RECOGNIZING A SWAN: SOCIALLY-BIASED LEARNING

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Socially-biased learning is widespread in the animal kingdom and important in behavioral biology and in evolution. However, common misconceptions about socially-biased learning stand in the way of its effective study by psychologists. Our aim in this paper is to recruit psychologists' interest in socially-biased learning by (1) defining this domain, and distinguishing it from imitation, (2) explaining the significance of socially-biased learning in behavioral evolution, (3) recommending comparative methods to analyze socially-biased learning in natural settings. Linked examination of the varying social contexts of practice and the forms and rate of change in individual practice can indicate the extent to which social context accounts for differences in learning. We close with a model of how social bias might modulate learning, and suggest ways of testing this model. ·

Key words: social learning, niche construction, associative learning, social relationships, traditions

In "The Ugly Duckling", a popular European children's fairy tale by Hans Christian Andersen, a swan gosling is reared by a mother duck along with her clutch of ducklings. Unbeknownst to all of them, the gosling is not an "ugly duckling", although all the ducks perceive him that way, and they make his life rather miserable on account of his unusual appearance and awkward manner. Eventually, he grows to adulthood, encounters other swans, and realizes that he never was a duck, but was always a swan. The swan accepts his new identity and (we are led to infer) lives happily ever after.

In some ways *socially-biased learning* (the term we suggest should replace *social learning,* the generic term customarily used for all learning aided by the activities of others — Box, 1984) suffers from being mis-identified as an "ugly duckling" among learning phenomena. First, it suffers from being considered less relevant to human behavior by many psychologists than imitation. Below, we criticize the notion that imitation is necessary for the maintenance of shared practice. Second, it suffers from the mistaken assumption that a distinction exists in process, outcome, or domain between "social" learning and other forms of learning. There is no way to distinguish "social" learning from "asocial" learning. Instead, we should focus on the biases produced in learning that result from individuals acting in specific social contexts.

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that social learning appears to be when it is mistakenly viewed as a lesser phenomenon than imitation, and as composed of an ill-defined group of "special" processes. After clarifying what we mean by this term, we explain the significance of socially-biased learning in behavioral evolution and suggest using a broader range of comparative methods to study it. Finally, we discuss how social factors bias learning, and provide examples of studies illustrating this process.

Defining the phenomenon

Socially-biased learning is a change in behavior contingent upon a change in cognitive state associated with experience (the definition of learning — Shettleworth, 1998) that is aided by exposure to the activities of social companions (Box, 1984). Socially-biased learning is distinguished by the context in which learning occurs, not by distinctive cognitive processes. Socially-biased learning occurs in a wide spectrum of animals, from primates to cephalopods. Acquired dietary preferences following exposure to eating-related cues provided by others (such as scent deposits at feeding sites, flavors in milk, odors in breath, ingestion of partially digested foods left by another, and even prenatal exposure to specific foods eaten by the mother) are paradigmatic examples of the phenomenon (Hudson, Schaal & Bilko, 1999; Galef, 1996). Examples in many other domains of behavior are readily available, including techniques of foraging, search sites, travel routes, vocal communication, and mate choice copying (see examples in Heyes & Galef, 1996; Box & Gibson, 1999). The conclusion that the social context affects learning is supported in some of these cases by experimental evidence comparing groups of individuals exposed to specific opportunities to learn (as in Hudson et al. & Galef's works, cited above). In many other cases the conclusion is based on observations of temporally persistent behavioral differences across groups, and/or on the basis of observed shifts in behavior of individuals to be more like those of others with which they associate.

Socially-biased learning as defined above is distinct from imitation (learning to do an act from seeing it done — Thorndike 1911; or response learning by observation — Heyes & Ray, 2000) in that imitation is conceived to require a process whereby observed action is translated into produced action (Heyes & Ray, 2000). Reproducing an act from seeing it done requires close coupling of attention to the other's act and to the movements of one's own body. Humans can translate a limited set of observed actions into produced actions from birth (Meltzoff & Moore, 1977). This indicates that imitation in humans is not dependent on a complex history of individual experience, but rather it is a species-normal activity in humans. As humans mature, imitation contributes in myriad ways to social interactions and to the development of skills (Meltzoff, 1990, 1996; Metlzoff & Gopnik, 1993). Some writers suggest that imitation represents a critical cognitive achievement of humans to which we can attribute culture, technology, and many other distinctly human characteristics. They seek evidence for continuity in imitative capacities among humans and great apes in particular (e.g. Byrne & Russon, 1998; Boesch & Tomasello, 1998; van Schaik, Deaner, & Merrill, 1999; Whiten, Goodall, McGrew,

Nishida, Reynolds, Sugiyama, Tutin, Wrangham, & Boesch, 1999). One difficulty with this approach is that the best examples of imitation in nonhuman animals do not come from primates, but from other orders (birds and cetaceans — Moore, 1996; Akins & Zentall, cited in Heyes & Ray, 2000; Janik & Slater, 2000; Rendall & Whitehead, in press). This suggests that imitative capacities might have evolved several times. Janik and Slater (2000) suggest that imitative capacity (as seen in vocal production learning, such as producing the calls of others) might be linked to a suite of social conditions that occur in several families of long-lived, intensely social taxa, and that the primary use of this ability might be to coordinate activities and maintain cohesion with group members. Meltzoff and Gopnik (1993) similarly suggest that early imitative activity in humans has social-cognitive functions (for example, identifying others as social companions).

Understanding how attention to observed action is coupled with produced action (as occurs during imitation) is an important goal for cognitive scientists and neuroscientists (e.g., Rizzolatti, Fadiga, Gallese, & Fogassi, 1996; Heyes & Ray, 2000; Byrne, 1999; Myowa-Yamakoshi & Matsuzawa, 1999). Understanding the developmental trajectories, functional outcomes, and evolutionary pathways leading to imitation are also of value, particularly because imitation is a rare phenomenon. However, we can dismiss the notion that imitation is the *sine qua non* for traditions (shared behavioral patterns maintained in part by socially-supported learning). A complete understanding of imitation will not lead to understanding how socially-maintained knowledge and practice arise in humans or any other taxon (Heyes, 1993, Heyes & Ray, 2000; Ingold, 1998). "Copying" behavior of others (as in imitation) is not a sufficient basis to produce skill; rather, skill requires repeated individual practice (Bernstein, 1996). Traditional practices are generated by each individual; they can not be handed down as "units" from one individual to another, any more than the corporal bodies that perform them can be handed down (Ingold, 1998). Understanding how traditional knowledge and practice can be maintained requires a dynamic conception of the individual as engaged with its world, both social and asocial elements, in ongoing commerce. Our task as psychologists is to understand the processes by which individuals generate activity, and how social context impacts those processes. In short, to understand the genesis of culture we should strive to understand the nature of social bias in learning (broadly construed to include skill development).

What does socially-biased learning contribute to behavioral biology and to evolution?

The idea that socially-biased learning impacts fitness has been with us a long time. So has the idea that individual variations in learning propensities are subject to natural selection, and as an inevitable consequence different species will possess characteristic patterns of learning in accord with each species' history of natural selection. These ideas can be found worded in similar ways in any contemporary textbook on learning (e.g., Domjan, 1998; Shettleworth, 1998). In the usual scenario, learning affects the behavior, and therefore the fitness, of the individual

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learner. In addition, however, an individual's behavior can be an informational resource to others about significant aspects of the environment. Ecologists recognize that one individual's activity can inform others' use of resources or assessment of risks. Giraldeau (Giraldeau, 1997; Giraldeau & Caraco, 2000) coined the label "information ecology" to identify this phenomenon and to urge its empirical study and mathematical modeling of its fitness consequences.

Laland, Odling-Smee, and Feldman (2000) suggest an additional impact of one individual's behavior on others, beyond the immediate informational resource value of an individual's behavior to its near neighbors. They note that many species modify their environments through their behavior, a process they label "niche construction" (similar to what Jones, Lawton, & Shachak, 1997 refer to as "ecosystem engineering"). For example, many mammalian species (e.g., rats, badgers and opossums, among others) construct multi-tunnel burrows. A complex of behaviors in these animals concerns defense and maintenance of these burrows, and regulation of the environment inside the burrow system. These behaviors reflect response to selection pressures that arose in conjunction with the construction of burrows (Nowak, 1991). The elaborated burrow-construction and burrow-defense behaviors among these animals reflect a "legacy of natural selection pressures that have been modified by ancestral niche construction" that constitutes an "ecological inheritance" (Laland et al., 2000, p. 133).

Niche construction can apply to other aspects of the environment beyond "hard construction" of shelters such as hives, nests, dams, or burrows that are used by multiple generations. For example, animals that alter the environment in ways that increase the abundance of their own foods have contributed to construction of a niche. The aye-ayes (*Daubentonia madagascariensis*), a nocturnal prosimian from Madagascar, alter their habitat in this sense (Erickson, 1995). Aye-ayes create sizeable cavities in dead logs by gnawing into the wood while searching for and extracting woodboring larvae, which they eat. The cavities thus created are later inhabited by the larvae of other insects and sometimes even larger creatures, such as frogs, that the aye-ayes also eat or are suspected to eat (Pollock, Constable, Mittermeier, Ratsirarson, & Simons, 1985). Through their excavation activities, aye-ayes alter their habitat in ways that promote the abundance of their own food sources. Each generation of aye-ayes can benefit from the excavation activities of the previous generations.

One consequence of niche construction is that the organism is conceptualized not merely as the target of natural selection. It also modifies, through its behavior, the environment for subsequent generations, so that behavior is conceptualized as contributing to the process of selection. As Laland et al. (2000) put it, the evolutionary significance of niche construction rests on the feedback that it generates. "In the presence of niche construction, adaptation ceases to be a one-way process, exclusively a response to environmentally imposed problems: Instead, it becomes a two-way process, with populations of organisms setting as well as solving problems." (p. 135).

Socially-biased learning is likely to support niche construction and enhance its

feedback potential in natural selection. When the constructed niche includes behavioral traditions, the behavior of individuals is affected across generations as well as, or rather than, the physical environment. For example, where acquisition of foraging skills is supported by social context, group-specific specializations in resource use are likely to appear, as in toothed whales (Boran & Heimlich, 1999), rats (Terkel, 1996), orangutans (van Schaik, Fox, & Sitompul, 1996) and perhaps (a provocative but unproven case) vampire finches (Schluter & Grant, 1984; Grant, 1986). Where socially-biased learning enables individuals to locate distant or rarely-used food or water resources effectively, animals can make use of seasonally available resources (e.g., brown bears; Gilbert, 1999). Where socially-biased learning permits individuals to learn production details about vocal signals, they can acquire group-specific "dialects" that support group cohesion, as in humpback whales (Payne & Payne, 1985) and horseshoe bats (Jones & Ransome, 1993). Social bias has the potential to impact the generation of behavior in every individual. According to the niche-construction model, those species with strong susceptibility to social biases in learning are likely to have socially-maintained practices that impact fitness positively, so that the socially-maintained practices are part of the "constructed niche". Keep in mind, however, that along with beneficial practices, we cannot rule out that some socially-maintained practices may be selectively neutral or even costly (Laland & Williams, 1998). Just as the selective impact of any particular trait must be examined, rather than considering all traits "adaptive" (Gould & Lewontin, 1979), the selective impact of each socially-maintained behavior must be examined on its own merits.

How can we evaluate the contribution of social bias to learning?: Experimental designs and comparative designs

Social aids to learning are rarely necessary for individuals to acquire a specific behavior pattern. There are redundant paths to virtually any behavioral outcome. Therefore, the scientific task in the study of socially-biased learning is to understand what contribution social context can provide to learning. In studies of social contributions to learning, most often a comparison of two groups suggests a difference in the MAGNITUDE of learning, rather than the presence vs. the absence of the learned behavior (as would be necessary to make a claim of causal necessity). For example, Terkel (1996) reports that about 60% of naive black rats encountering partially stripped pine cones on their own become proficient at stripping the seeds from complete pine cones. When naive black rat pups encounter the same cones in the presence of their mother, and the mother is proficient at stripping cones, virtually 100% of the rats become proficient at stripping cones. In this case, social bias in learning is evident in the probability of learning in the two groups. The pups that encounter cones with the mother were more likely to acquire skill at stripping the cones of their seeds than the rats that worked by themselves on partially opened cones. We can conclude that being with the mother as she processes the cones supports the pups' learning better than individual activities without the mother. We can not

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conclude, however, that the benefit to learning provided by supportive social context is sufficient to maintain a practice in a population. That requires studying the learning process in several individuals over a period of time (i.e., repeated generation of the same behavior in different individuals).

Here we come to an important point. We have used only a few experimental paradigms to show that social bias impacts learning. Most studies, like those of Terkel cited above, have concerned a single learning "event", where subjects in one group interact with or observe a "demonstrator" encountering some challenge (such as finding food) or making a choice (such as choosing food or a mate). Subsequently the subjects encounter the challenge or choice on their own. Subjects in a comparison group experience the same challenge or choice in a different social context (e.g., without a skilled demonstrator, or with a demonstrator using a different solution to the same problem). Laland (1999; see also Galef & Allen, 1995) argues for the value of studying multiple learning events, where the continuance of a socially learnt behavior is charted across "transmission chains". This design allows one to consider the time course of social influence, as well as its magnitude at any particular point. Studies with this paradigm constitute empirical demonstrations of traditions. Laland (1999) has also suggested the value of looking at the various proposed sources of social bias as additive elements. For example, rats acquire a preference for foods eaten by others most effectively if they are exposed to the others' breath after eating, AND are able to search for food in a site where they encounter the scent marks of others (Laland & Plotkin, 1993). Both elements are normally present for foraging rats sharing a communal den site.

Experimental designs that make use of multiple "transmission" events and that consider the additive effects of different aspects of social influence open up how we think about learning in social settings. Our view of socially-biased learning shifts from a single-event horizon to a process with a temporal dimension and with a collection of interacting elements. The broader experimental space of the latter view can be used to analyze socially-biased learning in situations that bear closer resemblance to conditions in the natural world than the traditional single-event design.

In addition to a broader experimental approach, we need more directed use of comparative methods to study socially-biased learning in natural settings. Phenomena in the natural world rarely lend themselves to the precise and powerful method of experimental analysis. In the case of learning, the experimental method makes use of manipulated independent variables, specific comparison groups, and before-and-after evaluations of the behavior of individuals. These elements are rarely, if ever, available from observations in natural settings. For example, observers of animals in natural settings cannot determine with certainty that the changes they observe across time in an individual's proficiency or form at some particular task reflect learning. Changes in behavior over time may also reflect some concurrently varying feature of the situation (such as seasonal changes in the availability of resources; physical changes in the individual; and so on). Moreover,

unlike in experimental studies, the observer of animals in natural circumstances usually does not know any individual's level of experience or degree of skill with a task prior to the start of observations. Thus linking behavioral changes with learning, and even more so socially-biased learning, requires more than observation of behavioral changes over time in some members of a group of individuals.

Does this mean that behavioral biologists should not attempt to study socially-biased learning in natural settings? Not at all! But we must be clear about the kinds of information we can gain from such studies, and the best ways to collect it. Field observers can provide three important kinds of information that cannot be collected readily in captive situations. First, they can document the social contexts in which the relevant behaviors typically occur when individuals are free to regulate their associations with others in species-normal ways (as Inoue- Nakamura & Matsuzawa, 1997, have done for chimpanzees cracking nuts). Second, they can document intragroup variation in behavior at a particular time and changes over time in individual performance, to identify shifts in practice towards homogeneity (as the Paynes have done for the songs of humpback whales — Payne & Payne, 1985). Third, they can seek comparable evidence about specific behavioral patterns in other groups of the same species or of related species (as Huffman, 1996, has done for Japanese macaques, with reference to stone-handling). With these data, we could determine (a) how rapidly new practitioners develop the behavior with differing forms of social support, (b) how close the behavioral resemblance remains across practitioners and through time, and (c) how different the patterns are in different social units. This last task is easier if the behavior is present in some groups and not others. All the tasks (a — c) are easier if a behavioral innovation is observed at the outset, and its spread followed within a group. All are still possible, however, even if the behavior is always present in all the groups observed.

Associative processes supporting socially-biased learning: Emotional contagion and conditioned modulation

Associative learning allows an individual to detect and use distinctively causal relationships (*sensu* Hume) between events occurring in its environment (Dickinson, 1980; Rescorla, 1988; Shettleworth, 1998). Many aspects of context are known to affect Pavlovian conditioning (i.e., what the individual detects as "causally related", in the terms of associative learning theory). For example, the "belongingness" of stimuli affects how easily associations are learned: pigeons more readily associate visual cues with food and auditory cues with danger (Lolordo, Jacobs, & Foree, 1982). The individual's history of exposure to particular features of the environment may impact how attention is directed during learning, so that the individual is more likely to attend to some cues than to others. The nature of the behavior system activated by the unconditioned stimulus affects how the individual responds to the conditioned stimulus. This principle accounts, for example, for the difference in behavior by several different species of rodents to a moving ball that signaled the arrival of food (Timberlake & Washburne, 1989). According to Shettleworth (1998), the animal's

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Pavlovian expectation of a specific outcome can facilitate a whole behavioral system in the operant setting, where the subject encounters an opportunity to produce an outcome by its actions. The instrumental contingency (between action and outcome) can strengthen any activity within it. In other words, the Pavlovian expectation of a specific outcome promotes a suite of activities that do in fact increase the probability of that outcome. In a practical sense, the animal is prepared to learn that some actions in this suite are linked more closely with the anticipated outcome than are others.

Returning to socially-biased learning, we suggest two different ways in which "social" elements in the learning context could support associative learning, so that learning occurs more effectively in social situations than when the individual encounters the same events and opportunities for action on its own. The first concerns the special contribution of social companions to the learner's affective or emotional state as it encounters events. Social partners provide, on a constant basis, salient information about their own affective status. Expressed affect serves as an unconditioned stimulus to others who are present, as captured in the phrase "emotional contagion" coined by Hatfield, Cacioppo, and Rapson (1994) with reference to humans. Emotional contagion is a family of psychophysiological, behavioral, and social phenomena that result in a pervasive tendency in one person to mimic and synchronize expressions, vocalizations, postures, and movements with another person, rapidly, automatically, unintentionally, and out of awareness (Hatfield et al., 1994). Emotional contagion can produce alterations in the function of the autonomic nervous system, as measured in heart rate, skin conductance, and so forth. Here, then, is a psychological "primitive", a foundational feature of social responsiveness that can bias learning. In the language of associative learning, the properties of the social companion that elicit contagion serve as unconditioned stimuli and elicit unconditioned responses. Functionally, emotional contagion leads to a convergence of affective state among the interactants.

Emotional contagion can bias learning because the unconditioned response to the social partner's expressed affect can be associated with the immediately antecedent or concurrent events or stimuli: The learner "catches" the other's affect *and* the "target" of that affect, when a salient environmental correlate is evident. Thus, to the extent that an observer experiences emotional contagion, it can form Pavlovian associations between its own new affective state and salient contextual variables. It can learn a "value" of an object or event from the other, and this learning persists after the "contagion" episode ends. Mineka & Cook's (1988) work with rhesus monkeys (*Macaca mulatta*) serves as an example of emotional contagion contributing to effective socially-biased learning: Monkeys acquired a strong and long-lasting fearful response to a previously neutral stimulus (an image of a snake) from a single, very brief (15 seconds or less) exposure to another monkey behaving fearfully in the presence of this stimulus. Translating the procedure into the Pavlovian paradigm, we have:
The Demonstrator's expressed affective state (fear) = Unconditioned stimulus
The Observer's state during exposure to the demonstrator = Unconditioned response

= Fear

The Observed/experienced contingent stimulus or event = Picture of a snake = Conditioned stimulus

The Observer's state following exposure to the conditioned stimulus alone = Conditioned response = Fear

Emotional contagion can contribute to socially-biased learning of action, in line with its ability to engage a whole behavioral system of flight, defensive attack, feeding, etc. (see Suboski, 1990, for a similar model). Curio's (1988) classic studies of "mobbing" in birds illustrate the phenomenon. Curio showed that blackbirds that observed a conspecific attack ("mob") an innocuous novel bird behaved similarly when they later encountered the same object. Blackbirds that had not viewed an attack ignored the same object. According to the contagion model, the original attacker's behavior invoked a matching affective state in the observer. The unconditioned (affective) response to the conspecific's behavior activated a suite of behaviors directed at the environmental feature linked associatively by the learner to its own affect. It seems likely that many cases in the literature described as "imitation" can be accounted for in this way, without a need to invoke copying of a specific action or sequence of actions from seeing the actions performed (the signature requirement of imitation). To evaluate this idea we need first to confirm that observation of expressed affect (as in signalling) or affect-related behavior (as exemplified in attack) in another individual produces an unconditioned affective response in the observer. We know that this is the case in humans (Hatfield et al., 1994), but we have only a few examples of confirmation in other species, most clearly in chimpanzees, whose expressions of affect are rather similar to our own (Parr & Hopkins, in press; Parr, in press). For any species in which affective UCR's are confirmed, we can determine if blocking or enhancing the affective unconditioned response in the observer reduces or increases, respectively, socially-biased learning. Behavioral pharmacological studies could contribute here.

The second way in which social context can bias learning is through conditioned modulatory influences derived from individual histories of social interaction. [Domjan, Cusato, & Villarreal (2000) pursue a similar line of reasoning with regard to how individuals regulate social behavior.] We illustrate the idea here with one well-documented modulatory influence, "occasion-setting" (reviewed in Holland, 1992). Occasion-setting occurs when one conditioned stimulus modifies the efficacy of associations between other cues and the unconditioned stimulus. This modulatory function has been shown by Peter Holland and colleagues to be distinct from the familiar elicitation functions of conditioned stimuli. A paradigmatic example of occasion-setting is provided by an experiment conducted by Ross and Holland (1981). The experiment involved training food-deprived rats in an appetitive situation. Rats that heard a tone and then received food consistently spontaneously tossed their heads (called a "head jerk") during the interval between the tone cue and delivery of the food. Rats that saw a light and then received food consistently spontaneously reared on their hind legs during the interval between light cue and food delivery. When the

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rats experienced both cues in sequence (e.g., saw a light come on briefly, a few seconds later heard a tone, and then a few seconds later received food), they consistently reared on their hind legs after the light came on, and jerked their heads after the tone came on. In the occasion-setting situation, after the CR to the tone alone was extinguished (i.e., head jerk did not occur), the rats again experienced the compound presentation of light-pause-tone-pause-food delivery. In this circumstance, the rats jerked their heads when the tone came on in the compound stimulus condition, but when the tone came on without the light preceding it, they did not jerk their heads. In Holland's terminology, the first CS, the feature cue (light, in this example) "sets the occasion" for the conditioned response to the second CS, the target cue (tone) in the compound CS. Occasion-setting is a robust phenomenon, appearing over a broad range of timing intervals between feature and target cues, so long as (a) the feature cue (that sets the occasion) occurs before the target cue (that immediately precedes the US) and (b) the feature cue is a better predictor of the US than is the target cue. In general, contemporary learning scientists recognize that conditioned emotional responses can modulate ongoing operant responding, or the acquisition and performance of other Pavlovian responses; occasion-setting is but one example of this family of phenomena (Shettleworth, 1998). This source of social support for learning seems particularly likely for individuals that maintain social relationships based on individual recognition. Recognized individuals, and their familiar behaviors, are rich sources of predictive information about environmental conditions and events.

Finding a likely example of occasion-setting where the social partner's behavior is a better predictor of an important outcome than any particular other cue (supporting the social partner serving as an occasion setter) is easy. To illustrate, we consider research findings with three different groups of animals (black rats, scrub jays, and Mongolian gerbils). For the first example, we return to the finding that a young black rat with its mother while she processes whole pine cones is able to obtain and eat some pine seeds; a young black rat by itself with the same whole cones does not learn to strip the seeds from the cones (Terkel, 1996). Let us interpret the learning context encountered by the rat pup in Terkel's studies in the language of occasion setting. For the young black rat, the seeds are the US; foraging activity directed at the seeds is the UR. The mother, when she is acting on the pine cone, is the probable occasion setter; the pine cone is the probable target cue, preceding appearance of the seeds when the mother is present but not when the cone is encountered otherwise. The pup's conditioned response (CR) is foraging activity, directed in this case at the target cue (the cone). This CR occurs most reliably while the mother is foraging on cones herself (even when no seeds are immediately present). In functional terms, the mother's presence and actions support the young rat's conditioned responsiveness to pine cones beyond that supported by the presence of the cones or the seeds alone. By promoting the pup's foraging-related behaviors directed at the cones at just those times that the mother is providing partially opened cones for the pup to work on, this process eventually enables the pup to learn to strip seeds from

the cones itself.

Interpreting the black rat's learning process has been a thought exercise, but the propositions are testable. For example, if the foraging mother serves as an occasion-setter in this situation, as we have proposed, then we should find stronger responsiveness to the cones while she is manipulating cones than when she is merely present, or in her absence. Differential responsiveness should be evident during the period that pups are eager to eat the seeds but before they become proficient at stripping seeds themselves.

The second example, a recent study by Midford, Hailman, & Woolfenden (2000), illustrates another way that associations influenced by social context can be layered to support particular learning. These authors report that under certain conditions, some juvenile wild Florida scrub jays (*Aphelocoma coerulescens*) learned to forage in a specific place (in the center of a plastic ring) for buried food (bits of peanuts). They were able to acquire this skill when they encountered the rings with other family members that foraged successfully in these places, and the juveniles were able to eat some of what the adults obtained. Under these conditions, virtually all of the juveniles entered the rings, and about 20% of them dug in the center of the ring (the baited area). Only about 20% of the juveniles that encountered the rings in family groups without "demonstrators" entered the ring, and they did not dig in the ring. The presence of older individuals foraging in the rings most strongly affected the probability that juveniles would enter the rings. However, even when accompanying skilled adult foragers, if juvenile birds were prevented from scrounging bits of food from others foraging in the prepared sites, they did not learn to search there themselves. Adult scrub jays feed their nestlings until the nestlings are about 85 days old (McGowen & Woolfenden, 1990). The juveniles studied by Midford et al. first succeeded at digging up peanuts at about the same age.

Consider this sequence of experiences in terms of the possibilities for associative learning by the young birds in the group in which scrounging was permitted. (1) Young birds saw the adults that routinely fed them and that they routinely followed enter the rings and (perhaps) the adults vocalized or otherwise indicated behaviorally the positive value of the place. (2) The adults permitted juveniles to take food from the site that adults had uncovered. The first condition supports the young bird's attraction to the rings, via observational conditioning. The second condition supports the young bird associating the rings (and more specifically, the center of the rings) as places where food is to be found, thus engaging the behavioral system associated with foraging. As the young birds began to obtain their own food routinely, they began to search more vigorously (i.e., dig) in these attractive places, leading (occasionally) to the young bird succeeding at obtaining food itself. Young birds that observed adults foraging in the ring but that had no opportunity to obtain food were still likely to enter the ring. However, they were far less likely to engage in foraging activity once in the ring than were the birds that were allowed to scrounge. Evidently observing others foraging was not sufficient for the young bird to associate the ring with food.

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The third example illustrates how socially-biased associative learning can be manipulated in an experimental setting. The study concerns the effects of an anxiolytic drug, chlordiazepoxide, on acceptance of a novel food in Mongolian gerbils, *Meriones unguiculatus* (Choleris, Valsecchi, Wang, Ferrari, Kavaliers, & Mainardi, 1998). Choleris et al. (1998) report that a gerbil will accept a novel food quickly if it observes a familiar conspecific eating the food. It will not accept the novel food if it observers a stranger with the food, rather than a familiar animal, even though it sniffs the strange "demonstrator's" mouth as often as it does the familiar "demonstrator's" mouth. Administration of the anxiolytic drug obliterated the differences in learning associated with the two different kinds of demonstrators; drug-treated animals accepted the food as readily after sniffing a stranger as after sniffing a familiar animal. Administration of the drug did not affect consumption of familiar foods (both treated and untreated animals ate familiar foods) nor acceptance of the novel food in singly-tested animals (neither treated nor untreated animals ate novel food). Thus, the drug only affected acceptance of the food when the conspecific was unfamiliar, and it enhanced the effectiveness of the unfamiliar animal as a cue of acceptability. The authors note that benzodiazepine drugs (of which chlordiazepoxide is a variety) usually impair learning in a variety of learning tasks employing aversive motivation (i.e., escape tasks). The situation presented by Choleris et al. (1998) assessed an appetitive behavior (feeding), and performance was assessed sooner after exposure to the learning situation (same day, vs. next day) than in the previous studies using aversive motivation. Thus there are many points about the findings that require further work to sort out the mechanisms of action of the drug. The interest of this study for the present discussion is that the familiarity of the partner impacts the salience for the learner of the information that it provides about food. This phenomenon might be interpreted along the lines of a differing unconditioned affective response by the observer to the familiar vs. the unfamiliar animal. An unconditioned positive affective response to the familiar demonstrator could result in conditioned affective response to the odors associated with that individual, evident as acceptance of the novel food. The unconditioned affective response to the stranger demonstrator might not support associating the odor of the food with a conditioned appetitive state. The effect of the drug is to provide the same positive or supportive affective reaction to the stranger as to the familiar animal, so that the odor of the food is associated with a pleasant or an appetitive state in both cases. Additional pharmacological interventions might show that a drug which blocks positive or appetitive affect would block the effectiveness of the familiar partner to impact the observer's acceptance of a novel food. In this case we would predict that neither kind of demonstrator would result in the observer accepting novel foods.

The associative model of socially-biased learning that we are promoting predicts variation across individuals and across species in accord with how strongly social relationships modulate the affect-regulating properties of certain individuals for others. For example, in many mammalian species, the mother's behavior is a particularly potent regulator of her dependent offspring's internal state (Hofer, 1987).

The model predicts that differences in affect-regulating properties impact the likelihood of forming associations between the individual's internal state and external events, and so impacts the likelihood of socially-biased learning. According to this model, the prevalence of "vertical" socially-biased learning, where young animals generate behaviors like those of their older kin (most often the parents), can reflect an asymmetry in the modulatory effectiveness of young animal's social companions. (It may also reflect a difference in the number of opportunities to learn while near specific others — young animals often spend most of their time near the mother.) In general, we predict that (a) species exhibiting emotional contagion (defined as unconditioned affective responsiveness to the presence or behavior of a conspecific) will exhibit socially-biased learning; (b) within these species, those individuals eliciting the strongest emotional contagion will support the most effective socially-biased learning; and (c) under appropriate conditions, conspecifics' presence and activities can modulate the effectiveness of other associative cues, either enhancing or suppressing an individual's conditioned responsiveness to environmental events and objects. Understanding how social relationships and social dynamics impact socially-biased learning will surely be a growing point in this area of research (Coussi-Korbel & Fragaszy, 1995).

Convergent models

We are not the first to link conditioning mechanisms with socially-biased learning. We have already mentioned Suboski's (1990) model of releaser-induced recognition learning (see also Suboski, Muir, & Hall, 1993). Suboski's model is particularly appropriate for circumstances in which the target of consummatory behavior is learned. Owren and Rendall (1997) provide an elegantly developed model of the ontogeny of signalling behavior in nonhuman primates that relies upon a similar reading to ours of the relation between individual A's ability to affect individual B through signalling, and the production of a conditioned emotional response in individual B. A major difference between our model and Owren and Rendall's (1997) model is that the signaller in their model is producing "private" information, directed at a particular individual. They are particularly concerned with the problem of how a young animal learns to direct specific kinds of calls to specific others. We are considering the more general case, wherein neither party produces a communicative "signal" (e.g., a vocalization), and no directional specificity is necessary.

Summary

Socially-biased learning is hardly an "ugly duckling" in the family of learning phenomena. Rather, it is a widespread and biologically important variation of a powerful system of learning (that is, associative learning). Socially-biased learning can contribute to the repeated generation of adaptive behaviors across generations by promoting convergent systems of behavior (such as foraging or defense), and convergent valuation of objects, events, and activities. In this sense, socially-biased

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learning participates in the construction of niches, and in continuing behavioral evolution. For psychologists and biologists alike, socially-biased learning is a "swan"; an elegant, effective member of the learning family. Here elegance derives from the simplicity of the mechanisms involved. Gigerenzer, Todd, and the ABC Research Group (1999) provide many examples of elegant (simple) cognitive processes in humans that support sophisticated decision-making and behavior. Nonhuman animals share many of these processes with humans, and social biases in learning are among them.

Socially-biased learning has been assessed experimentally for many years. However, we must strive to broaden the array of experimental designs we use to assess this form of learning. Current designs most often restrict analysis to singular learning events. We need additional designs that address how social influences can be layered with each other and with other normally varying contextual features, and how socially-biased learning can contribute to the maintenance of behavioral traditions. We also need to analyze patterns of variation across groups in natural settings to determine the probability and importance of social bias in their generation, and to identify probable aspects of social relationships and behavior that are responsible for the social bias observed. This aspect of socially-biased learning has been particularly neglected by psychologists.

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We have proposed that social partners can impact associative learning in at least three ways. First, one individual can acquire conditioned affective responsiveness to features in the environment that are linked temporally with a partner's display of affect. This kind of conditioning is apparently widespread in the animal kingdom, and it is a versatile mechanism promoting adaptive behavior (for example, recognition of hazards, and conversely, recognition of desirable resources). A second way that social partners can impact learning is through modulatory influences on the formation of associations, as when the partner or its activities acquire occasion-setting properties. Finally, partners can influence learning indirectly when they promote activation of a behavioral system so that the learner generates appropriate behaviors to learn relevant relations between its own actions and outcomes. In this way learners generate behaviors that match, functionally and sometimes topologically, the behaviors of their more proficient partners. We have given a few examples that support our model, and look forward to prospective analyses that will test these ideas.

REFERENCES

Bernstein, N. 1996. *On dexterity and its development.* Mahwah: Erlbaum.

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Boesch, C., & Tomasello, M. 1998. Chimpanzee and human cultures. *Current Anthropology, 39,* 591–614.
Boran, J. R., & Heimlich, S. L. 1999. Social learning in cetaceans: Hunting, hearing, and hierarchies. In H. Box & K. Gibson (Eds.), *Mammalian social learning* (pp. 282–307). Cambridge: Cambridge University Press.
Box, H. O. 1984. *Primate Behaviour and Social Ecology.* London: Chapman and Hall.
Box, H. O., & Gibson, K. 1999. *Mammalian social learning.* Cambridge: Cambridge University Press.
Byrne, R. W. 1999. Imitation without intentionality. Using string parsing theory to copy the

organization of behaviour. *Animal Cognition, 2,* 63–72.

Byrne, R. W., & Russon, A. 1998. Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences,* **21,** 667–721.

Choleris, E., Valsecchi, P., Wang, Y., Ferrari, P., Kavaliers, M., & Mainardi, M. 1998. Social learning of a food preference in male and female Mongolian gerbils is facilitated by the anxiolytic, chlordiazepoxide. *Pharmacology, Biochemistry and Behavior, 60,* 575–584.

Coussi-Korbel, S., & Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour, 50,* 1441–1453.

Curio, E. 1988. Cultural transmission of enemy recognition in birds. In T. Zentall & B. G. Galef, Jr. (Eds.), *Social learning: Biological and psychological perspectives* (pp. 75–97). Hillsdale, New Jersey: Erlbaum.

Dickinson, A. 1980. *Contemporary animal learning theory.* Cambridge: Cambridge University Press.

Domjan, M. 1998. *The principles of learning and behavior* (4th. ed.). New York: Brooks-Cole.

Domjan, M., Cusato, B., & Villarreal, R. 2000. Pavlovian feed-forward mechanisms in the control of social behavior. *Behavioral and Brain Sciences* **23,** 235–282.

Erickson, C. 1995. Feeding sites for extractive foraging by the aye-aye, *Daubentonia madagascariensis. American Journal of Primatology, 35,* 235–240.

Galef, B. G. Jr. 1996. Social enhancement of food preferences in Norway rats: A brief review. In *Animal Social Learning: The Roots of Culture* (pp. 49–64). New York: Academic Press.

Galef, B. G. Jr., & Allen, C. 1995. A model system for studying animal traditions. *Animal Behaviour, 50,* 705–717.

Gigerenzer, G., Todd, P., & the ABC Research Group. 1999. *Simple heuristics that make us smart.* Oxford: Oxford University Press.

Gilbert, B. 1999. Opportunities for social learning in bears. In H. Box & K. Gibson (Eds.), *Mammalian social learning* (pp. 225–235). Cambridge: Cambridge University Press.

Giraldeau, L-A. 1997. The ecology of information use. In N. Davies & J. Krebs (Eds.), *Handbook of behavioral ecology* (pp. 42–68). Oxford: Blackwell Scientific.

Giraldeau, L. A., & Caraco, T. 2000. *Social Foraging Theory.* Princeton, New Jersey: Princeton University Press.

Gould, S. J., & Lewontin, R. 1979. The spandrels of San Marcos and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London, 205,* 581–598.

Grant, P. 1986. *Ecology and Evolution of Darwin's Finches.* Princeton, New Jersey: Princeton University Press.

Hatfield, E., Cacioppo, J., & Rapson, R. 1994. *Emotional contagion.* New York: Cambridge University Press.

Heyes, C. 1993. Imitation, culture, and cognition. *Animal Behaviour, 46,* 999–1010.

Heyes, C., & Galef, B. G. Jr. 1996. *Animal social learning. The roots of culture.* New York: Academic Press.

Heyes, C., & Ray, E. 2000. What is the significance of imitation in animals? *Advances in the Study of Behavior* **29,** 215–245.

Hofer, M. 1987. Early social relationships: A psychobiologist's view. *Child Development, 58,* 633–647.

Holland, P. C. 1992. Occasion setting in Pavlovian conditioning. *The Psychology of Learning and Motivation,* **28,** 69–125. New York: Academic Press.

Hudson, R., Schaal, B., & Bilko, A. 1999. Transmission of olfactory information from mother to young in the European rabbit. In H. Box & K. Gibson (Eds.), *Mammalian social learning* (pp. 141–157). Cambridge: Cambridge University Press.

Huffman, M. 1996. Acquisition of innovative cultural behaviors in nonhuman primates: A case study of stone handling, a socially transmitted behavior in Japanese macaques. In C. Heyes & B. G. Galef, Jr. (Eds.), *Animal social learning. The roots of culture* (pp. 267–289). New York: Academic Press.

Ingold, T. 1998. Chimpanzee and human cultures: Comment. *Current Anthropology, 39,* 606–607.

Inoue-Nakamura, N., & Matsuzawa, T. 1997. Development of stone tool-use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology,* **111,** 159–173.

Janik, V., & Slater, P. 2000. The different roles of social learning in vocal communication. *Animal Behaviour,* **60,** 1–11.

Jones, G., & Ransome, R. D. 1993. Echolocation calls of bats are influenced by maternal effects and change over a lifetime. *Proceedings of the Royal Society of London, B,* **252,** 125–128.

Jones, C., Lawton, J. ecosystem enginee

Laland, K. 1999. Exp *Mammalian Social*

Laland, K., Odling-S cultural change.

Laland, K., & Plotkin *Animal Learning an*

Laland, K., & Willia *Behavioral Ecology,*

Lolordo, V., Jacobs, *Learning and Behav*

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Meltzoff, A. 1990. F other and the valu & M. Beeghly (E Chicago Press.

Meltzoff, A. 1996. Tl with implications *learning. The root*

Meltzoff, A., & Gopni of mind. In S. *Perspectives from at*

Meltzoff, A., & Moor 198, 75–78.

Midford, P., Hailmar of free-living Flo:

Mineka, S., & Cook Zentall & B. G Hillsdale, New J

Moore, B. R. 1996. *learning in animals*

Myowa-Yamakoshi, I chimpanzees (*Pa*:

Nowak, R. M. 1991.

Owren, M. J., & Rer In D. Owings, N 299–346). New

Parr, L. in press. (*troglodytes*). *Anin*

Parr, L., & Hopkii chimpanzees, *Pa*

Payne, K., & Payne Bermuda. *Zeitsi*

Pollock, J., Constabl feeding behaviol 435–447.

Rendall, K., & Whit

Rescorla, R. 1988. 151–160.

Rizzolatti, G., Fadig; actions. *Cogniti*

Ross, R. T., & H discriminations.

Jones, C., Lawton, J., & Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**, 1946–1957.

Laland, K. 1999. Exploring the dynamics of social transmission with rats. In H. Box & K. Gibson (Eds.), *Mammalian Social Learning* (pp. 174–187). Cambridge: Cambridge University Press.

Laland, K., Odling-Smee, F., & Feldman, M. 2000. Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences*, **23**, 131–146.

Laland, K., & Plotkin, M. 1993. Social transmission in Norway rats via excretory marking of food sites. *Animal Learning and Behavior*, **21**, 35–41.

Laland, K., & Williams, K. 1998. Social transmission of maladaptive information in the guppy. *Behavioral Ecology*, **9**, 493–499.

Lolordo, V., Jacobs, W., & Foree, D. 1982. Failure to block control by a relevant stimulus. *Animal Learning and Behavior*, **10**, 183–193.

McGowen, K., & Woolfenden, G. 1990. Contributions to fledgling feeding in the Florida scrub-jay. *Journal of Animal Ecology*, **59**, 691–707.

Meltzoff, A. 1990. Foundations for developing a concept of self: The role of imitation in relating self to other and the value of social mirroring, social modeling, and self practice in infancy. In D. Cicchetti & M. Beeghly (Eds.), *The self in transition: Infancy to childhood* (pp. 139–164). Chicago: University of Chicago Press.

Meltzoff, A. 1996. The human infant as imitative generalist: A 20-year progress report on infant imitation with implications for comparative psychology. In C. Heyes & B. G. Galef, Jr. (Eds.), *Animal social learning. The roots of culture* (pp. 347–370). New York: Academic Press.

Meltzoff, A., & Gopnik, A. 1993. The role of imitation in understanding persons and developing a theory of mind. In S. Baron-Cohen, H. Tager-Flusberg, & D. Cohen (Eds.), *Understanding other minds: Perspectives from autism* (pp. 335–366). New York: Oxford University Press.

Meltzoff, A., & Moore, M. 1977. Imitation of facial and manual gestures by human neonates. *Science*, **198**, 75–78.

Midford, P., Hailman, J., & Woolfenden, G. 2000. Social learning of a novel foraging patch in families of free-living Florida scrub jays. *Animal Behaviour*, **59**, 1199–1207.

Mineka, S., & Cook, M. 1988. Social learning and the acquisition of snake fear in monkeys. In T. Zentall & B. G. Galef, (Eds.), *Social learning: Biological and psychological perspectives* (pp. 51–74). Hillsdale, New Jersey: Lawrence Erlbaum.

Moore, B. R. 1996. The evolution of imitative learning. In C. Heyes & B. G. Galef, Jr. (Eds.), *Social learning in animals. The roots of culture* (pp. 245–265). New York: Academic Press.

Myowa-Yamakoshi, M., & Matsuzawa, T. 1999. Factors influencing imitation of manipulatory actions in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **113**, 128–136.

Nowak, R. M. 1991. *Walker's mammals of the world* (5th. ed.). Baltimore: Johns Hopkins University Press.

Owren, M. J., & Rendall, D. 1997. An affect-conditioning model of nonhuman primate vocal signalling. In D. Owings, M. Beecher, & N. Thompson (Eds.), *Perspectives in ethology: Vol. 12. Communication* (pp. 299–346). New York: Plenum Press.

Parr, L. in press. Cognitive and physiological markers of emotional awareness in chimpanzees (*Pan troglodytes*). *Animal Cognition*.

Parr, L., & Hopkins, W. in press. Brain temperature asymmetries and emotional perception in chimpanzees, *Pan troglodytes*. *Physiology and Behavior*.

Payne, K., & Payne, R. 1985. Large-scale changes over 19 years in songs of humpback whales in Bermuda. *Zeitschrift für Tierpsychologie*, **68**, 89–114.

Pollock, J., Constable, I., Mittermeier, R., Ratsirarson, J., & Simons, H. 1985. A note of the diet and feeding behavior of the aye-aye *Daubentonia madagascariensis*. *International Journal of Primatology*, **6**, 435–447.

Rendall, K., & Whitehead, H. in press. Culture in whales and dolphins. *Behavioral and Brain Sciences*, **24**.

Rescorla, R. 1988. Pavlovian conditioning: It's not what you think it is. *American Psychologist*, **43**, 151–160.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. 1996. Premotor cortex and the recognition of motor actions. *Cognitive Brain Research*, **3**, 131–146.

Ross, R. T., & Holland, P. C. 1981. Conditioning of simultaneous and serial feature-positive discriminations. *Animal Learning and Behavior*, **9**, 293–303.

Schluter, D., & Grant, P. 1984. The distribution of *Geospiza difficilis* in relation to *G. fuliginosa* in the Galapagos islands: Tests of three hypotheses. *Evolution,* **36,** 1213–1226.

Shettleworth, S. 1998. *Cognition, behavior, and evolution.* New York: Oxford University Press.

Suboski, M. D. 1990. Releaser-induced recognition learning. *Psychological Review,* **97,** 271–284.

Suboski, M.D., Muir, D., & Hall, D. 1993. Social learning in invertebrates. *Science,* **259,** 1628–1629.

Terkel, J. 1996. Cultural transmission of feeding behavior in the black rat (*Rattus rattus*). In C. Heyes & B. G. Galef, (Eds.), *Social learning in animals. The roots of culture* (pp. 17–47). New York: Academic Press.

Thorndike, E. L. 1911. *Animal intelligence: Experimental studies.* New York: MacMillan.

Timberlake, W., & Washburne, D. L. 1989. Feeding ecology and laboratory predatory behaviour toward live and artificial prey in seven rodent species. *Animal Learning and Behaviour,* **17,** 2–11.

van Schaik, C., Deaner, R., & Merrill, M. 1999. The conditions for tool use in primates: Implications for the evolution of material culture. *Journal of Human Evolution,* **36,** 719–741.

van Schaik, C. Fox, E., & Sitompul, A. 1996. Manufacture and use of tools in wild Sumatran orang-utans. *Naturwissenschaften,* **83,** 186–188.

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E., Wrangham, R., & Boesch, C. 1999. Cultures in chimpanzees. *Nature,* **399,** 682–685.