



Review

Imitation and local enhancement: Detrimental effects of consensus definitions on analyses of social learning in animals



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ABSTRACT

Development of a widely accepted vocabulary referring to various types of social learning has made important contributions to decades of progress in analyzing the role of socially acquired information in the development of behavioral repertoires. It is argued here that emergence of a consensus vocabulary, while facilitating both communication and research, has also unnecessarily restricted research on social learning. The article has two parts. In the first, I propose that Thorndike's (1898, 1911) definition of imitation as "learning to do an act from seeing it done" has unduly restricted studies of the behavioral processes involved in the propagation of behavior. In part 2, I consider the possibility that success in labeling social learning processes believed to be less cognitively demanding than imitation (e.g. local and stimulus enhancement, social facilitation, etc.) has been mistaken for understanding of those processes, although essentially nothing is known of their stimulus control, development, phylogeny or substrate either behavioral or physiological.

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The past three decades have witnessed enormous progress in our knowledge of social learning in animals. Development of a widely accepted vocabulary for discussion of relevant phenomena has both contributed to and reflected that progress, permitting organization of the plethora of information collected over the decades and facilitating communication among investigators with backgrounds in fields ranging from anthropology to zoology (e.g. Galef, 1988; Hoppitt and Laland, 2008; Whiten and Ham, 1992; Zentall, 2006). However, as I shall suggest below, consensus as to terminology may also have had some less-obvious, potentially pernicious consequences.

In the first and surely more controversial section of this article, I consider historical reasons why the consensus definition of imitation “as learning to do an act from seeing it done” (Thorndike, 1898, 1911) may have unnecessarily limited discussion of the behavioral processes underlying traditions of animals observed in the wild and led to use of methods in laboratory studies of the diffusion of behavior that may have precluded investigation of important aspects of the processes involved in the production of copies of observed behavior. I suggest modifications of such methods to bring them more into line with classic approaches to the study of avian song learning.

In part 2, I examine the possibility that consensus definitions of types of social influence on behavior that are generally believed to be less cognitively demanding than imitation may have led to the inappropriate conclusion that those types of social learning are well understood impeding experimental work on the phenomena to which those definitions refer.

1. Part 1: imitation

1.1. Edward Thorndike and the definition of imitation

Edward Thorndike’s (1898, 1911) two classic monographs, both entitled *Animal Intelligence* and both discussing the implications of the results of his doctoral research, are often read as concerned with the outcomes of a series of experimental investigations of imitation in animals. However, it is important to note that Thorndike did not undertake his thesis to study imitation per se. Rather, Thorndike’s goal was to challenge the notion, widely held during the late 19th century (e.g. Romanes, 1884), that animals, like humans, are cognitively sophisticated beings able to solve problems by manipulating representations.

Why should we care about Thorndike’s motivations for research undertaken more than a century ago? Because, ever since, research on social learning in animals has been dominated by one of the two questions concerning animal imitation that Thorndike proposed in 1898 and again in 1911: first, whether animals can “from an act witnessed, learn to perform that act” (Thorndike, 1911, p. 79), and second, whether “the idea of an act or the result of an act [italics added], . . . tends in itself to produce the act” (Thorndike, 1911, p. 250). For Thorndike’s purposes, the two questions were equivalent. Both asked whether animals could use representations to guide their actions. Consequently, it mattered little to Thorndike whether those representations were of actions or of goals. Only many decades later (Tomasello, 1994) did investigators of social learning make explicit a distinction between “imitation” (learning to do an act from seeing it done) and “emulation” (reproducing the results of a model’s behavior rather than reproducing the behavior that produced those results).

1.2. Discovering evidence of imitation in animals

Thorndike failed to find evidence of learning by imitation, and subsequent generations of experimental psychologists found Thorndike’s failure an irresistible challenge undertaking

innumerable experiments using more sophisticated versions of Thorndike’s puzzle boxes to investigate the question of whether animals could, in fact, learn to perform an act from observing others perform it. Unfortunately, all serious discussions found evidence of learning by imitation that emerged from such early studies relatively unconvincing (for review, see Galef, 1988). It was simply impossible to exclude simpler forms of social learning than imitation as explanations of observed social influences on the acquisition of behavior.

Indeed, persuasive evidence of imitation in animals became available only in the latter part of the 20th century, some decades after Dawson and Foss (1965) first reported that naïve budgerigars (observers) that had watched a trained conspecific (a demonstrator) use either its foot or its bill to depress a lever and obtain food tended to use the same appendage as had their respective demonstrators. Reintroduction of Dawson and Foss’s “two-action method” in the mid-1980s (Galef et al., 1986) produced a dramatic change in the experimental paradigm used to study animal imitation. Observer rats watched demonstrator rats push joy sticks either to left or right (Heyes and Dawson, 1990); observer pigeons and quail watched conspecific demonstrators either step on or peck at treadles (Atkins and Zentall, 1996; Zentall et al., 1996); chimpanzees and children watched adult humans as they either pushed or pulled at artificial fruit (Whiten et al., 1996), etc. and subsequently acted as had their respective demonstrators.

The two-action method provided evidence, contrary to the conclusion Thorndike had reached in his thesis work, that for a surprising range of avian and mammalian species, observing an act tended to produce that act. However, because the alternative acts witnessed in such two-action experiments (e.g. stepping and pecking, pushing and pulling, etc.) are likely to have been present in the behavioral repertoire of subjects before they participated in experiments, such experiments fail to directly address the question of whether animals “from an act witnessed, learn to perform that act.” They provide evidence only that observing an act can increase the relative probability that an animal will express that act rather than others in its repertoire. Although such evidence is surely consistent with the notion that representations of actions or goals can influence behavior, thus answering the question in which Thorndike was interested, such findings do not address the issue of whether an act can be learned from watching others perform it.

1.3. Too little too late

Long before the results of two-action experiments produced evidence that the idea of an act could motivate animals to produce that act, the stranglehold of radical behaviorism on the study of animal behavior had been broken, and animals had been shown to use representations to solve problems in navigation, timing, counting, classical conditioning, etc. (for review, see Shettleworth, 2010). Indeed, by the time that evidence from two-action situations became available indicating that animals could use representations to guide their behavior these other procedures had already provided ample evidence of that fact. Consequently, investigation into learning by imitation had, in a non-trivial sense, lost much of their original theoretical rationale (i.e. demonstration of representations influencing behavior) and were in danger of becoming an autonomously motivated enterprise perseverating in something of an intellectual vacuum. As others have noted (e.g. Heyes, 1993, 2005, 2013), although the two-action method provided opportunities for major advances in appreciation of the nature of the representations utilized by animals and, possibly, of the relationship of such representations to those used by humans, such prospects were rarely exploited. For the most part, the two-action method was used only to explore the range of species able to imitate, not the nature of animal cognition.

1.4. What now?

Although demonstration of imitative abilities in the limited sense indicated above occurred too late in the day to have much impact on the study of animal cognition, by the end of the 20th Century, work on animal imitation had become relevant in an important new context.

During the decades following reports from Japan of sweet-potato washing by Japanese macaques on Koshima Islet (e.g. [Kawai, 1965](#)), and from the UK of milk-bottle opening by various species of small birds ([Fisher and Hinde, 1949](#)), field researchers amassed impressive bodies of data indicating that groups of free-living primates might be able to sustain traditions functionally similar to the culturally transmitted patterns of behavior seen in humans (e.g. [Perry et al., 2003](#); [Van Schaik et al., 2003](#); [Whiten et al., 1999](#)). Such ethnographic studies of animals led many to question the uniqueness of human culture (for review, see [Laland and Galef, 2009](#)) and provided a compelling rationale for further investigation of animal imitation.

1.5. Cumulative culture and learning to do an act from seeing it done

One of the more unusual characteristics of human culture is its cumulative nature, i.e. the ability of succeeding cultural generations to learn socially and then improve upon innovations developed by their predecessors. As [Tomasello \(1994\)](#), [Boyd and Richerson \(1996\)](#), [Tennie et al. \(2009\)](#) and others (for review, see [Caldwell and Millen, 2008](#)) have proposed, cumulative culture requires an ability to precisely copy the behavior of others (See also [Galef, 1992](#)). The same authors have argued that precise copying of observed behavior requires either pedagogy (deliberate tuition) or imitation. If for example, an animal tradition rests, on local enhancement or emulation, each individual must learn for itself how to interact with the portion of the environment to which the behavior of a previous 'cultural generation' directed its attention. Consequently, when a tradition is transmitted by local enhancement or emulation, there is rarely a possibility of cumulative improvement. (An interesting possible exception, which will not be considered further here, can be found in the social learning of paths through the environment resulting from (e.g. [Helfman and Schultz, 1984](#)) together with incidental learning.)

Although there is no convincing evidence of pedagogy in non-human animals, the results of numerous two-action experiments suggest that members of many species of both primate and non-primate animals are able to learn by imitation. If cumulative culture can be supported by imitation, and many species of animal can imitate, why imitating animals lack cumulative culture becomes something of a mystery.

In the remainder of this section, I discuss the possibility that two-action method, although as Thorndike intended, is sufficient to reveal the use of representations in social learning, it is not an adequate test for imitation of the sort that produces precise copies of observed behavior, i.e. the kind of imitation that supports human culture. If so, understanding the imitation underlying the evolution of human culture requires a shift in focus of studies of animal imitation from questions concerning the possibility of animals using representations to direct their behavior ([Thorndike, 1898, 1911](#)), now a generally accepted fact ([Shettleworth, 2010](#)), to questions concerning how animals might learn to precisely copy the observed acts of others.

1.6. Learning motor acts: an introspection

Since my teen years, I have tried to acquire two fairly complex and surely novel (for me) motor skills: alpine skiing and Tai Chi. The

two skills are quite different, and I believe each offers insight into the role of observation in supporting the acquisition of motor skills.

Bitter personal experience has taught me that I could watch for decades as expert skiers gracefully descended steep inclines thigh-deep in fresh powder snow, and still not be able to navigate with grace even a moderate slope blanketed with relatively forgiving packed powder. I suggest that although, watching expert skiers is inspiring, such observation is in no way sufficient to produce similar performance in a neophyte.

Consideration of the role of observation of skilled practitioners in learning to ski proficiently seems relevant to understanding of chimpanzees' acquisition of skills such as nut cracking, termite fishing, and ant dipping, because in both humans and apes the development of proficiency in such behaviors is guided by feedback from the physical environment as a result of natural shaping processes ([Galef, 1980](#)) as discussed further in S1. In any case, thinking about learning to ski makes it clear that even humans cannot learn to perform complex acts proficiently by watching such acts performed.

Tai Chi is quite different from skiing in that the physical world provides the novice martial artist with little differential reward of behavioral variants to guide development of behavior to match that of an expert model. The simplest of Tai Chi movements is called a donue. A donue involves standing with legs slightly bent, hips thrust forward a bit to straighten the back and simultaneously, in time with your breathing, bending and straightening the legs and raising and lowering your relaxed arms.

If you attend a novice Tai Chi class and watch students try for the first time to imitate an instructor as she demonstrates a donue, you will see the students doing all sorts of strange things. Some bend at the waist and keep their arms straight rather than keep their back straight and raise and lower their arms. Others raise and lower their arms, but keep them straight and rigid rather than supple and flexible, etc.

It takes a surprising amount of practice to learn to do a reasonable approximation of a donue and months of further practice to learn to do a great one. As in the case of skiing, there is no learning to do an act from seeing it done. Rather, there is learning by observation that an act is possible. At first, the best a novice can do is to select from within her available repertoire of movements one close to that demonstrated by the instructor. Then, over time, she can bring that first approximation into greater accord with the demonstrated act.

Watching an expert perform donues results in "learning that an act can be done from seeing it done." However, that is not at all the same thing as imitation in Thorndike's sense of learning to perform an act from seeing that act performed.

Donues are not physically demanding, so any failure of neophytes to perform donues properly cannot be attributed to a lack of strength or dexterity. Donues are also of interest because they are similar in many respects to the arbitrary greeting gestures, grooming patterns and other social conventions (e.g. [McGrew et al., 2001](#); [Perry et al., 2003](#)) that have been interpreted as providing conclusive evidence of learning an act by seeing it performed or of the role of the role of patient watching in the acquisition of behavior. We do not know how primates acquire such social conventions. Consequently, to assume that such acts are learned from seeing them performed is premature. Indeed, if humans cannot learn to perform a relatively simple act like a donue from seeing it done. It is not likely that non-human animals can learn similar acts simply by observation.

1.7. Cumulative modifications of Thorndike's definition of imitation

Refinement of [Thorndike's \(1898, 1911\)](#) definition of the term imitation "as learning to do an act from seeing it done," is not

particularly original. Twenty-first century authors not only distinguish “imitation” (reproducing a model’s behavior) from “goal emulation” (reproducing the results of a model’s behavior; [Whiten and Ham’s, 1992](#)). They are also, to use [Janik and Slater’s \(1997\)](#) or [Byrne’s \(1995\)](#) terminology, not so interested as was Thorndike in “contextual imitation” (learning by observation to perform a familiar act in an unfamiliar context) as in “production imitation” in which the actual form of a novel action is learned through observation. And as discussed earlier, understanding the propagation and refinement of novel behaviors provides the contemporary intellectual rationale for further studies of learning by imitation.

Learning in which observation of a motor pattern is combined with trial and error resembles in important respects to [Tomasello’s \(1994\)](#) “emulation,” or [Whiten and Ham’s \(1992\)](#) “goal emulation.” In both, an individual learns by observation about what is possible, then generates behavior to achieve a desired outcome. However, in Tai Chi, alpine skiing, or other motor skills, the ‘goal’ is not, as in goal emulation, to reproduce some change in the environment, but to reproduce an observed behavior ([Shea, 2009](#)).

For the purposes of the next few paragraphs I shall refer to, as “performance emulation” social learning in which a neophyte learns from observation of an accomplished individual that a behavior can be performed and relies on subsequent trial-and-error learning to reproduce that behavior. It is not my intention to introduce yet another term into an already probably overly elaborate vocabulary describing ways in which social influence can affect the acquisition of behavior. Rather, I wish to call attention to the likelihood that what we call ‘imitation’ reflects not learning to do an act from seeing it done, but learning that an act can be performed as a result of observing others perform that act. Consequently, there is no reason not to continue to use the term imitation for such learning, though for the present paragraphs using the term “performance emulation” to refer to such learning may serve to focus awareness that the kind of imitation that might lead to faithful copying and cumulative culture is not Thorndike’s imitation and is not illustrated by the two-action method. Rather, performance emulation provides a behavioral mechanism for faithful transmission of behaviors (which goal emulation does not) and, therefore, might form a basis for cumulative culture (which goal emulation cannot).

Performance emulation is similar to [Byrne’s \(2002\)](#) “production imitation” but differs in at least two potentially important ways. First, labeling performance emulation as a type of emulation rather than of imitation emphasizes that acquiring a motor skill can be a goal approached via individual learning. Given the history of definition of imitation, “production imitation” suggests, to the contrary, that acquisition results directly from observing another demonstrate a behavior. Second, in [Byrne’s \(2002, p. 77\)](#) view, production imitation is “the kind of imitation that enables us to learn by apprenticeship, patiently watching a skilled practitioner.”

I know of no evidence that even humans can learn any unlikely motor skill [including how to make sushi ([De Waal, 2001](#))] by “patient watching” alone (Evidence consistent with the view that performance emulation, rather than Thorndikian imitation is involved in traditions of free-living primates is provided in S2). Rather, in both goal emulation and performance emulation, to accurately copy a performance, an observer has, first, to produce a behavioral variant from within its existing repertoire and then modify that behavior to bring it into correspondence with the behavior it observed. In goal emulation, guidance for elaboration is provided by the environmental consequences of behavioral variants; in performance emulation, guidance is provided at least in part, by a stored representation of an observed behavior. Further discussion of the relationship of goal and performance emulation can be found in S3.

1.8. Evidence of faithful copying in animals

To date, little laboratory evidence suggests that something other than imitation, in Thorndike’s sense of learning to do an act from seeing it done may be involved in animals’ social learning of improbable acts. However, this absence of evidence may reflect a failure to seek it. In the one experiment of which I know expressly designed to examine the social learning of behaviors with some of the complexity and novelty of many traditional behaviors in free-living apes, [Whiten \(1998\)](#) presented chimpanzees with an “artificial fruit” that had two defenses which subjects had to remove in succession if they were to gain access to the rewards that the artificial fruit contained. Each subject observed a human demonstrate one of two methods for removing each defense and one of two sequences of defense removal. Subjects exhibited no evidence of sequence copying on their first two test trials, but on the third trial, all four copied (or almost copied) the sequence that they had seen demonstrated. As [Hoppitt and Laland \(2008, p. 146\)](#) noted, “Perhaps the chimpanzees formed a template of the demonstrator’s behavior and then modified their behavior to match the template.” In other words, perhaps the chimpanzees in [Whiten’s \(1998\)](#) experiment engaged in performance emulation as defined above.

1.9. Avian song learning

The notion of “template matching” that [Hoppitt and Laland \(2008\)](#) used in discussing the results of [Whiten’s \(1998\)](#) experiment on sequence copying in chimpanzees is, of course, derived from classic analyses of song learning in passerine birds ([Marler, 1976](#)). In the past, such analyses have been largely ignored in the literature on imitation (e.g. [Heyes and Galef, 1996, 2004](#); [Zentall and Galef, 1988](#)).

[Thorndike \(1898\)](#) may well have been responsible for initiation, if not maintenance, of a ‘tradition’ in experimental psychology of disregarding avian song learning when discussing animal imitation. If Thorndike proposed, “a bird out of a lot of random noises that it makes chooses those for repetition which are like sounds that he has heard, it is. . . a mystery why, though not. . . a mystery how, he does it” (1911, p. 76), an assertion that has, I suspect, led generations of students of non-vocal imitation to ignore the possibility that the development of bird song might provide insight into the social learning of other motor acts.

As is well known, male nestlings of some species of song bird store a representation (a template) of a species-typical song after hearing an adult male of their species sing that song ([Marler, 1976](#)). Months later, these now sexually mature individuals learn to produce a copy of the song that they heard as nestlings. At first, the yearlings produce only subsong, a relatively disorganized string of species-typical notes and trills, and only gradually do they come to match their vocal output to the stored template of adult song heard while nestlings. Importantly, if a juvenile male is to develop adult song, he has to be able to hear his own voice during the period of subsong production, strongly suggesting that development of adult song out of subsong involves matching song output to a template stored in memory ([Marler, 1976](#)).

Because, as Thorndike indicated, a bird can directly compare the sound of its own vocal production with a stored auditory template it is not difficult to imagine how a young bird might gradually bring its subsong production to match a song template. The “how” of song imitation appears self-evident, and recent work on the neuroanatomy of subsong production provides findings consistent with the common-sense view that selection among song variants is crucial to development of adult song ([Brainard and Doupe, 2002](#)). I propose that in performance emulation (i.e. imitation) generally, as in bird-song learning, distinct processes are involved

in acquisition of the idea of a behavior and in development of an ability to perform that behavior.

Again as Thorndike suggested, the “why” of song learning remains problematic, as does the “why” of performance emulation more generally. Recent findings suggest that, in juvenile songbirds release of endogenous opioids following subsong production may be involved in maintaining singing while learning to produce adult song (Riters, 2009; see also Dayan and Balleine, 2002). Although the role, if any, of release of endogenous opioids in guiding development of subsong into adult song has not been explored, it would be enlightening if the intensity or duration of opioid release were to increase with increased similarity of subsong to an adult song heard while in the nest.

Recent neural imaging studies in humans indicate that activation of reinforcement-learning circuitry in the ventral striatum is associated with both receiving a valued object and learning that others agree with our valuation of an object (Campbell-Meiklejohn et al., 2010). Such linkage between rewards associated with one's own behavior and the behavior of others suggests a further possible avenue to explore in understanding the motivation for behavioral matching.

Understanding the how as well as the why of production of motor acts other than song is problematic. As Heyes and Ray (2000) state, because an observer's view of its model's behavior is quite different from its view of its own behavior, imitated motor acts are often “perceptually opaque,” and those acquiring a behavior have to match their motor output to a visual template that is not isomorphic to the behavior they are to produce. Ultimately, work on mirror neurons (Fogassi et al., 2005) may provide insight into how such cross-modal matching takes place. Much work remains to be done before the processes resulting in the development of perceptually opaque mimetic actions are fully understood (Press et al., 2010).

1.10. Conclusion to part I

One thing is clear; birds do not learn to sing precise copies of adult song by imitation alone at least not in the historical sense of that word. Similarly, I suggest, chimpanzees do not learn to fish for termites, crack nuts or dip for ants by imitation alone (again in the historical sense of that word). A match between one's own performance and that of a model, whether of bird song or other traditional behavior, requires sophisticated interaction between social and individual learning. Consequently, to achieve face validity in controlled studies of social learning of behaviors that resemble the traditions of free-living animals, we need experimental paradigms that, like those currently used to explore birds' achievement of adult song, both require subjects to acquire unlikely patterns of behavior following multiple demonstrations (Enquist et al., 2010) and provide opportunities to assess performance throughout a process of gradual acquisition (Whiten, 1998).

The suggestion that social learning of unlikely acts in both humans and other animals is a result of the same process (performance emulation) leads naturally to the question of why evidence of cumulative culture is so prominent a feature of the products of human social learning and is essentially absent from the traditions even of our great-ape cousins. “No animal comes close to having humans' ability to build on previous discoveries and pass the improvements on. What determines those differences could help us understand how human culture evolved” (Anonymous, 2005, p. 99). From the perspective proposed here, other animals must lack either the human capacity for: (1) constructing or maintaining templates of observed motor acts, or (2) the motivation or ability to learn to generate precise copies of observed behaviors.

Empirical approaches to study of possible dissimilarities in the ability to construct behavioral templates and in motivational

processes supporting human and animal behavior follow naturally from the analysis suggested above. For example, Whiten's (1998) demonstration of novel sequence copying in chimpanzees suggests that they may more easily form templates of sequences of familiar actions than of the details of novel performance. The ‘overimitation’ of human children suggests exceptional motivation to match behavior to a template once one is acquired (e.g. Over and Carpenter, 2013; Lyons et al., 2007).

2. Part 2: understanding cognitively less demanding social learning

Although for many years many laboratories have examined instances of social learning that are the result of local enhancement, social facilitation, stimulus enhancement, goal emulation, etc. (e.g. Frigaszy and Visalberghi, 1990; Galef and Clark, 1971b; Laland and Plotkin, 1990; Tomasello et al., 1987), such processes have rarely been treated as phenomena worthy of analysis in their own right. Consensus as to the definition of types of social learning believed to reflect cognitive processes less demanding than those involved in imitation has contributed to the illusion that we understand such processes more deeply than we actually do. Indeed, agreement on labeling seems to have concealed the need for further analyses. Here, I focus on local enhancement, though a similar case could be made for any number of “mimetic processes” (Whiten and Ham, 1992).

Ever since Thorpe (1963, p. 134) defined local enhancement as “apparent imitation resulting from directing the animal's attention to a particular object or to a particular place in the environment,” we all “know” what local enhancement is. Except for some relatively minor disagreement as to the importance of attentional processes as a defining feature of local enhancement (e.g. Galef, 1988; Zentall, 2004 vs. Hoppitt and Laland, 2008), Thorpe's definition has been widely accepted. Such agreement serves to conceal our near-total ignorance of: (1) the behavioral process (or processes) that support local enhancement, (2) the stimuli that control local enhancement, (3) its development, (4) neural substrate, or (5) phylogeny. An entire “field” of local enhancement awaits exploration. Analyses of other types of social learning carefully defined in the numerous linguistic dissections of social learning (e.g. Galef, 1988; Whiten and Ham, 1992; Zentall, 2006) are similarly restricted.

2.1. Mechanism

We do not know even whether across either species or situations instances of either local or stimulus enhancement reflect a single underlying process or several different processes. Although some disagree (e.g. Hoppitt and Laland, 2008), learning whether any two instances that are described using a single term are the outcome of similar behavioral processes or rest on separate neurological substrate seems likely to meaningfully enhance our understanding. For example, by many definitions, both species whose members come in contact with parts of the environment because they tend to remain in close physical proximity (e.g. guppies) and species whose members approach others when those others engage in unusual or interesting activities (e.g. chimpanzees) would be said to exhibit local enhancement if such socially biased experience increases the probability that group members subsequently behaved similarly to one another. However, such differences in underlying process supporting “local enhancement” could profoundly affect the rate at which behavioral innovations diffuse through social groups.

Application of network-based diffusion analyses of the type currently championed by Hoppitt and Laland (2008) offers promise of successful empirical examination of such alternatives (e.g. Atton et al., 2012). Effects of individual differences in ‘personality’ (e.g. in

boldness or hierarchical position) on diffusion paths should also differ markedly between species that are simply socially cohesive and those that attend to specific individuals engaged in salient activities and are thus open to bias in their social learning (Coussi-Korbel and Fragaszy, 1995).

2.2. Development

Susceptibility to social influence requires response to the behavior of others. Early experience may directly influence the development of behavioral phenotypes (e.g. boldness, aggressiveness, etc.), and behavioral phenotype might, in turn, affect reliance on socially acquired information. Alternatively, experiences early in life might directly promote or retard the tendency to use others as sources of information. For example, my students and I examined effects of hand rearing Norway rats from birth to weaning (thus denying opportunity early in life for interaction with conspecifics) on their subsequent tendency to prefer feeding sites that others of their species were exploiting. We found that normally reared, 25-day-old rats strongly preferred to feed at sites scent marked by conspecific adults, whereas pups reared without social contact failed to show such preference. Importantly, the influence of social cues on the feeding site choices of pups reared in social isolation could be fully reinstated by exposing them to age mates for a few days (Galef, 1981).

In a conceptually similar experiment, Chapman et al. (2008) examined the role of social interactions early in the early life of guppies on development of susceptibility to social influence. The authors report that guppies reared at low densities show a significantly greater tendency than guppies reared at higher density to both shoal and use socially acquired information to locate food. Chapman et al. (2008) suggest that a direct effect of rearing density on social learning provides the most parsimonious explanation of their data. It is, however, also possible that increased shoaling results in greater opportunity for incidental learning and thus indirectly rather than directly enhances social learning.

So far as I know, and unfortunately, the preceding two examples represent all the research undertaken expressly to examine the development of susceptibility to social influence on learning, though studies of the effects of early experience on schooling in fishes (e.g. Williams and Shaw, 1971) suggest interesting avenues for future research as does Katsnelson et al. (2011) recent work on the relationship between individual learning in house sparrows and their probability of being 'producers' or 'scroungers' when foraging socially.

2.3. Stimulus control

2.3.1. External stimuli

Information concerning the stimulus control of cognitively less demanding types of social learning is as impoverished as is information concerning its development. We know, for example, that Norway rats seeking a feeding site can use both visual (Galef and Clark, 1971b) and olfactory cues (Galef and Heiber, 1976) to identify sites that others are utilizing. We also know (although the data were never published) that rats do not use auditory cues others produce when gnawing on food to select a feeding site. Sound spectrograms of the noise sound of rats chewing are quite distinctive and are readily distinguished from background noise. Still, playback of high-quality audiotape recordings of the sounds of rats chewing on pellets failed to increase the preference of other rats for a feeding site where the sounds were played (Galef and McQuoid, unpublished).

2.3.2. Internal stimuli

Effects of internal state on social learning are also poorly explored. Food-deprived rat pups seeking food are more susceptible to social influence than are water-deprived rat pups seeking water (Galef, 1978), suggesting that in rats, local enhancement of feeding sites is domain specific rather than a result of a general tendency of young rats to affiliate. Possibly, in species that exhibit a strong tendency to flock or shoal (presumably to avoid predation) the conditions under which local enhancement occurs are broader than in rats.

If so, use of the term local enhancement to describe effects of the actions of conspecifics on bringing one another into contact with particular portions of the environment has served to obscure possible differences in the behavioral substrates supporting such phenomena.

2.4. Phylogeny

Comparison of the tendency of members of closely related species to rely upon social information has seldom been used as a tool for understanding the functions of social learning processes. Galef and Clark (1971a) compared the tendency of wild and domesticated Norway rats to use social information in selecting feeding sites and foods to understand why young wild rats show durable preferences for the food that adults of their colony are eating, while similar preferences in domestic rats are ephemeral. The "neophobia" of wild rats (Barnett, 1958) leads them to continue to reject foods they have not previously eaten long after their domesticated congeners have accepted such unfamiliar alternatives. In a similar vein, Coolen et al. (2003) examined three- and nine-spine sticklebacks use of public information, concluding that the greater reliance of the former on social information is a consequence of their greater vulnerability to predation and tendency to remain under cover and observe the behavior of others.

2.5. Conclusion to part 2

The general message in this brief section is that consensus as to how various instances of non-imitative social learning should be labeled has served to conceal profound ignorance of the causation, development, and phylogeny of behaviors so described. There are lifetimes of work awaiting those who wish to provide a deeper understanding of non-imitative processes in social learning which may well be of greater importance in the lives of non-human animals than is imitation, an aspect of social learning which has received an inordinate share of researchers' attention.

3. Conclusion

More than 125 years have passed since George Romanes (1884) observed his coachman's cat open a garden gate and interpreted the cat's behavior as a product of imitation. In intervening decades, extraordinary progress has been made in describing possible mechanisms of social learning, formally modeling social learning processes and understanding the role of social learning in the development of behavioral repertoires of free-living animals. Consensus as to the definition of terms describing various behavioral processes involved in social learning has not only facilitated discovery and analysis of relevant phenomena but has also restricted thinking about mechanism, concealing profound ignorance as to the development, physical substrate and expression of behaviors whose labeling is no longer controversial. Much remains to be done before we achieve as complete an understanding of social learning and its role in the lives of animals that even contemporary empirical tools allow. Freeing thinking about phenomena of interest from

constraints inherent in our ways of talking about them may prove a useful first step.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2013.07.026>.

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