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## On the Nature and Evolution of Imitation in the Animal Kingdom: Reappraisal of a Century of Research

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### I. INTRODUCTION

Clearly important in transmissions of human culture such as language acquisition, yet apparently traceable in humbler forms in other parts of the animal kingdom, imitation was an obvious early target for study in the post-Darwinian beginnings of comparative psychology. Attempts to construct mental *scala naturae* for the whole animal kingdom, culminating in Romanes' *Mental Evolution in Animals* (1883), were based principally on casual or anecdotal observations of animal behavior. These soon incorporated a diverse collection of phenomena under the heading of "imitation." Several of these were due to Darwin himself, who had bequeathed to Romanes his unpublished manuscripts on psychological subjects. Darwin gave a delightful description of the behavior of honey bees, quick to "mimic" bumble bees who had been cutting open flowers to get at their nectar; and Romanes added this and other observations by Darwin to a long catalogue of apparently imitative phenomena, such as puppies adopting the washing pattern characteristic of their cat foster parents.

However, the nineteenth century was to see much more than these anecdotal beginnings. Important theoretical and experimental advances were also made. We shall begin our review by examining several of these in some detail, for they appear to have set the investigation of animal imitation onto certain pathways that, as the twentieth century progressed, became deeper ruts along which researchers traveled perhaps too unquestioningly. In recent years, however, the conclusions of a century of research have been disputed from a variety of concep-

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tual and methodological perspectives, and it is this new ferment we review here, reappraising the earlier work in its light.

Our strategy is to begin at the beginning, first delineating the nineteenth-century origins of the fundamental issues to which we shall keep returning. Only then do we jump forward to summarize the thinking of today on the most basic of these issues: conceptualizing the nature of imitation, in comparison with the plethora of related psychological processes that may explain why one animal's behavior comes to resemble that of another. With this conceptual scheme in place, we step back again to review the methods and findings of research undertaken through the twentieth century up to the present day.

## II. FOUR INFLUENTIAL LEGACIES OF NINETEENTH-CENTURY COMPARATIVE PSYCHOLOGY

Early work on imitation learning is not only of historical interest. The latter half of the 19th century saw the formulation of alternative approaches to the study of imitative phenomena that, even today, shape research in the area. The views of major figures in the behavioral biology and psychology of the last century provide an important foundation for understanding the origins of much contemporary disagreement and confusion as well as a benchmark from which to measure a century's progress in the study of imitative behavior (Galef, 1988, p. 4).

Accordingly, Galef (1988) quoted at some length, and set in context, the contributions of three major figures, in turn: Romanes, Thorndike, and Morgan. Rather than reiterate Galef's account, we pick out what seem to us the four influential legacies that the nineteenth century has bequeathed to our own: (1) the classification of imitative phenomena; (2) experimental paradigms; (3) the apparent imitative superiority of primates; and (4) the contrast in vocal versus non-vocal imitation, raised particularly in the case of bird behavior. These then provide a framework for the rest of this article.

### A. DEFINING AND DISTINGUISHING IMITATIVE PHENOMENA

Romanes (1882, 1883) did not trouble to define imitation: to him the word was a perfectly ordinary, everyday expression. When Thorndike (1898) came to define imitation to test empirically for it, he used an expression that we are happy to adopt also as our basic definition of nonvocal imitation because it is concise and corresponds to everyday usage: imitation is "learning to do an act from seeing it done" (p. 50).

By the end of the century however, Baldwin (1895) and Morgan (1900) had appreciated that, whatever circumscribed definition one likes to apply to imita-

tion, there are then many imitation-like processes with which we need to contrast it carefully in any sophisticated conception of animal behavior.

J. M. Baldwin's monumental attempt to achieve an integrated understanding of ontogenetic and evolutionary processes of behavioral change and their interactions (e.g., 1895, 1902) bequeathed the "Baldwin Effect" to evolutionary biology and laid the foundations for Piaget's (1951, 1967, 1974, 1976) equally far-reaching biological conceptions of the nature of psychological development, including imitation. In Baldwin's grand scheme, imitation played a central role. The 1895 volume devoted over one hundred pages to the subject of imitation, including one whole chapter devoted to "organic imitation," which was contrasted with "conscious (i.e., mental) imitation." What Baldwin argued was that there is an essentially imitative quality in *all* adaptation by processes of selection, because this involves a certain *replication* of previous states: thus, "we may say that all organic adaptation in a changing environment is a phenomenon of *biological or organic imitation*" (p. 278). Although the breadth of this conception of imitation was soon challenged by Morgan (1900, pp. 179–183), imitation could never again be seen as an inherently narrow and easily circumscribed phenomenon!

Morgan (1890, 1896, 1900) developed his own three-way dissection of the phenomenon of imitation, although, like Baldwin, he applied his analysis to both ontogeny and evolution—a common enough endeavor of the period, given the ascendancy of the idea that "ontogeny recapitulates phylogeny" (Gould, 1978). Thus, according to Morgan:

In the case of the human child we may see three stages in the development of imitation. First, the instinctive stage, where the sound which falls upon the ear is a stimulus to the motor-mechanism of sound production. Secondly, the intelligent stage . . . if we assume that the resemblance of the sounds he utters to the sounds he hears is itself a source of pleasurable satisfaction (and this certainly seems to be the case), intelligence, with the aid of any higher faculty, will secure accommodation and render imitation more and more perfect. And this appears to be the state reached by the mocking-bird or the parrot. But the child soon goes further. He reflects upon the results he has reached; he at first dimly, and then more clearly realizes that they are imitative; and his later efforts at imitation are no longer subject to the chance occurrence of happy results, but are based on a scheme of behavior which is taking place in his mind, are deliberate and intentional, and are directed to a special end more or less clearly perceived as such. He no longer imitates like a parrot; he begins to imitate like a man (Morgan, 1900, pp. 192–193).

This third stage Morgan called "reflective imitation." His analysis of progress from simple to complex levels of imitation was the forerunner of more elaborate schemes of developmental and evolutionary stages that have followed in this century, including those of Piaget (1951) and, most recently, Mitchell (1989).

In the context of such distinctions between simple and complex, "clever"

imitation, it is instructive to recall that Romanes (1883), while neglecting any explicit definition of imitation, clearly implied that for him (as for Darwin before him), imitation was a process of only relatively mindless and unintelligent stamp. He noted that human infants imitate very early, but in later life the imitative tendency "may be said to stand in an inverse relation to originality or the higher powers of the mind. Therefore among idiots of a higher grade (though of course not too low) it is usually very strong and retains its supremacy through life . . . the same thing is conspicuously observable in the case of many savages" (p. 225). The everyday expression "to ape" still seems to carry this particular connotation of imitation as simple-minded, rote copying, a situation contrasting ironically with the advanced cognitive abilities that, as we shall detail later on, have recently been suggested to underlie certain forms of imitation special to highly encephalized species.

## B. EXPERIMENTAL PARADIGMS

The approach of Darwin and Romanes (1883) to using anecdotal evidence did not have to wait for twentieth-century behaviorism to be dismissed as uncritical. Of their new animal psychology, Wundt, for example, remarked that "its implicit principle . . . is precisely the opposite of the approved maxim of the exact natural sciences that we should always have recourse to the simplest explanation possible" (1894, p. 345).

The answer of Thorndike (1898) was to experiment. His essential paradigm represented an important advance in rigor and imagination—although we suggest that this was not often matched by the way it was copied by others, with only minor modifications, for much of the experimental work that followed in the present century! The technique was first to allow one animal to learn the behavior required to escape from a "puzzle box" (a cat might have to pull a particular string with its paw, for example); observer cats were then allowed to watch an animal who had become competent in this way and were later compared with naive cats, who had not observed, in their success at escaping when put in the puzzle box themselves. Two types of measure were available: similarity of action pattern and speed of escape. Thorndike emphasized that, while judgments were somewhat subjective as to whether the acts of the observer were copies of the other animal, "we have in the impersonal time records sufficient proofs of [in the case of the cats' latency to escape] the absence of imitation." It is only in the very recent work we describe in the following section that experiments have overcome the difficulty inherent in the distinction Thorndike made: that while speed of learning can be easily and objectively measured, it is insufficient to discriminate imitative copying from alternative types of social learning. To achieve this in the Thorndike paradigm, the experimenter is still thrown back on subjective judgments of similarity in behavioral patterns of the "demonstrator" and putative imitator.

### C. MONKEY SEE, MONKEY DO

Despite the early optimism, the nineteenth century closed with a negative verdict on the ability of animals truly to imitate, according to the only experiments conducted so far—those of Thorndike. The failures included chicks, cats, and dogs. However, Morgan noted that it was still the case that:

Professor Thorndike is of the opinion that monkeys are probably imitative in ways beyond the capacity of dogs and cats, but, at the time of writing, he had not substantiated his opinion, by analogous experiments. If so, it will perhaps prove that they are rational beings in the narrower sense defined in a previous chapter of this work. For it appears that the kind of imitation which Mr. Thorndike's experiments go far to disprove, is what we may term reflective imitation . . . the cat had not in any sense grasped the nature of the problem before it, had no notion of just where the difficulty lay, had not the wit to see that the performance of the other cat supplied the missing links (1900, pp. 185–186).

Perhaps monkeys *would* have the wit?

Visalberghi and Fragaszy (1990) noted that in many different languages the words for imitation and monkey (or ape) have common roots. In English, we have the expression “to ape” and the saying “monkey see, monkey do.” We do not know how far back such assumptions go, but they are vivid in the earlier treatises we have considered: “Allied, perhaps to the emotions, is what Mr. Darwin calls ‘the principle of imitation.’ It is proverbial that monkeys carry this principle to ludicrous lengths, and they are the only animals who imitate for the mere sake of imitating” (Romanes, 1882, p. 477). “as the faculty of imitation depends on observation, it is found in greatest force, as we should expect, among the higher or more intelligent animals—reaching its maximum in the monkeys” (Romanes, 1883, p. 225).

“As we should expect” (Romanes’ words), the twentieth century did produce experimental results in support of the superiority of primates in imitation, to which were added ethological observations of protocultural behaviors in wild populations presumed to be transmitted by imitation (see Nishida, 1987, for a review). Animal behavior textbooks have tended to present a story of primate imitativeness prefigured in the observations of Romanes (e.g., Manning, 1979; McFarland, 1985).

Recently, however, the superiority of both monkeys and apes has been challenged (Whiten, 1989) and we shall need to discuss the evidence in some detail. Most of the research on imitation this century has, in fact, concerned primates rather than other taxa, excepting the case of vocal imitation in birds.

### D. THE SPECIAL CASE OF VOCAL IMITATION IN BIRDS

“The psychology of imitation is difficult of analysis, but it is remarkable as well as suggestive that it should be confined in its manifestations to monkeys and certain birds among animals” (Romanes, 1882, p. 477).

However, there is an obvious difference between these two apparently gifted taxa: almost without exception, research has focused on *vocal* imitation in the case of birds and on *visual* imitation (performance of actions previously watched) in the case of primates and other mammals. Thorndike was eventually to conclude that the two were not deeply connected and that birds' facility, although a "mystery" deserving further study, was a specialization rather than a reflection of a general (and thus "true") imitative ability:

though the imitation of sounds is so habitual, there does not appear to be any marked general tendency in these birds. There is no proof that parrots do muscular acts from having seen other parrots do them . . . we cannot, it seems to me, connect these phenomena with anything found in the mammals or use them in advantage in a discussion of animal imitation as the forerunner of human (Thorndike, 1911, p. 77).

"In what follows they will be left out of account," Thorndike continues. In this we shall follow him, omitting studies of vocal imitation, a huge research industry in its own right (for reviews, see Kroodsma and Miller, 1982; Slater, 1986). However, it is very relevant for us to assess (1) recent explanations offered for *why* the bird-vocal/primate-visual dichotomy might exist, and (2) recent studies that *have* examined the imitation of "muscular acts" in birds, as Thorndike advocated.

### III. DEFINING AND DISTINGUISHING IMITATIVE PHENOMENA TODAY

We now revisit each of the four fundamental issues previously discussed. In the case of the first two—the conceptual and the methodological issues—we concentrate on the position today. With this in mind, we shall then examine the empirical evidence gathered through this century for imitation, respectively, in mammals (principally primates) and in birds, where a smaller and more recent literature has emerged.

The classification of mimetic phenomena has been reviewed and revised recently. Galef (1988) analyzed the many terms used to distinguish imitation and imitation-like behavior, and Mitchell (1989), in the spirit of Morgan as described before, distinguished a number of levels of complexity in imitation. The following owes much to these thoughtful and comprehensive essays, although we have to disagree with Galef and with Mitchell on some fundamental points. The array of terms and concepts generated by a century of writing still remains potentially bewildering (Table I). In the next section, our intention is thus to classify all the major concepts in one coherent scheme.

TABLE I  
SOME VARIATIONS IN TERMINOLOGY FOR MIMETIC PROCESSES<sup>a</sup>

Preferred terms	Related terms
Mimicry (Wickler, 1968)	First-level imitation (Mitchell, 1989)
Social mimetic processes (implicit in Fig. 1)	Observational learning (Hall, 1963) Imitation (Morgan, 1900) Social learning (Box, 1984)
Social influence (Fig. 1)	Social enhancement (Galef, 1988)
Contagion (Fig. 1: Thorpe, 1963)	Instinctive imitation (Morgan, 1900) Imitation (Humphrey, 1921) Imitative suggestion (Guillaume, 1926) Mimesis, allelomimesis (Armstrong, 1951) Pseudo-vicarious instigation (Berger, 1962) Social facilitation (Thorpe, 1963) Coaction (Zajonc, 1965) Stages 2 and 3 imitation (Piaget, 1951) Second-level imitation (Mitchell, 1989)
Social support (Fig. 1)	Social facilitation (Zajonc, 1965)
Stimulus enhancement (Fig. 1: Spence, 1937)	Local enhancement (Thorpe, 1963)
Imitation (Fig. 1)	
a. Third-level imitation (Mitchell, 1989)	Intelligent imitation (Morgan, 1900) Persistent imitation (Baldwin, 1902) Trial-and-error imitation (Guillaume, 1926) Stage 4-5 imitation (Piaget, 1951)
b. Fourth-level imitation (Mitchell, 1989)	Reflective imitation (Morgan, 1900) Internal persistent imitation (Baldwin, 1902) Symbolic imitation (Guillaume, 1926) Stage 6 imitation (Piaget, 1951) Pretence (Mitchell, 1989)
Goal emulation	Emulation (Tomasello <i>et al.</i> , 1987) Fourth-level imitation (Mitchell, 1989)

<sup>a</sup>This is not an exhaustive list but illustrates the proliferation of expressions. Note that by calling terms "related" we mean just that: they are not necessarily synonymous, but rather have significant (and potentially confusing) overlap of meaning.

## A. CLASSIFYING SOCIAL MIMICRY: DESCRIPTION AND EXPLANATION

Galef (1988) advocated distinguishing what he calls *descriptive* terms from a number of other terms that refer to possible *explanations* for the behavioral changes so described. The three descriptive terms (see Table I for alternative terms used by others) are *social learning*, *social enhancement*, and *social transmission*. We agree with Galef that, having merely described a behavioral change such as the emergence and spread of a novel act in a population, the question remains open of just what type of transmission process is responsible.

However, we would dispute that his "descriptive" terms are really only descriptive. The term *social learning*, for example, surely invokes a certain explanatory mechanism: that is, that an animal has acquired a behavior through processes involving both learning and social influence. We suggest that all three of Galef's "descriptive" terms are better regarded as *generic* explanatory terms for why animals have come to act as they do. Within each generic term, more *specific* explanatory distinctions can be made, these including processes that Galef himself is happy to consider "explanatory." Thus, all the (22!) terms that Galef reviews can, in principle, be rearranged into a hierarchically organized explanatory classification along the lines of (although not identical to) our own taxonomy set out in Fig. 1. We still need a supergeneric term for the apex of this taxonomy, and here we use *Mimetic Processes*. By this we mean *all processes whereby some aspect of the behavior of one animal, B, comes to be like that of another, A*, and "mimetic" here implies no more than this. *Mimicry* in the sense of B's behavior being in some sense *copied from A's* is just one specific case among such processes generating behavioral conformity between A and B.

## B. A TAXONOMY OF MIMETIC PROCESSES

Figure 1 provides a map of our scheme, which the reader is advised to use in conjunction with the rationale that follows.

### 1. *Nonsocial Mimetic Processes*

We shall deal with these relatively briefly. They are not of central interest in this article, but it is obviously important to distinguish them. They are defined by exclusion: they do not involve social interaction between A and B.

At the most general level, we must acknowledge the possibilities of *convergence*, where natural selection has caused B to resemble A in its behavior through the exploitation of similar ecological niches and the facing of similar selective pressures, and *common descent*, where B resembles A because of evolutionary descent from a common ancestor. Flying in birds and bats would be an example of the former, and flying in different taxa of birds an example of the latter.



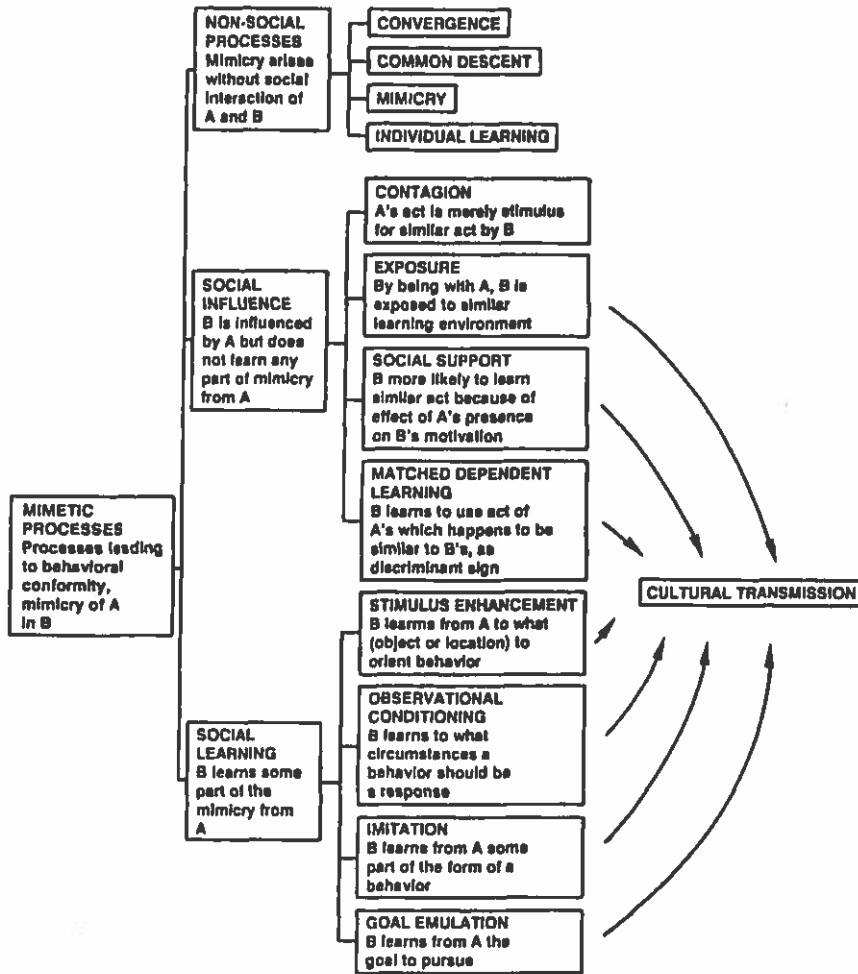


FIG. 1. A taxonomy of mimetic processes. Three layers of categorization are shown. Logically, a category of "Social Processes" should be included, creating four layers. This has been omitted here for simplicity. Seven subcategories have the capacity to produce cultural transmission of behavior (in which behavioral conformity spreads nongenetically through a population and/or across generations), as indicated on the right.

A more specific category is *mimicry*, where natural selection has led members of one population to resemble, and through this means exploit, the behavioral strategy of another. One species may in this way mimic another, as when female fireflies of the genus *Photuris* replicate the female courtship signals of other firefly species, so capturing males of those species for food (Lloyd, 1965).

Alternatively, one sex may mimic the other within a single species: male scorpion flies, for example, mimic females' behavior and then steal food from other males so attracted (Thornhill, 1979). Unlike similarity of behavior achieved through convergence or common descent, mimicry of A by B is maintained and refined by natural selection *because* of the resemblance. In this sense, B can be said to be a copy or imitation of A, and so Mitchell (1989) calls this *level 1 imitation*, the only one of the nonsocial processes we list here to be included in his scheme of imitative phenomena. Although imitation as a learning mechanism (see Fig. 1) is commonly distinguished from mimicry by the criterion that B's imitation of A is derived from B's *observation of A*, Mitchell notes that the existence of a mimic B also depends on observation of A; however, in this case, the observation is not *by B*, but by other individuals whose mistaking of B for A is the basis of the shaping process of natural selection.

Finally, turning to nonsocial processes operating within a single individual's lifetime, we have *individual learning*, where each of two or more individuals independently acquire the same behavior through encountering and being shaped by similar learning environments. This is the ontogenetic analogue of phylogenetic convergence described earlier. Such individual learning can, of course, be further subdivided into many different processes (e.g., trial-and-error, insight, and so forth: Thorpe, 1963), but these need not detain us further here.

## 2. *Social Mimetic Processes: Social Influence and Social Learning*

*Social processes* (see Fig. 1) in which the mimicry of A by B is dependent on social effects of A on B is subdivided, in turn, into *social influence* versus *social learning*. The difference between social learning and social influence is that in the former, B *learns* some aspect of the behavioral similarity *from A*, whereas in *social influence* B does not learn the similarity from A, but is nevertheless subject to one or other sort of social influence from A that, in concert with nonsocial processes such as trial-and-error learning, brings about a similarity in the behavior of A and B. *Social influence* includes what Galef labels *social enhancement* ("a generic to refer to all social influences on performance of established responses" 1988, p. 13), but we avoid his expression to avoid confusion with *local* or *stimulus enhancement*, one of the accepted subcategories of social learning (see Fig. 1 and the following).

We can subdivide processes of *social influence* in terms of the *type of influence* that occurs between A and B, giving us four categories: *contagion*, *exposure*, *social support*, and *matched dependent learning*. We subdivide *social learning* using the same principle, but here the social effects can be expressed specifically in terms of *what B learns from A*; this gives us *imitation* and three other categories.

Before we describe these categories of social learning and social influence, we

wish to make explicit two of our attitudes to classification and definition. These attitudes are those we take to all of scientists' technical analyses of phenomena like "intelligence," "play," and "imitation," which are already covered, less precisely, by everyday language (see also Whiten and Byrne, 1988b).

First, we believe it is futile to argue about what imitation "really" or "truly" is: the question of what scientists or other people usually mean by "imitation" is a legitimate and empirical one, but the business at hand, instead, is to make certain important *conceptual distinctions* between categories, to the clear definition of which we then need to attach convenient labels, one of which happens to be the everyday word "imitation."

Second, it does not follow that anybody can set themselves up to "legislate" on what, henceforth, the formal distinctions and definitions shall be. Distinctions are likely to be adopted and maintained in the discipline just so long as they do a useful job. There is no *absolute* meaning of "imitation" that we might waste time debating. Each investigator will be well advised to define such terms at the time of each new application of them.

### 3. *Types of Social Learning*

Earlier in this paper we adopted Thorndike's simple definition of imitation: "learning to do an act from seeing it done." But we must be careful to discriminate a number of ways through which B may have learned from A the basis of a subsequent similarity between their actions.

*a. Stimulus Enhancement (Local Enhancement).* This is the category perhaps most often confused with imitation in practice. Its nature is nicely illustrated by the example of milk-bottle opening by tits (*Parus caeruleus*: Fisher and Hinde, 1949; Hinde and Fisher, 1951), the cultural spread of which seemed difficult to explain by anything other than a process corresponding to Thorndike's definition. However, following Krebs *et al.* (1972), Sherry and Galef (1984) showed that the transmission of such behavior could be explained by an observer bird simply having its attention drawn to open bottle tops: trial-and-error learning could achieve the rest.

Thus, if we make a distinction between the actions involved in opening a milk-bottle top and orientation to milk bottles, it is only the latter that B learns from A in the case of local enhancement. A subdivision may be helpful in some contexts, between *local enhancement*, as defined by drawing attention to a particular locale in the environment, and *stimulus enhancement*, where attention is drawn to an object or part of an object, irrespective of its location.

The term imitation would thus be reserved for cases where B learns something about the *form* of the act: about *how* to open milk bottles, for example, as opposed to a mere concentration of attention on the bottle tops themselves. We shall see that the imitation/local enhancement distinction is a crucial one when we come to survey evidence across the animal kingdom. However, we should

also emphasize that in practice it may be difficult or impossible, in a case of local enhancement, to distinguish whether animal B is indeed *only* having its attention drawn to some environmental features (learning nothing about behavior *per se*) or is, in fact, learning to *orient its behavior* to those environmental features. We could think of the latter as a form of imitative copying restricted just to the specific behavioral feature of *orientation* with respect to the environment. Thus, when we normally use the term imitation, we imply more than this: we imply that B has learned something of the intrinsic form of an action from A, apart from any extrinsic aspects of orientation to features of the environment.

*b. Observational Conditioning.* Mineka *et al.* (1984) found that juvenile monkeys (*Macaca mulatta*) who initially showed no fear of snakes, did so when observing their wild-born parents acting fearfully in the presence of snakes, and continued to react fearfully themselves when later exposed to snakes without the parent present. The juveniles' actions were mimetic of their parents' on a number of measures, including avoidance and facial expression. Mineka *et al.* called this "observational conditioning": a form of classical conditioning in which an unconditioned response (in this case, fearful behavior as a response to fearful behavior in others) becomes associatively conditioned to a new stimulus (in this case, the snake). Later work has indicated constraints on the flexibility of such learning: fear is not so readily conditioned to biologically irrelevant objects like flowers (Cook *et al.*, 1987; Mineka and Cook, 1988).

Observational conditioning is similar to the process of stimulus enhancement insofar as B learns from A *to what* it should direct actions already in its repertoire; it is just that stimulus enhancement typically refers to appetitive actions and observational conditioning, as studied by Mineka *et al.*, to avoidance reactions. This is a trivial difference and if it were the only one, the two categories should be collapsed together. However, in observational conditioning, the animal learns more than just an *orientation* element: the monkeys in the snake experiment appeared to have learned something more general about the *significance* of the stimulus that led to other aspects of behavioral conformity, such as fearful facial expressions and bodily postures. More importantly, it is necessary for observational conditioning that B initially shows an unconditioned mimetic response contingent on A's reaction to the stimulus, whereas this appears not to be the case in stimulus enhancement, where B may merely watch A and then much later express its "latent learning" (Thorpe, 1963).

*c. Imitation.* We can distinguish from these processes the one in which B learns some aspect(s) of the intrinsic *form* of an act from A, and this is what we mean by imitation. This seems to be fully consistent with everyday usage as well as with Thorndike's definition, previously mentioned. Of course, no imitation of A by B will be perfect, and "some aspect(s)" in our definition is intended to acknowledge that imitative copying of the form of another individual's act may

vary between the faithful and the poor and encompass only a subset of the elements potentially copyable.

A further question is what is to be meant by "learning" in our (and in Thorndike's) definition. In the everyday sense, a person can imitate another doing some everyday act like waving, yet the imitator is not "learning to wave" insofar as some sort of waving is already in their behavioral repertoire. The sense in which this *is* learning is that of *being shaped through information transfer*: the form of the imitator's act is derived from the information gained in observing the other's waving. To be reasonably consistent with everyday usage it is this relatively broad notion of learning that we must prefer, noting as we do so that in the animal literature, the emphasis is often on learning in the more restricted sense of acquiring behaviors novel to the individual's repertoire. But imitation of acts that can be said to be already in B's repertoire must also be distinguished from the mere social influence involved in contagion (see the following).

*d. Goal Emulation.* One particular element whose copying deserves a special category is that which is the culmination of a goal-directed sequence. Tomasello *et al.* (1987) found that juvenile chimpanzees (*Pan troglodytes*) who had watched another chimpanzee use a stick to rake in out-of-reach food were then themselves quicker to do the same than control animals who had not watched; however, the youngsters invented their own ways of using the stick, rather than copying the particular form of the behavior they had previously observed. Tomasello *et al.* suggested that the chimpanzees were not attempting to reproduce the model's *behavior* so much as the *results* they achieved. Following a distinction made by the child psychologist David Wood, (1988) Tomasello *et al.* (1990) call the first of these "impersonation" (equivalent to imitation as we have defined it) and the second "emulation."

Two comments on this distinction must be made. First, we would argue that a distinction between copying *behavior* versus its *results* is not clear-cut in practice. Any "result" of an action sequence will have to be achieved by a final act in that sequence that, however variable the acts that precede it, will inevitably have some consistency of form. In the example under discussion, that might be described as "raking the food in." Put more generally, what we are saying is that any imitation is unlikely to be perfect and thus always to be partial; and partial imitative copies might include just the final act, or the final act and a subset of elements preceding it, or several of these elements without the final act. Thus, emulation as described by Tomasello could be redescribed as just *imitation* of the final act in a goal-directed sequence. It is for this reason, coupled with the fact that dictionaries tend to equate emulation with imitation, that we add "goal" to the label "emulation" to distinguish it from (other) imitation.

Indeed, our second comment is that imitation of only the "goal act" in a sequence *is* of sufficient interest to justify maintaining a special category called

emulation. Emulation may in some cases require sufficient intelligence to recognize a goal achieved by others (e.g., "getting the food raked in") as a goal—and a goal potentially achievable by one's own novel problem-solving attempts. This leads to an expectation different from the traditional one that imitation should be shown by particularly intelligent taxa of animals: if emulation is the mark of intelligence, thorough imitative copying of the form of others' acts may often be avoided by intelligent species—even if it is within their capability.

#### 4. *Types of Social Influence*

We must briefly distinguish from the processes discussed in the last section a number in which mimicry depends on some social influence of A on B, without B actually acquiring from A the information underlying the resemblance. We shall need to return to these distinctions later on when we discuss social facilitation.

*a. Contagion.* Thorpe (1963) defined contagion as the "unconditioned release of an instinctive behavior in one animal by the performance of the same behavior in another animal." *Social facilitation* is a common synonym. An example would be the chicken who is allowed to eat until satiated, but on being introduced to others that are feeding, resumes eating (McFarland, 1985). Actions subject to contagion are likely to be shared by populations (or subpopulations such as one sex). This distinguishes contagion from imitation based on acts already in the repertoire, which may occur between just two individuals (see the example of Fifi and Gilka on page 265).

*b. Exposure.* By simply being with (or following) A, B may be exposed to a similar learning environment and thus acquire similar behavior. As Galef (1988) says of one of Thorndike's (1911) own examples, "it seems unlikely that birds lose their fear of trains as a result of socially induced enhanced attention to them. Socially induced increased exposure to trains and consequent habituation to the threatening stimuli that trains emit seem a likely explanation of the observed social transmission of behavior."

*c. Social Support.* B may also be more likely to learn behavior like A's in the mere presence of A and its learning environment, because A affects B's motivational state. For example, the presence of conspecifics can reduce fear (Stamm, 1961). Zajonc (1969) suggested that the presence of companions may "energize" others, but this has proved difficult to distinguish from fear reduction (Galef, 1988).

*d. Matched Dependent Learning.* Miller and Dollard (1941) showed that a rat could learn through reinforcement to use the actions of another as a discriminative stimulus to guide its own behavior. Where the experimenter arranges that the two actions are similar (e.g., B learns that if A turns right in a maze, it should do the same to gain reinforcement), behavioral conformity is the result. The essential learning process is operant conditioning—B could just as well be

trained to act in this way (turning right) using rat A performing a different act (e.g., turning left) or even replacing rat A with a flashing light as the discriminative stimulus. However, this does not mean the process is an oddity produced only in the experimentalist's laboratory; indeed, Skinner (1953) showed that the requirements for learning matched dependent behavior are likely to be common in nature. It is often the case that an animal is reinforced when it uses an act (e.g., a foraging technique) like the one it has just observed a conspecific perform. However, no part of the similarity in the form of A's and B's behavior is based on B copying what it has observed A do; the similarity is entirely due to piggyback reinforcement contingencies.

#### IV. NEW METHODOLOGIES

##### A. VARIATIONS ON THORNDIKE'S PROCEDURE

The essential contribution of Thorndike in distinguishing among mimetic processes was the experimental design in which a "demonstrator" animal performed a task in front of a naive observer, the test then being whether the observer required a smaller number of trials to achieve some criterion of success on the task when compared with an animal who had not been allowed to observe the demonstrator. The eager acceptance of this method by comparative psychologists during the present century gave rise to several variations that, following Thorndike's negative results with nonprimates and optimism about primates' abilities, have almost exclusively been applied to monkeys and apes. However, none of these methods can satisfactorily distinguish imitation from all the alternative processes now arrayed before us (see Fig. 1).

In the Kline single-cage method (e.g., Haggarty, 1909), the naive individual is housed with the demonstrator so it can manipulate the task apparatus between episodes of demonstration. This is, perhaps, a more natural situation than the original Thorndike design where the observer watches from a separate compartment and is only later allowed access to the manipulandum itself. However, both designs suffer from an inability to distinguish imitation from local or stimulus enhancement. As in the case of tits and milk bottles, the observer may solve the problem more quickly than nonobservers because its actions are directed more often to the relevant area or object, thereby facilitating learning by trial-and-error.

Apparently circumventing this criticism, Warden and Jackson (1935) introduced a duplicate-cage approach in which the observer was provided with an identical task to that being performed at the time by the demonstrator in an adjacent cage—in this case, pulling a chain to expose food in a recess. But, as Galef (1988) has recently emphasized, although this may rule out local or stimulus enhancement (in the precise sense referring to the unique object manipulated

by the demonstrator), it does not do so in the more general sense where stimulus enhancement is taken to refer to the entire *class of objects* sharing the stimulus characteristics of the object manipulated by the demonstrator (the sense in which Spence (1937) actually defined stimulus enhancement). If an observer monkey's attention was directed in this fashion toward its duplicate chain apparatus, as seems plausible, the faster acquisition of chain-pulling that Warden and Jackson recorded still does not count as evidence for imitation as opposed to stimulus enhancement.

#### B. THE DAWSON AND FOSS "TWO-ACTION" TEST

It was not until 1965 that a design was offered by Dawson and Foss that explicitly distinguishes imitation from local enhancement. Dawson and Foss's experiment was also interesting in that it appears to be the first after Thorndike's to test for (nonvocal) imitation in birds. In their experiment, observer budgerigars (*Melopsittacus undulatus*) watched one of three trained demonstrators working with the same task of removing the lid from a dish of food; however, one did this with its foot, another by grasping with its beak, and the third by nudging with its beak. If observers tended to use a technique more similar to the one they had seen, rather than one they had not seen, this appears to be explicable only by imitation. Local enhancement is ruled out by use of the same manipulandum for each of the different types of action. Dawson and Foss did, in fact, find that their subjects used the techniques each had observed, although, with only five subjects, the authors interpreted their results as preliminary. A replication has been attempted that we shall discuss later.

#### C. HAYES AND HAYES' "DO-AS-I-DO" TEST

The important principle of the Dawson and Foss procedure is that alternative actions are performed with the same manipulandum. Two alternatives, as opposed to the three they used, would suffice for the logic of the design. However, as the number of alternatives is increased, the probability of chance concordance between demonstrator and observer techniques falls, and it should then be possible to demonstrate any imitative ability that exists with a relatively small number of subjects. An approach used by Hayes and Hayes (1952) with a single chimpanzee can perhaps be seen as an extreme extension of this logic. The Hayes' trained their home-reared chimpanzee, Viki, to imitate so that on the command "Do this!" she would usually attempt to copy the action the human performed next, such as clapping or pulling the mouth wide open. It took about 12 rewarded acts for Viki to grasp the general rule, after which imitation could be tested by recording only spontaneous, nonrewarded imitations. This continued through 70 different types of action, 55 of which were judged to be responded to with a



correspondingly similar act. The probability of such concordance occurring by chance is vanishingly small. This study is, therefore, often taken to be the most convincing demonstration of the fact that chimpanzees can imitate. Presumably, one cannot "train" an animal to imitate in this way unless it has some inherent imitative capacity. Unfortunately, like Dawson and Foss, Hayes and Hayes did not mention many details of procedure that (quite apart from the sample size!) means that the method, which appears powerful in principle, begs replication.

#### D. SYSTEMATIC FIELD OBSERVATION

The twentieth century has seen the emergence of systematic and quantitative field studies that have taken the study of cultural transmission and observational learning far beyond the naturalistic anecdotes of the preceding century (Nishida, 1987). Thus, for example, it has been possible to classify different subcultures of chimpanzees (*P. troglodytes*) that show variations in the use of certain tools and food types not explicable by the local availability of the raw materials (McGrew, *et al.*, 1979; McGrew, 1992). Cross-fostering showed that oyster catcher (*Haematopus ostralegus*) chicks adopt the particular technique of the local cultural group to which their parents belong—those that stab or those that hammer to open the shells of the mussels they eat (Norton-Griffiths, 1969). Perhaps most famous of all, the diffusion of new feeding techniques in groups of Japanese macaques (*Macaca fuscata*) has been documented in some detail (Kawai, 1965; Itani and Nishimura, 1973). The literature has become enormously rich with such observational evidence; in a nonexhaustive survey of foraging behavior alone, Lefebvre and Palameta (1988; Table 7.1) list 73 studies claiming social transmission in fish, reptiles, birds, and mammals.

The role of imitation or other mechanisms through which transmission occurs is much less well specified. However, with an increasingly refined understanding of the discriminations that must be made in the field between the alternative mimetic processes that may underlie the spontaneous behavior observed (see Section III), some fieldworkers have recently attempted the critical observations. Thus, in a group of vervet monkeys (*Cercopithecus aethiops*) previously observed for many years, Hauser (1988) was able to document the emergence and spread of the use of acacia pods to extract exudate from a hole in an acacia tree. The whole process was quite rapid, with four individuals adopting the technique within 9 days and another two within 22 days. Given continuity of observation, details of the first incorporation of the act into each animal's repertoire provided evidence that different individuals acquired the technique by different routes. One appeared to deduce what to do from observing the end product (the model finally eating dipped pods), whereas another watched the model prepare and consume pods "and then performed the whole behavior."

The latter observation is still not a watertight demonstration of imitation

because it must remain possible that some parts of the developing actions escaped observation and these might have been subject to other processes like trial-and-error learning; unless such a case study is seamlessly continuous, convincing field evidence for imitation may remain elusive. What such detailed case studies can achieve is to specify more clearly than before the scope for imitation and how it might interact with other mimetic processes—an important advance in field studies.

## V. THE DISTRIBUTION OF IMITATION IN THE ANIMAL KINGDOM

We have already noted that the preliminary conclusion of the nineteenth century has become the common “textbook” wisdom of the twentieth: primates, almost alone among animal taxa, have been seen as having a special aptitude for imitation. No experimental work appears to have even been attempted on invertebrates or on vertebrates other than birds and mammals. Even then, following early negative results, little work has been carried out with nonprimate species. Passingham’s (1982) review mentioned just a little evidence for imitation in cetaceans, in addition to that for primates.

In the past few years, however, the presumed special ability of primates to imitate has come under strong attack. At the same time, fresh attempts to investigate imitation in birds and in other mammals have offered positive results. Century-old received wisdoms suddenly appear questionable.

### A. MONKEY SEE, MONKEY DO?

#### 1. *Observational Studies of Imitation by Monkeys*

“Probably the single most impressive case of imitation on record concerns the changes in food technology of the Japanese macaques on Koshima Island” (Premack, 1984, p. 17). The novel potato-washing of a juvenile female, Imo (Kawai, 1965), “soon was imitated by other monkeys” (McFarland, 1985, p. 514); and the habit “was copied . . . subsequently by nearly all the younger members of her troop” (Manning, 1979, p. 199).

This flagship case of imitative cultural transmission in monkeys has recently been questioned from several directions. First, Green (1975) noticed that potatoes were selectively given by the provisioner only to those animals that washed potatoes, suggesting reinforcement as the potential shaper of the behavior. The proximity of particular age groups and matriline to the provisioner might even explain the social pattern through which the behavior spread. Second, Galef (1990) scrutinized the time course over which the novel act spread and noted that both mean and median times for acquisition of potato washing after Imo showed the behavior were about 2 years. A second habit called placer

mining, in which wheat grains were separated from sand by releasing them into the water, spread even more slowly. This is hardly consistent with acquisition by imitation, which, when investigated under experimental conditions, is assumed to require only moments for implementation (e.g., Warden and Jackson, 1935; Hayes and Hayes, 1952; Meltzoff, 1988). In short, although the behavior *may* have been transmitted by imitation, this remains unproved. Stimulus enhancement—in which the behavior of potato washers drew the attention of others to the potatoes, the water, and their conjunction—coupled with trial-and-error learning, possibly enhanced by caretakers, would appear sufficient to explain the phenomenon.

We have already noted that, even with careful attention to such distinctions in the case of a much more rapidly transmitted act—pod-dipping in vervet monkeys—Hauser (1988) had to concede that clear evidence for imitation was not forthcoming. Indeed, in another study where researchers were alert for signs of imitation, its absence was striking, given the use to which it could apparently have been put. Boinski and Fragaszy (1989) found that, although infant squirrel monkeys (*Saimiri oerstedii*) had ample time to observe adults using the technique of rubbing noxious spines off caterpillars using their tail tips, the infants did not themselves attempt this when starting to handle caterpillars. Instead, they appeared to have to learn through trial and error, involving direct experience of the noxious spines.

Despite monkeys' reputation, other studies in wild populations have actually generated rather few additional claims of imitative transmission (Table II). None provide stronger evidence for imitation than those we have just reviewed. Taken together with other studies on food selectivity, they do suggest that observational learning at the level of stimulus enhancement often plays an important role in the development of food selection and foraging behavior (Whitehead, 1986; Whiten, 1989). However, even at this level there is evidence that species-specific foraging patterns may develop without opportunity to learn by observation of elders (Milton, in press).

## 2. *Experimental Studies of Imitation by Monkeys*

Tables III and IV list experimental studies of monkeys' social learning, which have, respectively, claimed positive and negative evidence for imitation. The two lists are about equal in size and, given different reasons for doubting the basis for both kinds of results, do not hold promise of a clear verdict.

In the case of the positive results, the most common problem is, yet again, a failure to distinguish imitation from local or stimulus enhancement. Recall that even the duplicate cage method of Warden and Jackson (1935) does not avoid this problem, because it exactly duplicates the stimulus characteristics for the potential imitator.

This does not disprove imitation but, as in the case of the observational

TABLE II  
NATURAL OBSERVATIONS CLAIMED TO BE REPORTS OF IMITATION IN MONKEYS

Reference	Genus	Observation	Possible explanation <sup>a</sup>
Carpenter (1887)	Macaca	Learning to open oysters with stones	SE
Tinklepaugh and Hartman (1930)	Macaca	Young induced to eat afterbirth after observing mother	SE
Imanishi (1957)	Macaca	Potato washing, rice throwing, caramel eating	T&E, SE
Carner (1955)	Macaca	Trained by imitation to aid experimenter in his botanical collections	SE
Hall (1963)	Papio	Dug in the same place after observing another	SE
Marais (1969)	Papio	Cracking the fruit of the baobab tree by pounding it with stones	T&E
Hamilton and Tilson (1985)	Papio	Catching fish	T&E, SE
Hauser (1988)	Cercopithecus	Dipping pods into exudate from a tree	T&E, SE

<sup>a</sup>SE, Stimulus enhancement; T&E, trial and error.

studies, it means that imitation is not yet proved. What is required is application of the methods used either by Dawson and Foss or Hayes and Hayes, reviewed earlier. Strangely, neither of these approaches has been applied to the most studied group, the monkeys, until recently.

In using a Dawson and Foss "two-action" approach, Ham (1990) also aimed to avoid a criticism that can be made of most of the *negative* results in Table IV: that they require tool use such as using a stick to obtain food. By contrast with chimpanzees (to be discussed later), macaques and, indeed, most monkeys are not naturally extensive tool users. Ham therefore used a task designed to be an analogue of routine manipulation in food processing. Observer monkeys (*Macaca arctoides*) watched one of two types of model working at exactly the same manipulandum, essentially a T-bar that could be grasped with both hands like the handlebars of a bicycle. One model twisted this and the other pulled it forward and, in each case, the T-bar disgorged a peanut. Observers were then given access to the apparatus, and the effect of having watched either pulling or twisting was gauged through various measures of the effort put into pulling versus twisting.

This test for imitation by the observers was conducted without any reinforce-

ment being available, reflecting a further criticism of many of the earlier experiments where testing for "imitation" was continued, even after a successful performance gained a food reward. Warden and Jackson (1935), for example, quoted the results of six trials for each action; but if a reward is gained in the first trial, the other five are not independent tests of imitation because they are contaminated with the effects of reinforcement (not necessarily in an effective way, however: in only 3 of 11 cases was a successful first "imitation" of chain-pulling followed by "imitation" in the next trial!). In Ham's experiment, with no reward, whether the observer had watched pulling or twisting had no significant effect on the ratio of its own subsequent pulling versus twisting, either in the first few attempts or over the whole of the 3-min manipulation period.

Although further experiments of this type are now needed, combining the rigor of an unreinforced two-action test with a user-friendly food-processing analogue, the current verdict on monkey imitation must be "not proved." Note also, however, that nearly all the work (see, especially, Table III) has been restricted to the genus *Macaca*—the white rat of the laboratory primatologist. Other taxa may yet turn out to be (better) imitators.

## B. APING

### 1. *Observational Studies of Imitation by Apes*

Nearly all the evidence for imitation in apes comes from common chimpanzees (*P. troglodytes*). Chimpanzee tool culture often follows Japanese monkey potato-washing in the classic textbook accounts of primate imitation. Thus, for example, we hear of "the use of simple tools which is certainly learnt afresh when each new generation of young chimpanzees copies from its parents" (Manning, 1979, p. 199), and "the technique of fishing for termites is learned by imitation and is passed through the population by cultural tradition" (McFarland, 1985, p. 513). However, the basis for this conclusion is essentially that juveniles closely observe mature tool users and later come to adopt the behavior in a gradual step-wise manner (McGrew, 1977). This, however, is a process that takes many years, and it seems impossible to disprove that it results from trial-and-error learning directed by the actions of others toward certain stimulus arrays (termite mounds, sticks, and possibly their conjunction): in other words, by stimulus enhancement.

In addition, captive chimpanzees reared without access to models to imitate may show tendencies to poke sticks into holes (Lancaster, 1975). Social facilitation of this maturing tendency is thus another process that may be operative. This is a further general problem in identifying imitation in the wild. Consider the following (is it a case of imitation or local enhancement combined with social facilitation of a maturing tendency?):

TABLE III  
CLAIMED POSITIVE LABORATORY EVIDENCE FOR IMITATION IN MONKEYS

Reference	Genus	Task	Method <sup>e</sup>	Possible explanation <sup>b</sup>
Hobhouse (1901)	Various	Manipulative	B	SE, SF
Kinnaman (1902)	Macaca	Pulling a plug Pressing a lever Opening a box	B	SE, SF
Haggarty (1909)	Various	Manipulative, involving a rope, screen, plug, and button	A	SE, SF
Aronowitsch and Chotin (1929)	Macaca	Learned by observation to respond opposite to training	A	OC
Warden and Jackson (1935)	Macaca	Pulling a chain to expose a raisin in hole	C	SE, SF
Warden <i>et al.</i> (1940)	Various	Manipulative	C	SE, SF
Presley and Riopelle (1959)	Macaca	Avoiding an electric shock by jumping over a barrier	B	OC
Miller <i>et al.</i> (1959)	Macaca	Fear response	A	OC

Myers (1970)	Macaca	Learned to respond on a multiple reinforcement schedule	B	OC
Beck (1976)	Macaca	Throwing action of tool at inaccessible food	A	T&E
Cook <i>et al.</i> (1985)	Macaca	Fear of snakes	B	OC
Anderson (1985)	Macaca	Manipulating metal rods to reach otherwise inaccessible food	B	SE, SF
Chevalier-Skolnikoff (1989)	Ateles	Putting things in mouth, ringing bells, examining objects, interactions with a bucket (Piagetian Stages 3 and 4)	A	SE
	Cebus	Banging two objects together, putting tub in a moat, draping a cloth on a branch (Piagetian stages 5 and 6)	A	SE, T&E

<sup>a</sup>A, Kline Single Cage Method; B, Thorndike Observation Cage Method; C, Warden Duplicate Cage Method.

<sup>b</sup>SE, stimulus enhancement; SF, social facilitation; OC, observational conditioning; T&E, trail-and-error.

TABLE IV  
CLAIMED NEGATIVE LABORATORY EVIDENCE FOR IMITATION IN MONKEYS

Reference	Genus	Task	Method <sup>a</sup>
Thorndike (1898, 1901)	Cebus	Opening a box	B
Watson (1908, 1914)	Cebus	Manipulative	B
	Macaca		
	Papio		
Beck (1972, 1973a,b)	Papio	Use a tool to reach inaccessible food	A
Beck (1974)	Macaca	Reaching pan with stick	A
Antinucci and Visalberghi (1986)	Cebus	Cracking nuts	A
Visalberghi (1987)	Cebus	Cracking nuts	A
Westergaard and Fragaszy (1987)	Cebus	Probing for syrup	A
Adams-Curtis (1987)	Cebus	Mechanistic puzzle	A
Visalberghi and Trinca (1987)	Cebus	Displacing reward in a horizontal tube	A
Fragaszy and Visalberghi (1989)	Cebus	Cracking nuts using tools, displacing reward in tube using stick	A
Fragaszy and Visalberghi (1990)	Cebus		A

<sup>a</sup>A, Kline Single Cage Method; B, Thorndike Observation Cage Method.

"A three-year-old male (Atlas), for example, ran to the security of his mother as an adult male gave pant-hoots preceding a charging display, then watched as a male ran, slapping the ground with his hands, stamping with his feet, ending his display by jumping up and drumming with his hands on a tree-trunk. When the adult male had moved away, the infant left his mother, ran a short distance with much stamping of feet, then paused near the drumming tree. He gazed at it, approached, and—very cautiously and gently—hit it twice with his knuckles" (Goodall, 1986, p. 336).

Such ambiguities mean that much of the more convincing evidence of spontaneous imitation comes from studies of captive animals, whose adoption of human patterns of behavior cannot be explained away as the interaction of enhancement and maturation of species-specific tendencies. Such evidence is anecdotal by its very nature, yet it must be said that, taken as a whole, it goes significantly beyond anything described for any species of monkey, both in scale (numbers of records by different observers on different individuals: Table V) and



TABLE V  
OBSERVATIONAL REPORTS OF IMITATION IN CHIMPANZEES

Reference	Observation	Possible explanation <sup>a</sup>
Rothman and Teuber (1915)	Learned to open doors, insert keys into locks, use a lever to regulate water supply, scrub floor, sweep with a broom	SE, I
Shepherd (1915)	Opening a watch	SE
Furness (1916)	Learned to dig with a spade, screw with a screw, scrub, and sweep	I
Sheak (1923)	Learned to wipe nose with a handkerchief, drive nails with a hammer, and to sew	I
Kellogg and Kellogg (1933)	Learned to brush hair, open cupboards	I, SE
Kohler (1925)	Learned to use a paintbrush, to stack boxes to reach a banana	T&E
Yerkes (1943)	Learned to spit, to imitate facial expressions	I
Kearton (1925)	Learned to wash clothes	I
Hayes (1951)	Learned to brush hair, to apply lipstick, brush teeth, sharpen pencils	I
Hayes and Hayes (1951)	Imitated on command	I
Hayes and Hayes (1952)	Stick and tunnel, stick and string problems, ball throwing	SE
Hayes and Hayes (1953)	Imitation set series—patting head, clapping hands, protruding tongue	I
Gardner and Gardner (1969)	Soaping and drying a doll in imitation	I
Menzel <i>et al.</i> (1972), Menzel (1973)	Creation of ladders	SE
Tomasello <i>et al.</i> (1989)	Throwing chips as a way of initiating play	I, SE
<i>Locale-specific behaviors</i>		
van Lawick-Goodall (1973)	Termite fishing	T&E, SE
Sugiyama and Koman (1979)	Cracking nuts with stones, using various techniques to reach lower branches of a tree	T&E, SE

(continued)

TABLE V  
(continued)

Reference	Observation	Possible explanation <sup>a</sup>
de Waal (1982)	Limping gait	I, OC
Sumita <i>et al.</i> (1985)	Cracking walnuts with stones	SE, T&E
Nishida and Hiraiwa (1982)	Differences in population in preferred ant species	T&E
Fouts <i>et al.</i> (1989)	Acquisition of sign language	I

<sup>a</sup>SE, Stimulus enhancement; OC, observational conditioning; T&E, trial and error; I, imitation.

apparent accuracy and complexity of copying. Space permits support of the latter assertion with just a small selection of examples.

In one case, Hayes and Hayes (1952) described how the home-reared chimpanzee Viki "appropriated a lipstick, stood on the washbasin, looked in the mirror, and applied the cosmetic—not at random, but to her mouth. She then pressed her lips together and smoothed the color with her finger, just as she had seen the act performed" (p. 451) and "when she saw an experimenter sharpen some pencils, she could not imitate immediately; but within a minute she got a pencil from the next room, returned with it, put it in the sharpener, and turned the crank."

Goodall (1986) cites an incident "in which Maurice Temerlin was ill. After having been violently sick, he staggered to his bed, followed by a concerned Lucy. A few minutes later she went back to the bathroom, stood upright, leaned over the toilet (as he had done), opened her mouth wide, and made gagging sounds as if trying to imitate his vomiting (Temerlin, 1975)."

A common feature of such episodes as listed in Table V is that they have no obvious reward beyond performing the act itself. This is in contrast to the monkey records in Table 2, where all the imitation claimed is for cases in which obtaining food was the end, so that trial-and-error coupled with stimulus enhancement can be invoked as an alternative explanation. This is not the case for the chimpanzee records in which there is no extrinsic goal at stake. Perhaps it was really just chimpanzees that Romanes (1882) had in mind when he talked of "the only animals who imitate for the mere sake of imitating." Of course, if these records are taken for evidence of imitation, then it becomes likely that imitation does play an important part in the life of wild chimpanzees also, as suggested in other records cited in Table V; although "imitation for imitation's sake" can be quite persuasive evidence of the *ability* to imitate, we must presume

that the functional significance of imitation in the wild is *generally* to imitate behavior that *does* achieve useful ends. Unfortunately, it is exactly in such natural cases that it will be difficult or impossible for the scientist to discriminate imitation from other mechanisms.

This does not mean that an animal with the capacity to imitate in the wild will not adopt particular cultural "fashions" so long as they confer no selective *disadvantage*. Possible examples include the "grooming handclasp" (McGrew and Tutin, 1978), a special posture adopted in grooming, and the "leaf-clipping display" (Nishida, 1980), in which a courting male rapidly bites a large leaf: each pattern has been observed in some chimpanzee populations but not in others that have been studied for years. Goodall (1986) described a case that appeared to show the beginnings of such cultural transmission, through imitation: "At Gombe a juvenile, Fifi, suddenly showed *wrist-shaking* . . . Fifi used it when threatening an older female. A younger individual, Gilka, was with Fifi at the time. The following week not only was Fifi seen to wrist-shake again (in a similar context), but Gilka too used the gesture. Subsequently Gilka wrist-shook frequently and in a variety of contexts" (p. 145).

Claims for imitation based on observation of other apes (Table VI) are fewer, which may in part reflect the smaller number of studies on them. They also appear to lack the quality of those quoted above for chimpanzees, particularly the copying of arbitrary actions, with just one exception, digging by an orangutan (Furness, 1916). Yerkes remarked on the contrasts with chimpanzees in orangutans' failure to imitate stacking of boxes to reach bananas (1916) and gorillas'

TABLE VI  
OBSERVATIONAL REPORTS OF IMITATION IN OTHER APES

Reference	Genus	Observation	Possible explanation <sup>a</sup>
Vosmaer (1778)	Pongo	Spitting in imitation of man	T&E,*
Abel (1818)	Pongo	Imitation of a kiss	T&E,*
Furness (1916)	Pongo	Digging with a spade	
Yerkes and Yerkes (1927)	Pongo	Learned by observation to lift the lid of a sewage tank	SE
Carpenter (1937)	Gorilla	Synchrony of moods and play behavior	C, T&E, OC
Harrison (1960)	Pongo	Nest building and feeding habits	T&E, SE
Wright (1972)	Pongo	Flaking stone tools	SE, T&E
Galdikas (1982)	Pongo	Tool use	SE, T&E

<sup>a</sup>SE, Stimulus enhancement, SF, social facilitation; OC, observational conditioning; T&E, trial-and-error; C, contagion; \*, history of animal unknown.

failures to imitate the solving of lock and key problems (Yerkes and Yerkes, 1927), although these may reflect only a lack of chimpanzees' tool-using proclivities in these other apes. It would be premature to conclude that the chimpanzee is the only ape to imitate (Russon and Galdikas, 1991), although that is an intriguing hypothesis.

One final observation consistent with this is the recent reporting of intentional teaching in chimpanzees (Boesch, 1991) in which a mother was described as performing nut-cracking in a slower and more deliberate way following a display of incompetence by her infant. Boesch interprets this as *demonstration*, which has not been shown for any other nonhuman species. There would, of course, be no functional role for demonstration in a species that did not also have an imitative capacity.

## 2. *Experimental Studies of Imitation by Apes*

We should not have to agonize over whether the observational evidence adequately demonstrates imitation in chimpanzees (or other apes): if such ability is so apparent, it should be demonstrable experimentally. Yet the extraordinary fact is that, until recently, the only thorough experimental study was the unique "do-as-I-do" sequence, already described in our discussion of methodology (Hayes and Hayes, 1952). Moreover, Tomasello *et al.* (1987) pointed out that no experimental test of imitation of *conspecifics* had been attempted. Their effort to remedy this is important for a number of reasons. First, although we naturally assume that if a chimpanzee can imitate a human, the capacity has evolved to permit conspecific imitation, the nature of transmission may be different in the two cases (e.g., humans are likely to be better intentional demonstrators) and so conspecific imitation requires investigation in its own right. Second, to make fair comparisons with evidence for imitation in other species, we must standardize on conspecific imitation: the morphological similarity between human and chimpanzee clearly favors interspecific imitation in ways beyond the reach of more distantly related species. Third, as the natural function of imitation is (we assume, mostly) intraspecific, this is really what we should be focusing on.

The experiment of Tomasello *et al.* largely followed the conventions of monkey studies already described. Observers watched a model using a stick to rake in food, and were then compared with nonobservers in the way they responded to the problem of being presented with out-of-reach food. Observers clearly benefitted from observing and were quicker to use the rake and apply it successfully to rake in the food. However, Tomasello *et al.* emphasized that the manner in which they did so should not be called imitative in the sense of copying the form of the models' act; instead, observers appeared to develop their own techniques, and did not copy the two-part hooking approach of the model that appeared quite distinctive to the human observers.

The authors conclude that the observers did not attempt to copy the model's

behavior so much as attempt to recreate the *results* of their efforts, a process they call *emulation*. Presumably, the "results" in this case would be "food getting raked in," because the evidence for emulation was essentially that the observers spent more time than nonobservers directing the rake to the goal of pulling in the food. However, it is not so clear that local enhancement (of the food) coupled with stimulus enhancement (of the sticks) would not suffice to explain the actions of the observers. Further alternatives would seem to be either that what was enhanced was the *conjunction* of rake and food or that imitation was indeed taking place, but with respect to the form of the behavior described at a relatively general level (along the lines of "rake in food"), with the details of the technique provided by the individual.

Whatever the merits of these alternative explanations, what these chimpanzees acquired seems not dissimilar to what was gained by cebus monkey observers in an experiment by Visalberghi and Trinca (1987). Here the task was to use a stick to poke a reward out of a tube. Animals that had observed conspecifics demonstrate this did not imitate in the sense of then succeeding in the task, but they did make more contacts with both stick and tube than nonobservers.

In short, the only experimental tests of conspecific imitation in chimpanzees have not upheld the reputation of the species based on observational and experimental studies of human-to-chimpanzee imitation. No similar experiments are known for other apes.

### C. IMITATION IN OTHER MAMMALS

We are aware that, as primatologists, we may appear chauvinistic in lumping "the rest" under this one heading. However, the reason is simple. As Passingham (1982) notes, "well-authenticated accounts of imitation in mammals are hard to find": indeed, "the only reported case where we can be certain that true imitation occurred is in the dolphin (*Tursiops aduncus*) in captivity." This was reported by Tayler and Saayman (1973), who described the responses of a dolphin when it came to share a pool with a seal. One example is in the pattern of swimming. The dolphin normally uses its flukes to provide propulsion, only using its flippers to steer, whereas it is the flippers that the seal uses in propulsion. Yet, when the seal had been with the dolphin for a few months, the latter "was frequently seen moving forward very slowly on the surface, holding her flukes motionless and propelling herself with seal-like strokes of the flippers" (p. 288). Similar accounts are given of the dolphin apparently copying in some detail the comfort movements and sleeping style of the seal, as well as the swimming movements of a skate. The authors noted that "the clumsiness with which the dolphin executed these movements emphasised their unnaturalness" (p. 289). Another dolphin, "after repeatedly observing a diver removing algae growth from the glass underwater viewing port, was seen cleaning the window with a

seagull feather while emitting sounds almost identical to that of the diver's air-demand valve and releasing a stream of bubbles from the blowhole in a manner similar to that of exhaust air escaping from the diving apparatus" (p. 290).

It may be no accident that the quality of these apparent imitations—their arbitrary nature and complexity—seem alone to match those produced by the other highly encephalized species we discussed earlier—the chimpanzee. We shall consider the cognitive demands of such imitation in Section VI.

Unfortunately, there appears to have been no experimental investigation of cetacean imitation. Recently, however, experiments have been performed with other mammals—mice and rats. These are of great interest, not only because they use the "two-action" method we have already advocated in the case of primates, but because their theoretical framework of animal learning theory offers a different perspective on the distinctions at stake. Indeed, the bibliographies of these studies barely overlap with those of the other recent work we have reviewed, which have their roots more often in ethology, and it would now seem fruitful to attempt to bring the different approaches together (see Zentall and Galef, 1988, for an important step in this direction).

In Heyes and Dawson's (1990) experiment using rats, observers faced toward and watched one of two conspecific models. One model pushed a lever to the left for food reward, the other pushed it to the right. Observers were then tested in a number of phases, in all of which they had access to the lever themselves from the direction in which the model had operated it, which was thus the reverse of the direction they had viewed the modeling from earlier. In the first test, pushes to both left and right were rewarded until a set number had been achieved in the direction the model had pushed the lever. The proportion of left pushes was significantly higher for those who had watched left pushes (0.86) than for those who had watched right pushes (0.29). Similar evidence for an imitative effect was obtained in further tests in which reversal learning (pushing in the opposite direction) was speeded by intervening observation of a model pushing in the new direction, and extinction of a response was inhibited by watching a model perform the act. Collins (1988) performed a similar experiment with mice, finding that they pushed a pendulum door to the left more often after observing a model push it to the left, then after watching one pushing to the right. In this experiment, the observer mouse viewed the manipulandum from the same side as it later operated it.

Were these rats and mice imitating? The main concern of Heyes and Dawson is whether they have provided evidence for the observational learning of a response-reinforcer (R-S\*) relationship (e.g., push lever to left to obtain reward: what we would call imitation) or only of a stimulus-reinforcer (S-S\*) relationship (lever moving to left signals reward and may thus itself acquire reinforcing properties). An animal that has learned only the latter may then generate behavior appropriate to achieving that end (getting the lever to move to the left), but here

an imitative behavior would not actually be necessary. The rat could, in principle at least, push the lever with its nose or its paw, irrespective of the technique it had watched the model use (although natural constraints might well lead to the same action being used by both model and observer, giving a false impression of imitative copying). The plausibility of this second, S-S\* alternative is demonstrated in an experiment by Denny *et al.* (1983) in which there were two actions that *could* have been done by models, but in fact were not: rats observed either one or the other of two distinctive levers moved *automatically* to signal delivery of food. When given access to the levers the rats pushed the one whose movements had previously signaled food reward. Of course, if the levers had originally been pushed by "demonstrator" rats, the subsequent actions of the observers would likely have been similar and the results would probably have been interpreted as demonstrating observational learning—but at the level of stimulus enhancement, rather than the imitation of particular acts on the same single object that Heyes and Dawson (1990) claim to have demonstrated. In any case, these authors argue against the learning of only a S-S\* link in their experiment because the observers saw the lever originally from the opposite point of view to that from which they later operated it, and the cues to be seen in the two cases were rather different. This may be true, but there is a good deal of evidence that rats are actually rather good at defining absolute directions relative to the gross structure of their environment, even when they see the latter from various different points of view (Olton, 1979). As Heyes and Dawson admit, the matter can only be finally resolved by an experiment in which the lever is moved automatically.

Heyes and Dawson and Denny *et al.* (1983, 1988) thus raised a general criticism of the "two action" test. Where the two actions are done with the same part of the body on the same object, stimulus enhancement is nicely ruled out, but R-S\* and S-S\* learning are not discriminated. Until this is done with "disembodied" or automatic movement, imitative copying of the form of the action used has not been unequivocally demonstrated. Where, on the other hand, the two actions are done on the same object but with different parts of the body (as in the original study by Dawson and Foss, 1965), it could be said that here imitation is a rather special case anyway; that is, it involves copying *only of the part of body used* rather than the *form* of the act done with any particular body part.

These distinctions are discussed further in Section VI. To summarize the conclusions of the work reviewed so far, we have some surprising contrasts. As we have just seen, rats and mice have been shown apparently to "do an act from seeing it done" in a two-action test, which allows us to rule out stimulus enhancement. By contrast, the monkeys tested by Ham in a similar fashion did not do what they had seen done. Chimpanzees have not yet been tested properly in this way, but the one experiment using conspecific observation was interpreted by its authors (Tomasello *et al.*, 1987) as providing no evidence of imitation in

any case. Visalberghi and Fragaszy (1990) reviewing recent primate research, could conclude only that "apes probably do ape each other, at least in behaviors not involving tools. This is still nearly a statement of faith, however." It would seem that a century's assumptions about the supremacy of primate imitation have still to be experimentally confirmed.

## VI. EXPLAINING THE DISTRIBUTION OF IMITATION: COMPUTATIONAL REQUIREMENTS OF IMITATING THE SEEN VERSUS THE HEARD

### A. COMPUTATIONS INVOLVED IN IMITATING SEEN ACTS

The gloomy conclusion we have just reached about experimental evidence does, of course, ignore all the observations of spontaneous imitation, as well as Hayes and Hayes' human →ape "do-as-I-do" results, which suggest a very sophisticated imitative ability in chimpanzees, and perhaps dolphins also, although the latter evidence is based on a single report. Indeed, the achievement of the rats, just reviewed, in learning through observation to perform the simple act of pushing a lever to one side rather than the other (which in any case may be S-S\* rather than R-S\* learning) pales in comparison to the accurate reproduction of many complex and arbitrary acts by chimpanzees such as those described earlier. Thus, our working hypotheses are that (1) chimpanzees can indeed imitate, and do so well—a hypothesis admittedly requiring further experimental testing, particularly in the conspecific case; (2) dolphins may be able to imitate in a similar way, although we can be even less sure of this; (3) imitation is either absent in monkeys and other taxa or it is a much more fragile phenomenon, compared with that in chimpanzees, than has hitherto been recognized. The status of apes other than chimpanzees in this picture is currently unknown.

A similar judgement about the relative capacity of monkeys and chimpanzees to imitate appears in the context of Cheney and Seyfarth's (1990a) recent and independent review of primate social intelligence. What, then, is so special about chimpanzees' cognition? Whiten (1988) and Whiten and Byrne (1991) suggested that imitation is part of a larger pattern of cognitive differences, the background to which requires a slight digression.

#### *1. Mental Representation and Metarepresentation*

Leslie (1987) reviewed the findings of much recent work on children's development of a natural "theory of mind" (referred to by ethologists as "natural psychology" [Humphrey, 1980] or "mindreading" [Krebs and Dawkins, 1984; Whiten, 1991]). By the age of 5, children are usually capable of attributing beliefs different from their own to other people. The origins of this tendency to



mentally represent another's mentality (representation of representations, or metarepresentation) can be traced back to earlier years—even 2-year-olds attribute wants to others, for example (Wellman, 1991). Leslie suggests that the earliest manifestation of metarepresentation is seen in pretend play. Evidence for this in children includes the sequence of emergence of pretense and theory of mind in normal development and, perhaps more impressively, a dual deficit in theory of mind and pretend play in children afflicted with the social difficulties of autism.

This ontogenetic pattern finds a parallel in the phylogenetic contrast of chimpanzees with monkeys (Whiten and Byrne, 1991). Chimpanzees provide the only evidence of both true pretend play and mindreading. Records of spontaneous play with imaginary objects have been reported for chimpanzees by Hayes (1951) and Savage-Rumbaugh and McDonald (1988). The claim in the case of mindreading is that chimpanzees attribute intentional states to others, a claim supported both experimentally (Premack and Woodruff, 1978; Premack, 1988; Povinelli *et al.*, 1990) and by observational data on deception and counterdeception (Whiten and Byrne, 1988a, 1991; Byrne and Whiten, 1991). These latter studies do not suggest a similar ability in monkeys, and recent experiments with vervet and macaque monkeys are consistent with this monkey/ape difference (Cheney and Seyfarth, 1990a,b).

## 2. *Imitation as Mindreading*

Chimpanzees thus appear to have some facility in metarepresentation that monkeys do not, and Whiten and Byrne (1991) further suggested that this may be linked to the difference in imitative ability between the taxa. To imitate in the visual mode involves B copying an action pattern of A's that was originally organized from A's point of view (Bruner, 1972). It is necessarily a different pattern from B's point of view, yet it has then to be re-represented in its original organizational form so as to be performed from B's point of view. The expression "re-represented" seems unavoidable and is used advisedly: it translates as second-order representation or metarepresentation (Leslie, 1987; see also Dennett, 1988). To put the idea more graphically, we might say that B has to get the program for the behavior out of A's head: in other words, to engage in a type of mindreading. The hypothesis predicts that, as acts to be imitated become more complex, so it will be difficult to achieve imitation when the viewpoints of model and imitator differ, as opposed to B watching over A's shoulder.

## B. NEW DATA FOR BIRDS: IMITATING THE SEEN VERSUS THE HEARD

The preceding interpretation presents imitation of observed actions as a rather high-level cognitive achievement. This is consistent with a distribution restricted to only highly encephalized species. It thus fits with the apparent lack of imita-

tion in the visual modality in birds, despite the widespread capacity for imitation in the auditory modality, which it will be recalled, Thorndike (1911) wished to set aside as a "special case." As Palameta (1989) notes, "in order to copy a novel movement, a bird cannot rely, as in song learning, on comparing its own product with the perceived act in the same sensory modality." More specifically, in song learning, the bird does not have to represent what is in effect the model's representation of the act as it does in the case of visual imitation; instead, it need only adjust its own output until the sound of this matches what it originally heard (one level of representation). This may be an extra dimension in visual imitation that makes it more demanding than vocal imitation in its computational requirements.

The demonstration of visual imitation in birds would challenge this interpretation, insofar as relatively small-brained animals might lack the required computational power. As we have seen, Thorndike noted a lack of evidence for this type of imitation in birds. Rowley and Chapman (1986) have reported that galahs (*Coccyzoida roseicapilla*) raised by Mitchell's cockatoo (*C. leadbeateri*) foster parents "mimicked" the wing-beat motions of these foster parents; however, the report suggests the similarity resulted from learning to fly slower than normal so as to stay in the foster flock. This would appear to be an interesting version of "exposure" (see Fig. 1), in this case to slow travel times.

We earlier cited the work of Dawson and Foss on budgerigars, which did offer some support for what Thorndike called "doing muscular acts from seeing them done." In view of the tentative nature of Dawson and Foss's results, Galef *et al.* (1986) attempted to replicate it more thoroughly and with adequate numbers of subjects. They found a tendency for observer budgerigars to use the part of the body they had seen the model use, but this achieved significance only on the second of five trials (in all of which, we should note, reinforcement was given for success, so introducing a confounding factor of conditioning); overall, the 60% concordance between model and observer acts was not significant. Galef *et al.* generously concluded that this "relative fragility" of the Dawson and Foss finding "renders it unsuitable as a model system for exploring the phenomenon of imitation learning" (p. 191).

Palameta (1989) similarly found no signs of imitation in budgerigars performing acts like those used by Dawson and Foss, but had more success with pigeons. In an attempt to avoid the stimulus enhancement explanation for results of a previous study (Palameta and Lefebvre, 1985), an apparatus was designed in which not only did animals work at the same object, but even contacting it with the beak was held constant; what differed was what the beak did next, so this is an analogous procedure to Ham's in which monkeys pulled or twisted a bar. In one experiment, observer birds were pretrained to lift a stopper out of a depression to reveal a food reward. They then watched either a model who demonstrated a grasping and lifting action or another who, instead, grasped the stopper

and pulled down, rotating the disk into which the stopper was set and so revealing a second hole with a food reward in it. Both groups were then given an opportunity to perform under the second condition, where the stopper could not be removed but, instead, had to be pulled down to reveal the second hole. The group that had observed models performing the rotating action required a shorter time to solve this task and used fewer pecks, both differences being significant. This, together with the similarly positive results of a test with naive observers, Palameta interpreted as evidence, finally, for imitation in the visual mode in birds.

However, the design of the experiment is essentially similar to that of Heyes and Dawson in which rats pushed a lever to right or left, and in which we were forced to consider the possibility that what the observer had learned was an S-S\* rather than an R-S\* relationship. In the case of Palameta's experiment, the S-S\* link would be something like "disc rotating signals appearance of food," and the pecking actions of the birds that had been able to observe this would be interpreted as behavior directed toward getting the disk to rotate in this way, as distinct from the less purposeful efforts of the observationally naive controls. One way to exclude this possibility would appear to be to run the experiment without models, rotating the disk automatically as a demonstration.

Until this is done, the claim stands that imitation as evidenced in chimpanzees is not proved in other mammals (including monkeys and rats) or in birds.

### C. EMULATION: INFERRING OTHERS' GOALS OR NOTICING THEIR RESULTS?

Hogan (1988) gives a name to the S-S\* process referred to by Heyes and Dawson: "valence transformation." We have already noted that this involves more than stimulus enhancement, and also, of course, we have distinguished it from imitation (R-S\* learning in Heyes and Dawson's terms). We might then ask where it fits into the scheme illustrated in Fig. 1.

Our answer is that it is not yet obvious just how it differs significantly from "emulation" as defined by Tomasello *et al.* (1987). In both cases, it is suggested that what the animal learns is not the form of an act, but the nature of some desirable *result* of the model's act, which the observer later tries to recreate. It is just that in the case of Tomasello's chimpanzees, the animals came up with a variety of ways to do this, so imitation was not apparent, whereas in the case of the rat and pigeon experiments, such emulation could have led to similar behavior to that of the model because the tasks were sufficiently circumscribed that there was only one best way for the species to achieve them.

However, perhaps because "emulation" has been generated by human and chimpanzee workers and "valence transformation" by rat/learning theory workers, different assumptions will be made about their significance, and it is impor-

tant to make these explicit. Thus, on the one hand, valence transformation is interpreted as being a social phenomenon in a relatively trivial sense; indeed, the test suggested for it involves removing the model and having the manipulanda go through their movements automatically. At the other extreme, if emulation is seen as attempting to replicate the *goals* rather than the form of the models actions, then we are considering a rather sophisticated social interpretation in its own right—that the observer is perceiving the *aims* of the model. Cheney and Seyfarth (1990a), in a parallel argument to that of Whiten and Byrne (1991) previously described, suggest that “chimpanzees and other apes seem more adept than monkeys at learning to use tools through observation, possibly because they are more adept at imputing purposes to others” (p. 228).

Such distinctions raise a host of alternative hypotheses about what is occurring in episodes like those studied by Tomasello *et al.* Were observers learning nothing about how to behave (imitate), as such, but only about what movements the *objects* needed to make (that the rake had to catch the food in a certain way and then shift toward the cage)? Alternatively, were they imitating the form of the demonstrator's act, but only at a very crude level of resolution (“raking”), supplying idiosyncratic details of how to do this themselves? Or were they attempting to replicate the goal of the demonstrator (“trying to get food raked in”)? Or to recreate a result of the demonstrator's actions they themselves found attractive (“food getting raked in”)? Or perhaps some combination of these?

Such possibilities lead to a number of experimental refinements. We need to compare the effects of, for example: (1) a model that is seen (e.g., on videotape?) attempting to reach food (with no stick in view) and then wielding a stick (with no food in view), a display presumably sufficient for a “double” (food plus stick) stimulus enhancement effect; (2) a model wielding a stick near (or even touching) the food but not raking, thus providing local and stimulus enhancement, but presumably no basis for emulation; (3) the rake lined up with the food, or somehow automatically raking with no chimpanzee model in view (or with a chimpanzee in view but not doing the raking), which should be sufficient to elicit valence transformation; or (4) a model who is observed attempting to rake in food but not yet succeeding, presumably sufficient for an observer to infer the model's *goal*, yet not revealing the ultimate *result* of its actions.

#### D. SIMPLE VERSUS COMPLEX IMITATION

There is another way of looking at valence transformation. This is to argue that to limit the concept of “behavior” to bodily movements is arbitrary. When an animal acts, it moves its limbs, but it may also move tools or affect the environment in various ways. In the case of tool use like raking, we can regard the movements of the rake as just an extension or indeed part of, *the behavior of raking* [cf., Dawkins' (1982) concept of the extended phenotype]. It follows that

copying even the movements of the rake could be said to be "imitation of (part of) the form of the action." Similarly, pigeons copying the rotating of the disk itself and rats copying the movement of the lever in the experiments described would then count as imitation.

Whether imitation in monkeys, rats, or pigeons is confirmed either by accepting this semantic argument or by experimentally ruling out valence transformation, we would still appear to be left with a difference in the complexity of imitation demonstrated by chimpanzees when compared with other taxa. Of course there are inherent anatomical limits on complexity in each species—some have hands and others do not, for example. Nevertheless, it is the case that the rat and pigeon candidates for imitation, which we have been considering, involve movements whose simplicity can be characterized as almost two dimensional, by contrast with the many degrees of freedom involved in, say, Viki's lipstick episode. So far, much of the debate about phylogenetic differences in imitation has been of an all-or-none character, scrutinizing evidence for imitation as distinct from other mimetic processes, but it begins to look as if some formal way of comparing relative complexity will provide important insights into species differences and the mechanisms proposed to explain them; the computational demands of metarepresentation as discussed by Whiten and Byrne, for example, might become limiting only as the complexity of the action to be imitated places more demands on its mental representation.

## VII. CONCLUSION

What then, are the advances generated by a century of research? On the one hand, the verdict must be "very few." When we survey the scene with hindsight, we must admit how little is firmly empirically established about which species can and do imitate and through what mechanisms.

But the reason for this dull conclusion is an exciting revolution that has mainly taken place in the past decade in all of the four matters that have concerned us in this article as we traced their fortunes from the nineteenth century through the present one. With respect to our conceptualization of imitation in relation to a host of other mimetic processes, we have become much more sophisticated, and there are grounds for optimism that the major distinctions that need to be tackled empirically are recognized and laid out in some detail. In addition, we have seen that methods are now at hand to make progress on making these distinctions in practice, by contrast with the extensive series of studies we have reviewed from earlier times. Long-standing assumptions about the superiority of certain taxa have taken such a pounding that we can now proceed to judge the evidence in a less prejudiced fashion. And finally, those phylogenetic differences that we have taken as our "working hypothesis," together with differences in imitating the

seen versus the heard, have now provoked initial attempts to understand the cognitive mechanisms that underlie the process of imitation.

### VIII. SUMMARY

Systematic research on imitation has been pursued for over a century, but methods and conclusions generated in this time have come under strong attack in recent years. Among the most influential ideas have been several that date back to the beginnings of the field in the nineteenth century. In the present article, four of these are distinguished and their consequences and reappraisal in the present century are examined. First, despite early recognition of varieties of imitation, distinctions now made between a greater number of processes by which one animal can come to act like another mean that many conclusions drawn in the first half of this century require revision. Second (and closely related to these theoretical distinctions), experimental paradigms developed in the nineteenth century have been adhered to for much of the present one; only relatively recently have techniques been invented that can adequately distinguish imitation from a range of imitative-like processes. This is important because the latter have important social and cognitive implications in their own right. Third, early assumptions about phylogenetic differences in imitative ability—particularly the superiority of primates—have been reinforced by both observational and experimental studies for much of the present century. Results obtained in recent studies have combined with reappraisal of earlier ones to question these phylogenetic differences. We argue that imitation is as yet unproved in monkeys, whereas chimpanzees (and possibly other apes) share with humans an imitative capacity consistent with other aspects of social cognition examined in recent research. Fourth, it was early argued that auditory-vocal imitation (characteristic of many birds) is distinct from visual imitation (shown by mammals). We use recent research findings to suggest why visual imitation may exert greater computational demands, but also review new studies suggesting that a dichotomy between the vocal imitation of birds and the visual imitation of encephalized mammals is too simplistic to accommodate all the phenomena.

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