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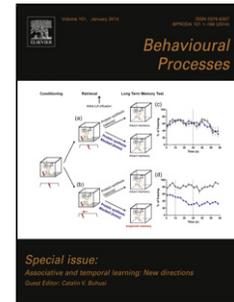
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How the two-action method became the gold standard for determining whether an animal can “from an act witnessed, learn to perform that act” (Thorndike, 1911)

Problems with the two-action method in understanding the development of traditional behaviors in free-living animals

Bird-song learning may provide a more appropriate model than classic Thorndikian imitation for understanding the role of social learning in the development of regional traditions in animals

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Laboratory studies of imitation/field studies of tradition: towards a
synthesis in animal social learning

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Here I discuss: (1) historical precedents that have resulted in comparative psychologists accepting the two-action method as the “gold standard” in laboratory investigations of imitation learning, (2) evidence suggesting that the two-action procedure may not be adequate to answer questions concerning the role of imitation in the development of traditional behaviours of animals living in natural habitat, and (3) an alternative approach to the laboratory study of imitation that might increase the relevance of laboratory studies of imitation to the work of behavioral ecologists/primatologists interested in animal traditions and their relationship to human cumulative culture.

Introduction

In 1988 Lawrence Erlbaum Associates published *Social Learning: Psychological and Biological Perspective*, a multi-authored text that Tom Zentall and I co-edited. The book, developed from a symposium that Tom had organized for the meetings of the Midwestern Psychological Association in Chicago in 1985, was the first of several edited volumes and special issues of journals focussed on animal social learning that were to appear in the following 25 years.

Periodic publication of collections of papers on social learning was useful because those interested in the role of socially acquired information in the development of adaptive patterns of behavior had backgrounds in fields ranging from anthropology to zoology. Consequently, relevant literature was widely scattered and difficult to follow in the primary literature.

The diversity of background of those interested in understanding social learning led Zentall and Galef (1988, p. ix) to suggest that “The process of creating a coherent field of social learning out of the diversity of current social learning research is likely to be both long and difficult.” Juxtaposition in edited volumes of work sampling broadly from the diverse social learning literature provided a potential antidote to intellectual provincialism.

As the subtitle to Zentall & Galef’s (1988) volume indicates, divergence of interests between those approaching the study of animal social learning from biological and psychological perspectives was particularly obvious. Investigators working in paradigms associated with experimental/comparative psychology were concerned almost entirely with social influences on animals’ acquisition of behaviors that are not seen outside the laboratory: bar pressing, key pecking, chain pulling, etc. More biologically oriented contributions focussed on the possible role

of socially acquired information in the development of presumably adaptive patterns of behavior seen in natural circumstances: predator avoidance, food handling, mate choice, etc.

Further, and as will come as no surprise to those with even a passing familiarity with the social-learning literature, the chapters in Zentall and Galef (1988) discussing the role of social information in the acquisition of arbitrary responses were preoccupied with the question of whether animals could imitate, whether in Edward Thorndike's (1911, p. 79) words, an animal "from an act witnessed, could learn to perform that act." For example, Zentall (1988) entitled his chapter in the Galef and Zentall (1988) volume "Experimentally manipulated imitative behavior in rats and pigeons" and David Hogan (1988) entitled his "Learned imitation by pigeons." To the contrary, chapters focussed on the role of social learning in the acquisition of patterns of behavior seen in natural circumstances never mentioned imitation in either title or text.

The field of social learning has changed dramatically over the last quarter century. In Laland and Galef's (2009) edited volume "*The Question of Animal Culture*" comprising chapters by both psychologists and biologists interested in the role of social learning in development of local traditions in free-living animals, imitation is discussed in every contribution, whether its author was trained in psychology, ecology, primatology, or philosophy.

The present manuscript has four goals: first, to explore the historical context that led those with a background in experimental/comparative psychology and an interest in animal social learning to focus almost exclusively on studies of imitation as first defined by Thorndike in 1898 rather than on other forms of social learning: e.g. local and stimulus enhancement, emulation), second, to ask whether

concentration on learning to perform an act from seeing it done was really such a good idea (I am going to suggest that it was not), and third, to explore the adequacy of Thorndikian imitation and the two-action method to which it led to analysis of the development of traditions in free-living animals. Last, I shall offer a suggestion as to where those interested in mechanisms of social learning that support development of local traditions in animals might focus attention in future.

My purpose in reviewing the historical material is to take a tentative, and I hope heuristic step towards integrating the work of those (primarily experimental psychologists) conducting laboratory experiments examining animal imitation with the contributions of those (primarily primatologists) providing information on the regional distribution (e.g. Whiten et al., 1999) and development (e.g. Lonsdorf, 2005, 2006) of traditional patterns of behavior in populations of free-living animals.

Edward Thorndike and the study of animal imitation

Edward Thorndike published two immensely influential monographs, both entitled *Animal Intelligence*, and both describing and interpreting the results of his dissertation research on animal learning. The title of both monographs poked not-so-subtle fun at similarly titled earlier monographs by such pioneers in the interpretation of animal behavior as C. Lloyd Morgan (1891) and George Romanes (1892). Indeed, the conclusion Thorndike reached in both his publications was that animals are not nearly as cognitively sophisticated (i.e. intelligent) as they had been portrayed by his contemporaries.

In the social-learning literature, Thorndike's classic papers are usually treated as describing the methods and results of a series of failed experimental investigations undertaken to determine whether, as a plethora of earlier anecdotal

reports of animals (e.g. Romanes, 1884) suggested, non-human animals (henceforth animals) could “from an act witnessed, learn to produce that act.”(Thorndike, 1911, p. 79), or alternatively “whether the idea of an act *or the result of an act* [emphasis added]...tends in itself to produce that act” (Thorndike 1911, p. 250).

Perhaps surprisingly, for decades, only the first of the two definitions of imitation Thorndike (1911) proposed captured the attention of those studying animal imitation. Not until 1996, when Tomasello introduced the term “emulation” (learning about the results of actions rather than about actions themselves) into the social-learning literature, did researchers and theoreticians begin to consider the possibility that observation of the result of an act, rather than of an act itself, might increase the probability that an observer would perform an act that it had observed.

Thorndike’s repeated failure to find evidence consistent with the hypothesis that cats, dogs, chickens or monkeys could learn by imitation proved an irresistible challenge to subsequent generations of comparative psychologists motivating myriad studies in apparatus, similar to (if more sophisticated than) Thorndike’s famous puzzle boxes. Discovery of convincing experimental evidence that any animal could learn to produce an act simply from observing another engage in that act became something of a Holy Grail in laboratory research on animal social learning.

However, as the second of the two quotations above from *Animal Intelligence* (1911, p. 250) suggests, Thorndike did not undertake his groundbreaking thesis research to determine whether animals could imitate. The issue that interested Thorndike was both broader and of greater general interest than that. Thorndike wanted to know whether, as his contemporaries largely believed,

animals other than humans could use representations to initiate actions. In Thorndike's view, evidence of imitation in animals would be consistent with interpretations of animal learning that included human-like cognitive capabilities; if animals could imitate, then the idea of an act (in the case of imitation, an idea formed by watching another behave) must be able to initiate and direct behavior.

Evidence of the breath of Thorndike's interest in undertaking his dissertation research is apparent in a second (perhaps wisely forgotten) paradigm that he used to investigate the ability of animals to use representations to organize their behavior. Thorndike argued that, if the idea of an act were sufficient to produce that act, then an inexperienced animal repeatedly "put through" (Thorndike, 1911, p. 103) some action leading to reward should subsequently show a reduced latency to learn to perform that action. "Putting through" involved manually moving an animal's limb to produce a desired action (e.g. a foot pulling on a string or stepping on a treadle). Thorndike considered his failure to find any evidence of an effect of "putting through" on latency to acquire behaviors as consistent with his failure to find evidence of imitation. Both suggested that in animals, the idea of an act did not lead to its production.

Thorndike's thesis data and his interpretation of them had tremendous impact on the study of behavior and resulted in a near-total rejection of cognitive interpretations of animal behavior during the decades when radical behaviorism dominated study of both animal and human learning. Second, and equally relevant to the present discussion, all researchers interested in animal learning adopted Thorndike's general method for studying imitation; naïve observers were allowed to watch demonstrations of a motor act leading to reward, and the latencies of such subjects to acquire the observed behavior was compared with that of control animals that had not seen demonstrations.

In the late-20th century, Thorndike's method of studying imitation as well as his perspective on animal intelligence more generally (Shettleworth, 2010), were to fall from favor. Critics of Thorndike's experimental paradigm for studies of imitation (e.g. Galef, 1988) argued that his methods could not provide convincing evidence of imitation learning. It was simply impractical to exclude all alternative explanations to imitation of any effect of watching a demonstrator perform a behavior on the latency of an observer subsequently to acquire that behavior. In particular, effects of increased attention paid to the portion of the environment following observation of activity of another there (local or stimulus enhancement, (e.g. Galef, 1988; Whiten & Ham, 1992; Zentall, 1996) proved impossible to exclude in traditional imitation experiments.

Credible evidence of imitation by an animal that had seen another engage in some activity was not available until some decades after Dawson and Foss (1965) first reported that naïve 'observer' budgerigars that had watched a trained conspecific demonstrator use either its foot or beak to depress a lever for a food reward tended to use the same appendage as had their respective demonstrators. A partially successful attempt to replicate the Dawson and Foss "two-action method" (Galef, Manzig & Field, 1986) led, over subsequent decades, to a dramatic change in the procedures used to seek evidence of animal imitation. The two-action method became standard in experimental studies of imitation; naïve rats watched trained demonstrators push joy sticks to left or right (Heyes & Dawson, 1990; Heyes et al. 1992), observer pigeons and quail watched conspecifics either step on or peck at treadles (e.g. Zentall et al., 1996; Atkins et al. 2002), and apes and children watched others push or pull at artificial fruit, (for review, see Whiten & Custance, 1996), then tended to act as had their respective demonstrators. Other potential methods for studying imitation [e.g. examining social transmission of

novel sequences of behaviors (e.g. Whiten, 1998) or examining the ability of animals to learn to “do as I do” (e.g. Custance et al., 1995)], may well be at least as convincing as the two-action method in demonstrating an ability of animals to imitate. However, the two-action method captured the lion’s share of attention in providing convincing evidence that, contrary to the conclusion that Thorndike had reached, for a surprising number of avian and mammalian species, observing a demonstrator engage in a behavior already in the observer’s repertoire increases the probability that the observer will subsequently engage in that behaviour.

Although, as discussed further below, such findings do not directly address the question of whether animals can “from an act witnessed, *learn to perform* [italics added] that act” [perhaps the sight of another performing an act simply leads to facilitation of that response if it is already in an individual’s repertoire. (e.g. Byrne, 1994), data from studies using the two-action method are consistent with the hypothesis that for animals, as for humans, representations of acts can influence behavior, thus answering the broader question concerning animal cognition that had motivated Thorndike’s thesis research in the late 19th century.

Too little too late

If two-action experiments had been conducted in the 1960s, they might have made a substantial contribution to the emerging evidence indicating a role for representations in the behavior of animals. However, by the time two-action experiments became standard in laboratory studies of animal imitation, decades of research in other laboratory situations [e.g. navigation, counting, timing, classical conditioning, etc.(Shettleworth, 2010)] had shown that animals use representations to guide their behavior.

The two-action method may have had potential as a tool for exploring the nature of animal cognition and its relationship to human cognition, but such potential has rarely been exploited (Heyes, 2005; Zentall, 2012). Instead, the two-action procedure was used, all but exclusively, to extend the range of species known to imitate. Consequently, the two-action method has, at least to date, contributed relatively little to our understanding of animal cognition, the possible existence of which had motivated Thorndike to undertake studies of imitation in the first place.

New uses for studies of imitation

By the end of the 20th century, primatologists working in field situations had gathered extensive observations consistent with the view that groups of free-living primates could sustain behavioral traditions similar in function 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). Discovery of regional differences in the behavioral repertoires of members of a single species (e.g. ; van Schaik et al., 2003; Whiten et al.,1999), not readily explained by differences in either their environments or genetics, led to intense debate as to the uniqueness of human culture (Laland & Galef, 2009) and provided a new and compelling justification for studying imitation in animals.

Such interest is likely to increase. Recent technological developments (Krause et al., 2013) all but assure that studies of the spread of novel patterns of behavior (innovations) through free-living populations will both increase in number and raise compelling questions as to the behavioral processes that support the development of such traditions of innovative behavior (e.g. Reader & Laland, 2003).

Development of passive integrated transponders and radio-frequency identification now permit essentially continuous monitoring, in real time, of the distances between most or all pairs of animals in a free-living population allowing detailed descriptions of social network structures (e.g. Ruiz et al., 2012; Krause et al., 2013). A variety of relatively new modelling techniques can be used to determine the effect, if any, of such social-network structures on the diffusion of experimentally introduced behaviors through a population (e.g. Krause et al., 2013; Hoppitt & Laland, 2013). Whether imitation plays a role in such diffusion is likely to be as contentious in the future as it has been in the past, in part because determining whether animals can precisely copy the behavior of innovators is important in understanding the relationship between socially transmitted traditions in animals and human culture (Laland & Galef, 2010).

One generally agreed-upon, possibly unique feature of human culture is its cumulative nature. Human populations can iterate technological improvement across cultural generations (Boyd & Richerson, 1985). There is no generally accepted evidence that any animal, even our chimpanzee cousins can do so (Whiten, xxxx). Although the uniqueness of human cumulative culture is debated by some (e.g. Boesch, 2012), humans are surely far more adept than other animals at copying a behavioral innovation and then improve upon it. As many have argued (For review of the issue, Dean et al., 2012; Dean et al., 2014), imitation and teaching are possibly the sole means of information transmission that have the potential to produce copies of behavior of sufficient fidelity to support the iterative modification of innovations so characteristic of human culture in general and of human material culture in particular.

When information transmission between ‘cultural generations’ results from processes such as stimulus/local enhancement or emulation (Whiten & Ham, 1992;

Zentall, 1996), individuals have to learn for themselves how to successfully interact with those portions of the environment towards which the behaviour of others has directed their attention. If all that is socially transmitted is attention to a particular portion of the environment (local enhancement) or information indicating that some goal can be achieved (emulation), then socially induced cumulative improvement over more than two successive behavioral generations [the initiator (generation one) and those who directly copy the initiator (generation 2)] is not possible. Of course individuals can gradually improve their performance on some task as a result of differences in the rewards the environment provides for alternative variants of a behavior (e.g. Pike et al., 2010), but that is not at all the same thing as cumulative culture.

Consequently, although studies of imitation in animals may have contributed relatively little to progress in understanding animal cognition, such studies do have the potential to answer important questions concerning the ability of animals to precisely copy the acts of others and thus to produce traditions potentially homologous to those seen in human social groups (e.g. Galef, 1992; Tomasello, Kruger & Ratner, 1993). If animals should prove unable to produce precise behavioral copies of observed behavior or are markedly less capable of doing so than are humans, then the qualitative difference in the complexity of animal and human traditions would be at least partially explained and important questions raised as to the potential utility of studies of animal traditions in understanding the evolution of human culture

Changing definitions

Those interested in understanding the role of imitation in maintaining traditions observed in free-living animals have not by and large been satisfied with

Thorndike's definition of imitation. Such researchers have distinguished "contextual imitation" (learning by observation to perform a familiar act in an unfamiliar context) from "production "imitation" [learning by observation the form of a novel behavior (e.g. Janik, 1995; Janik & Slater, 1997)]. The dependent variables in two-action experiments are motor patterns already present in the behavioral repertoires of subjects before they enter the experimental situation.

There is reason to question the generalizability of results of such experiments involving imitation of familiar acts to the unusual patterns of behavior, the production imitation, that is of interest of those trying to understand the diffusion of behavioral innovations through animal populations that result in traditions (Byrne, 1995). Indeed, if laboratory studies of imitation are to make contact with current interest in animal traditions, experiments will have to require animals to engage in behaviors that they are unlikely to produce without social input. Consequently, further integration of laboratory research on imitation with the study of animal traditions will require a change in research paradigm.

Evidence that something other than the two-action method is needed

Chimpanzee termite fishing is one of the more closely studied of regional behavioral innovations that may well be learned socially by young chimps observing adept elders engage in the behavior. Success in termite fishing involves a series of acts: (1) identifying a potentially productive hole in a termite mound, (2) making a suitable tool or picking up one previously discarded by a practitioner, (3) inserting the tool into a suitable hole in a termite mound, and finally (4) extracting the tool from the hole in a manner that results in the capture of termites (Lonsdorf, 2005).

After spending many months observing chimpanzees fish for termites, Teleki (1974), an early student of chimpanzee termite fishing, tried to fish for termites. He reports (admittedly anecdotally) that even after months of careful observation of chimpanzees fishing for termites, when he first tried the technique, he was unable to either select suitable probes or to locate appropriate tunnel openings. He learned to do so only after considerable trial and error.

Even after he learned to both create appropriate probes and locate active tunnels in a termite mound, he “spent many hours inserting probes [into tunnels], pausing for the designated interval and pulling them out again—without getting any termites. Only after some weeks of near total failure...did I finally grasp the problems involved” (Teleki, 1974, p.588). And Teleki is not the only one to experience difficulty capturing termites using twigs as probes even after spending many hours observing proficient adult chimpanzees use the technique.

Lonsdorf’s (2005; 2006) 4-year field study of young chimpanzees acquiring termite fishing provides an unusually detailed description of the development of this regional pattern of behavior in young apes. Lonsdorf reports (2005, personal communication) that even after exhibiting all four behavioral elements necessary for success in catching termites, young chimpanzees typically take more than a year to become proficient at the task and during this period, gain no extrinsic rewards from their attempts.. Before mastery, young chimps engage in numerous inappropriate behaviors: e.g. swiping at the mound with a discarded tool, inserting a tool into a termite mound to insufficient depth or withdrawing it too rapidly to capture termites, etc.

Consequently, there is no evidence that chimpanzees learn directly to succeed in fishing for termites from seeing others do so. Young chimpanzees seem

to get some idea of the actions necessary to capture termites, but then need an extended period of trial-and-error learning to shape their behavior to match the representation they hold in memory. And termite fishing is not unusual among purported traditional behavioral innovations in requiring something more than observation of others performing a behavior acquire that behavior.

Monkeys at Koshima, once they reached the age at which Imo initiated sweet-potato washing (and are thus sufficiently mature to engage in the behavior) still took, on average, more than 2 years before they first washed potatoes (Galef, 1992). Even 10 year old chimpanzees do not exhibit adult levels of proficiency when termite fishing (Lonsdorf, 2006) or nut cracking, and like tufted capuchins in Brazil (Perry, 2009), take more than 2 years to learn to crack nuts.

In general, the acquisition of behaviors such as potato washing, termite fishing and nut cracking seem to involve much more than simply learning to do an act from seeing it done. At best, Thorndikian imitation provides an incomplete picture of the development of the behaviors in question.

Now what?

As the preceding examples of the time course of acquisition of purportedly traditional behavioral innovations suggest, although observation of a pattern of behavior may result in learning something about its form, a prolonged period of asocial, trial-and-error learning during which a neophyte can reap little or no extrinsic reward for its efforts is often prerequisite to acquisition. The two-action method fails to capture this possibly fundamental aspect of the diffusion through populations of innovative behaviors that vary regionally and are of great contemporary interest. Unfortunately, we have few experimental investigations in laboratory situations of the role of social learning in the development of such

behavioral innovations (Reader & Laland, 2003) that are the raw material of traditions. Whiten (1998) gave four chimpanzees the opportunity to observe a human demonstrator use one of two methods to remove each of two defences from an artificial fruit and one of two possible sequences of defence removal. Although on first and second exposures to the artificial fruit, subjects showed no tendency to accurately copy the type and sequence of acts they had observed, on the third trial all four copied (or nearly copied) the sequence of acts they had seen demonstrated. Such delay in onset of evidence of social learning is consistent with what is often observed in the acquisition of traditional behaviors by members of natural populations.

As Hoppitt and Laland (2008, p. 146) proposed in discussing Whiten's (1998) findings, "Perhaps the chimpanzees formed a template of the demonstrators behavior, then modified their behavior to match the template." The use of template matching as a metaphor for the development of expression of observed behaviors is, of course, not new. It dates to Marler's (1976) classic analysis of the development of local dialects in the songs of white-crowned sparrows. In template matching, observation provides the idea of a response, but a period of trial-and-error learning is required to bring expressed behavior into correspondence with the behavioral representation stored in the template.

For historical reasons discussed below, template matching, introduced as a way of understanding the development of regional dialects in bird song, has not been considered as a mechanism for social learning. Thorndike (1898, 1911) dismissed bird-song learning as irrelevant to understanding imitation more generally thus setting the tone for subsequent generations' treatment of the phenomenon. In Thorndike's (1911, p. 76) view, "If a bird out of a lot of random noises that it makes chooses those for repetition which are like the sounds it heard,

it is...a mystery why, though not how he does it.” Although it would be more than a half century before evidence of how song birds come to learn the song of their species, Thorndike’s intuitions proved generally correct. Whilst in the nest, male songbirds store a representation (a template) of adult song and a year later begin to produce relatively disorganized strings of species-specific notes and trills (subsong), only gradually matching their vocal output to the template they have stored in memory (Marler, 1976).

Because a young bird can directly compare its own vocal productions with the memory of the song of an adult, as Thorndike (1911) indicated, it is not difficult to imagine how a young bird might gradually bring its vocal output to match the auditory template that it acquired whilst in the nest. As W. H. Thorpe (1963, p.136) , an early student of bird song learning proposed, “[the] very complex and elaborate imitation of sounds by birds may, in fact, be explicable essential on the basis of trial and error learning” together with a tendency to “utter the same sounds that it hears” (McDougall, 1936, p. 175).

As Thorpe and McDougall hypotheses concerning the mechanism of bird-song learning require, if a juvenile male is to develop normal adult song, it must be able to hear its own vocalizations during the period when it is producing subsong, suggesting that development of adult song does, in fact, involve matching song output to a stored representation of adult song (Konishi, 1965). The evidence suggests that during song development, a bird compares auditory feedback from its subsong production with the song template generating an error signal that it gradually reduces by modifying its vocal output. The result is a mature song that closely resembles the song stored as a template (Doupe & Kuhl, 1999).

Recent work on the neuro-anatomy of subsong production provides further evidence consistent with the view that selection among subsong variants is crucial to development of adult song (Brainard & Doupe, 2002). Juvenile zebra finches (*Taeniopygia guttata*): (1) begin to match their subsong to that of an adult male tutor after only 75-sec cumulative exposure to that song and increase the closeness of that match over the next 48 h, and (2) that early, crude copying plays a role in development of adult song (Deshpand et al., 2014).

Similar data from a controlled environment describing the course of behavioral development cannot be provided using the two-action method in which performance of a demonstrated behavior (one already in the subject's repertoire) is essentially instantaneous, but are needed to understand the social transmission of the sorts of behavior comprising traditions in natural populations.

Bird-song learning is a highly specialized activity occurring only during a sensitive period, with its own neural substrate, etc. I am not, of course, proposing that neural structures homologous to the "song system" of passerines (Bolhuis & Gahr, 2006) are involved in mammalian imitation; not even non-song birds have such structures. Rather, I am suggesting that imitation learning like song learning involves a two-stage process in which: (1) a template (or representation) of an observed behavior is stored in memory, and (2) there is intrinsic motivation to engage in trial-and-error learning to produce behavior that matches the template. That human children exhibit such intrinsic motivation to match their behavior to a stored representation is strongly suggested by the discovery of "over-imitation" in children who will precisely copy even totally ineffectual observed actions (e.g. Whiten et al., 2009). Young chimpanzees do not show similar copying of unnecessary actions. Whether animals exhibit even weaker intrinsic motivation than children to precisely copy an observed behavior is an open question.

Learning to copy motor acts that others have been seen (rather than heard) performing provides an additional challenge. Imitation of non-vocal demonstrations would often require matching to a visual template a motor output that is under proprioceptive rather than visual control. Indeed, even when an observer successfully matches the behavior of its demonstrator, the visual signal from its own behavior will not match the visual signal its demonstrator provided (Heyes & Ray, 2000; Heyes & Kilner, 2011; Nehaniv & Dautenhahn, 2002). Further understanding of the functioning of mirror neurons that fire when an individual either performs an action or merely sees another individual perform that action (Fogassi et al., 2005) are currently the most promising avenue for understanding such cross-modal matching

The motivation to copy the song of others, like the motivation to copy other instances of action imitation remains obscure. Recent findings indicate that endogenous opioids are released when juvenile songbirds produce subsong (Riters, 2009; Dyan & Balleine, 2002) possibly maintaining subsong production in the absence of extrinsic reward. If the intensity of opioid release were to increase with increasing similarity of subsong to a stored song template, then shaping of subsong to resemble the template would follow. An extensive series of studies (Howe et al., 2013) demonstrating an increase in the release of dopamine in the striatum of rats as they approach a goal in a maze is consistent with the hypothesis that intrinsic rewards can shape animals behavior.

Of course, proper performance of non-vocal motor acts can often lead to an increase in extrinsic rewards. If a demonstrator's behavior is, as might be expected (Galef, 1995) an efficient means of garnering rewards, then feedback from the environment should shape a neophyte's early, crude copies of behavior to match more precisely that of its demonstrator. Apparent template matching would be

emulation (learning from a model that a goal is achievable) followed by trial-and-error learning to achieve the goal and homogeneity of behavior in a social group would reflect only regularities in the feedback from the asocial environment. The distinction is important because template formation together with intrinsic motivation can produce high fidelity copies that are necessary for cumulative culture, whereas emulation together with shaping by the external environment is not. Further, if diffusion of behavioral traditions through populations of animals reflects only emulation plus environmental shaping, whilst imitation in humans involves formation of behavioral templates together with an intrinsic motivation to produce a behavioral match for the template, then the study of such phenomena in animals becomes largely irrelevant to understanding the evolution of culture

Conclusion

Birds do not learn to sing their local dialects by imitation, at least not in Thorndike's sense of that word. I propose here, that chimpanzees similarly do not learn directly to fish for termites or crack nuts or Japanese macaques to wash the dirt from sweet potatoes by learning to do an act from seeing that act performed. Producing a match between one's own performance and the observed motor act of another requires a sophisticated interplay between social and asocial learning.

If such an analysis is correct, then it follows that controlled studies of potential behavioral mechanisms supporting many of the more interesting traditions observed in free-living animals, must go beyond the two-action method as currently employed. Understanding the imitation of non-vocal behavior will require paradigms in which subjects acquire novel behaviors or novel sequences of familiar behaviors and can be observed while they gradually match their behavior to that of a model. Such controlled studies of performance rather than of

contextual imitation (Byrne, 1995) will be similar to Lonsdorf's (2005, 2006) field study the development of termite fishing in young male and female chimpanzees.

The suggestion that many traditional behaviors of animals, like those of members of our own species (Galef, 2013) rest on a combination of template construction and learning by trial and error to match the behavior represented in the template leads naturally to the question of why “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 to understand how human culture evolved.” (Anonymous, 2005, p. 99).

On the view proposed here, the failure of animals to exhibit cumulative culture suggests that they are relatively deficient in: (1) the ability to construct or maintain templates of observed motor acts, (2) the ability to match proprioceptive output to a stored visual template, or (3) the motivation to precisely match motor output to a stored template (E.G. Gergely et al., 2002; Whiten et al., 2009). Developing experimental procedures to test such hypotheses is likely to prove challenging but important.

Regardless of whether the use of bird song as a model system, emulation together with trial-and-error learning or some other process proves important in diffusion of innovative behaviors through free-living populations, “a coherent field of social learning” (Zentall & Galef, 1988, p. ix) will require abandoning the laboratory study of contextual imitation using the two-action paradigm to determine whether an animal “from an act witnessed, could learn to perform that act” (Thorndike, 1911, p. 79).

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