

What's Social About Social Learning?

Cecilia Heyes
University of Oxford

Research on social learning in animals has revealed a rich variety of cases where animals—from caddis fly larvae to chimpanzees—acquire biologically important information by observing the actions of others. A great deal is known about the adaptive functions of social learning, but very little about the cognitive mechanisms that make it possible. Even in the case of imitation, a type of social learning studied in both comparative psychology and cognitive science, there has been minimal contact between the two disciplines. Social learning has been isolated from cognitive science by two longstanding assumptions: that it depends on a set of special-purpose modules—cognitive adaptations for social living; and that these learning mechanisms are largely distinct from the processes mediating human social cognition. Recent research challenges these assumptions by showing that social learning covaries with asocial learning; occurs in solitary animals; and exhibits the same features in diverse species, including humans. Drawing on this evidence, I argue that social and asocial learning depend on the same basic learning mechanisms; these are adapted for the detection of predictive relationships in all natural domains; and they are associative mechanisms—processes that encode information for long-term storage by forging excitatory and inhibitory links between event representations. Thus, human and nonhuman social learning are continuous, and social learning is adaptively specialized—it becomes distinctively “social”—only when input mechanisms (perceptual, attentional, and motivational processes) are phylogenetically or ontogenetically tuned to other agents.

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Social learning in animals has been studied for more than a century, primarily by researchers interested in the evolution and adaptive functions of behavior. They have discovered a magnificent range of cases in which animals acquire biologically important information, not through teaching or explicit communication, but just from observing the actions of others.¹ Social learning has been found in animals as diverse as insects, birds, fish, rodents, cetaceans, and primates. It provides information about where to live, what and where to eat, how to obtain inaccessible food, who is a predator, who would make a good mate, and how to behave in a particular social group (for reviews see Galef, 1976; Galef, 1988; Heyes & Galef, 1996; Galef & Heyes, 2004; Hoppitt & Laland, 2008).

Research on social learning has been largely untouched by cognitive science. A great deal is known about the adaptive functions of social learning, including its role in the social or cultural transmission of behavior, but very little is known about the cognitive mechanisms that make social learning possible. Taxonomies

of social learning typically distinguish types according to what is learned by observation. For example, in stimulus enhancement, the observer learns “to what (object or location) to orient behavior,” and in imitation, the observer learns “some part of the form of a behavior” (Whiten & Ham, 1992). These taxonomies delineate social learning effects, not social learning mechanisms. They focus on what are thought to be the cognitive results of social learning, but say nothing about the cognitive (or neurological) processes producing those results. In this sense, taxonomies of social learning are “behaviorist”; they are silent about what goes on between the learner’s ears.

Social learning has been isolated from cognitive science, not just by the usual barriers to cross-disciplinary integration, but by the long-standing and largely implicit assumption that it depends on social—cognitive adaptations—learning mechanisms distinct from

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Correspondence concerning this article should be addressed to Cecilia Heyes, All Souls College, Oxford, OX1 4AL, United Kingdom. E-mail: cecilia.heyes@all-souls.ox.ac.uk

¹ *Social learning* refers to learning about other agents or the inanimate world that is influenced by observation of, or interaction with, another individual or its products (e.g., Heyes, 1994; Hoppitt & Laland, 2008). These products can include deposits, such as scent marks, and the effects of actions on objects and environments. Social learning is commonly contrasted with *asocial learning*, *individual learning*, *trial-and-error learning*, and *innovation*; that is, with learning about other agents or the inanimate world that is not influenced by observation of, or interaction with, another individual or its products. It is also common, as I do here, to distinguish social learning from *teaching*, *signaling*, and *communication*. In these cases, but not in social learning, the behavior of the observed individual, the *demonstrator*, is adapted or intended to communicate information to the observer. Thus, neither social learning nor asocial learning includes cases in which learning is mediated by language or other forms of symbolic communication.

those mediating asocial learning (see Footnote 1) that have evolved many times in different taxonomic groups as adaptive specializations for group living (Klopfer, 1959, 1961; Templeton, Kamil, & Balda, 1999; Wilkinson, Kuenstner, Mueller, & Huber, 2010). This assumption has discouraged investigation of the similarities between social and asocial learning, and fostered the view that adult humans—the principal targets of cognitive science—generally do not learn from others in the same way as nonhuman animals. Humans are thought to learn from others predominantly via teaching and imitation. Teaching is distinct from social learning (see Footnote 1), and it is often claimed that imitation occurs only in our close primate relatives.

Recent evidence challenges the assumptions that social and asocial learning, and human and nonhuman social learning, depend on different learning mechanisms. It shows that social learning ability and asocial learning ability covary, across and within species; that social learning occurs even in solitary animals; and that social learning has the same key features in diverse species, including humans. Drawing on this evidence, I argue here that social and asocial learning depend on the same basic cognitive mechanisms; these mechanisms are adapted for the detection of predictive relationships in all natural domains; they are associative mechanisms—processes that encode information for long-term storage by forging excitatory and inhibitory links between event representations; and they mediate human as well as nonhuman social learning.

If social learning depends on the same mechanisms of associative learning as asocial learning, then what is special about social learning? What, at the cognitive level, is “social” about social learning, and how does this social characteristic evolve or become adaptively specialized? In the final part of this article, I suggest that social learning is distinctive when input mechanisms—perceptual, attentional, and motivational processes—are biased or tuned to a particular channel of social information, and review some recent evidence that this kind of tuning can be achieved phylogenetically or ontogenetically, by evolution or via developmental processes.

Social and Asocial Learning Covary

If there were distinct social and asocial learning mechanisms that evolve independently, one would expect social and asocial learning abilities to be unrelated. For example, species that are good at social learning should be no more likely than poor social learners to be good at asocial learning. In contrast with this prediction, a number of studies of birds and primates have found that social learning ability and asocial learning ability covary across species (e.g., Lefebvre & Giraldeau, 1996; Reader & Laland, 2002; Reader, Hager, & Laland, 2011). In the latest study of this kind, Reader et al. (2011) estimated the social and asocial learning (or *behavioral innovation*) abilities of 62 primate species via a comprehensive survey of all papers published between 1925 and 2000 in leading primate behavior journals (*Primates*, *American Journal of Primatology*, *Folia Primatologica*, and the *International Journal of Primatology*). They found a strong positive correlation between social and asocial learning ability, even after controlling for body mass, brain volume, phylogeny, research effort, and other potential confounds.

Evidence is beginning to emerge that social and asocial learning abilities also covary across individuals within species. Studying male zebra finches, which learn their song by listening to other males, Boogert, Giraldeau, and Lefebvre (2008) found that song complexity (social learning) was associated with rate of learning in an extractive foraging task (asocial learning). Individuals with more phrase elements in their song required a smaller number of trials to learn to flip a lid off a food well than individuals with fewer song phrase elements. Similarly, Bouchard, Goodyer, and Lefebvre (2007) found a strong, positive correlation between the rate at which pigeons learned by conspecific observation to use their beaks to remove a stopper from a test tube (social learning), and the speed at which they learned via their own efforts to access a seed box (asocial learning). This relationship remained when the analysis took account of variance due to sex, dominance rank, and individual differences in neophobia.

Interspecific covariation is inconsistent with the assumption that social and asocial learning are mediated by cognitively distinct learning mechanisms that evolve independently. However, it is compatible with two alternative hypotheses: that social and asocial learning depend on different cognitive mechanisms that evolve together, or that they depend on the same cognitive mechanisms. Intraspecific covariation favors the second of these hypotheses. It suggests that the very same mechanisms encode information that is gained via the observation of other animals’ behavior (social learning), and information that is gained exclusively through the learner’s own interactions with the world (asocial learning).

Social Learning in Solitary Animals

If social learning depended on cognitive adaptations—on learning mechanisms that are cognitively distinct from those mediating asocial learning, and that evolve independently in response to selection pressure from the social environment—one would not expect social learning to occur in solitary species. When there is minimal contact between individuals within a species, there is very little opportunity for social learning to yield the fitness advantages that would promote the evolution of dedicated social learning mechanisms. However, there is evidence that at least two solitary species—the common octopus and the red-footed tortoise—are capable of social learning. When presented with two objects of different colors, octopuses are more likely to attack the object they have seen attacked by a conspecific (Fiorito & Scotto, 1992). Wilkinson et al. (2010) gave red-footed tortoises a detour problem in which they had to walk around one of two fences to get to a food reward. Four of the tortoises were given the opportunity to solve this problem by themselves, and none of them succeeded. In contrast, four tortoises who first observed a trained tortoise solving the problem, not only made the detour, but also tended to take the same right turn as the demonstrator.

It would be helpful to know more, not only about the small amount of social contact that occurs among free-living members of these species, but also about the social experience of the particular animals used in these experiments (Fiorito & Scotto, 1992; Wilkinson et al., 2010). However, given our current knowledge of octopus and tortoise social ecology, these studies indicate that social learning ability is not confined to taxa in which it would yield substantial fitness advantages.

Social and Asocial Learning Come in the Same Varieties

Imagine you are a U.S. citizen visiting the U.K. and wondering if when the locals say *aubergine* they are referring to the vegetable you know as *eggplant*. If you knew that eggplants normally come in three varieties (e.g., globular purple, long white, and small green), and then discovered that aubergines come in the same three varieties, it would increase your confidence that aubergine and eggplant refer to the same vegetable. Similarly, an analysis showing that social and asocial learning each come in the same three basic varieties (Heyes, 1994)—that types of social learning map onto types of asocial learning—provides evidence that they depend on the same mechanisms of learning.

Animal learning theory, which is concerned primarily with asocial learning, distinguishes three basic types of learning according to the kind of experience that provokes a change in behavior: exposure to a single stimulus (S learning, e.g., habituation and sensitization), to a relationship between two stimuli (S-S learning, or Pavlovian conditioning), or to a relationship between a stimulus and a response (S/R; instrumental learning or habit formation; Rescorla, 1988).

Stimulus enhancement, a traditional category of social learning (Spence, 1937; Thorpe, 1956), corresponds to single stimulus learning. Observation of another animal exposes the observer to a single stimulus, rather than a relationship between two events, and this socially mediated stimulus exposure results in a change in the observer's subsequent behavior—typically an increase in the frequency or intensity of the observer's interaction with the exposed stimulus. For example, after observing a conspecific manipulating one object in a cluttered array, monkeys are more likely to contact the manipulated object than the other objects in the array (Warden & Jackson, 1935).

Observational conditioning, the second traditional category of social learning (Cook, Mineka, Wolkenstein, & Laitsch, 1985), corresponds to S-S learning. Observation of another animal's behavior facilitates exposure to a relationship between two stimuli, and exposure to this relationship results in a change in the observer's subsequent behavior. For example, when monkeys see a snake (first stimulus) paired with another monkey behaving fearfully (second stimulus), they subsequently avoid snakes (Cook et al., 1985). In this example, the relationship between the two stimuli is positive—the occurrence of one predicts the occurrence of the other—and the second stimulus, fearful behavior, is aversive. However, like asocial S-S learning, observational conditioning can also occur when the relationship is negative—the first stimulus predicts that the second will not occur—and when the second stimulus is attractive. For example, in an environment where food is hidden beneath one of two objects, monkeys who have seen a conspecific searching under one object and failing to find food there tend to search under the alternative object (Darby & Riopelle, 1959).

The third major category of social learning, observational learning, corresponds to S/R learning (Galef, 1988; Heyes, 1994). Observation of another animal's behavior facilitates exposure to a relationship between a stimulus and a response, and exposure to this relationship results in a change in the observer's subsequent behavior. As in asocial learning, the relationship may be between an action and its outcome (R-S), or between a stimulus and a

response that occurs selectively in the presence of that stimulus (S-R). Socially mediated exposure to an R-S or S-R relationship sometimes results in the observer exhibiting behavior that is topographically similar to the behavior of the demonstrator; the parts of the observer's body move in the same way, relative to one another, as the parts of the demonstrator's body. In these cases, observational learning is also known as "imitation" (Galef, 1988; McGregor, Saggerson, Pearce, & Heyes, 2006). For example, as a visitor in your house, I might see you using your foot to close a particular cabinet door, and then begin to use my foot to close that door. This would be R-S observational learning, or *goal-directed imitation*, if what I had learned from observing your behavior was a relationship between a response (foot movement) and its outcome (door closing). It would be S-R observational learning, or *blind imitation*, if what I had learned was a relationship between a stimulus (a distinctive feature of the door) and a response (foot movement). Examples of R-S and S-R observational learning in animals are discussed below.

Thus, as one would expect if social and asocial learning depend on the same learning mechanisms, the three principal types of social learning occur under the same observable conditions as the three principal types of asocial learning (Heyes, 1994): through exposure to a single stimulus (stimulus enhancement), a relationship between two stimuli (observational conditioning), and a relationship between a stimulus and a response, (observational learning/imitation).

Each Type of Social Learning Is Found in Diverse Species

Recent research has shown that each of the three principal types of social learning occurs in diverse species, including humans. These types of social learning are distinguished according to the conditions in which they occur (Heyes, 1994). Therefore, in so far as common conditions of learning indicate common mechanisms of learning, the occurrence of each type of social learning in diverse species implies that the mechanisms of social learning are taxonomically general.

Stimulus enhancement has been found in a wide range of taxa (see Hoppitt & Laland, 2008, for review) including greylag geese and humans. Goslings that have observed a human hand opening a box explore more at the location where the hand contacted the box than control goslings who have not seen box opening (Fritz, Bisenberger, & Kotrschal, 2000). Similarly, computational modeling has shown that humans often influence one another's attitudes via *interdependent sampling* (Denrell & Le Mens, 2007; Denrell, 2008). For example, if I have a positive view of a particular restaurant, my friend is likely to develop a preference for that restaurant, not because I tell him it is good, or look satisfied when we are both there, but simply because my friend is more likely to sample the restaurant—to go there and discover the restaurant's merits for himself.

In the case of *observational conditioning*, there is even more striking evidence of taxonomic generality. For example, recent studies show that observational conditioning occurs in humans and in damselfly larvae. The human studies indicate that participants can learn an aversion to a stimulus such as a blue square not only as a result of experiencing electric shocks in the presence of the blue square (asocial learning/Pavlovian conditioning), but also by

observing a demonstrator wince, as if in pain, in the presence of the blue square (social learning/observational conditioning; Olsson & Phelps, 2007). Similarly, damselfly larvae learn to avoid pike, one of their predators, through exposure to pike stimuli (chemical cues in water) in conjunction with injured damselflies (Wisenden, Chivers & Smith, 1997).

No one is surprised by evidence of *imitation* in adult humans. Indeed, many researchers continue to believe that imitation is found only in humans (Thorndike, 1911), or that the imitative behavior of apes is qualitatively different, and significantly more complex, than the imitative behavior of other nonhuman animals. However, recent research in cognitive science and comparative psychology challenges this view in two ways: it provides evidence of simple imitation in adult humans, and of complex imitation in animals that are distantly related to humans.

Simple Imitation in Humans

In studies of *automatic imitation*, human participants are required to perform body movements in response to arbitrary stimuli, but the arbitrary stimuli are accompanied by photographic images of the body movements in the response set (e.g., Stuermer, Aschersleben, & Prinz, 2000; see Heyes, 2011, for a review). For example, in an experiment where participants were instructed to open their mouths whenever they saw a blue square and to open their hands whenever they saw a red square, presentation of each color was accompanied in some trials by an image of mouth opening and in other trials by an image of hand opening (Leighton & Heyes, 2010). The action images were not relevant to the task, and participants were told to ignore them. However, when the action image matched the incorrect response (e.g., a hand-opening stimulus was presented with a blue square requiring a mouth-opening response), responding was slower and less accurate than when the action image matched the correct response (e.g., a mouth-opening stimulus was presented with a blue square requiring a mouth-opening response). Automatic imitation effects of this kind have been found in more than 70 experiments, involving a range of action pairs (Heyes, in press). They indicate that adult humans engage in blind S-R imitation. We tend to imitate observed body movements even when this interferes with performance of an ongoing task.

Research on *unconscious mimicry* in naturalistic social situations suggests that blind S-R imitation is pervasive in everyday human life, and that it plays an important role in promoting cooperation among social partners (see Chartrand & van Baaren, 2009, for a review). These studies show that, when in conversation, people are constantly imitating one another's incidental body movements, such as foot bobbing and face touching, and that this occurs without the awareness of either party. Furthermore, participants who have been imitated in this way report greater enjoyment of the interaction (Chartrand & Bargh, 1999; Tanner, Ferraro, Chartrand, Bettman, & van Baaren, 2008), are more willing to help the partner, and donate more money to charity (van Baaren, Holland, Kawakami, & van Knippenberg, 2004) than participants who have not been imitated.

Studies demonstrating automatic imitation in birds and dogs, using experimental procedures analogous to those employed with human participants, underline the taxonomic generality of this kind of simple imitation (Mui, Hazelgrove, Pearce, & Heyes, 2008;

Range, Huber, & Heyes, 2011). For example, budgerigars that are rewarded for counterimitation—pecking whenever they see a conspecific stepping, and for stepping whenever they see a conspecific pecking—show a persistent, inefficient tendency to imitate—to peck when they see pecking, and to step when they see stepping.

Automatic imitation is simple in two respects: the observer does not intend to imitate, and the imitated action is familiar; that is, it consists of a short sequence of movements that was part of the observer's behavioral repertoire before imitation was recorded. Other recent studies of human imitation indicate that these factors can be dissociated; humans can imitate novel action sequences without intending to imitate and without being aware of what they have learned (Bird & Heyes, 2005; Bird, Osman, Saggerson, & Heyes, 2005). In these experiments, participants observed a demonstrator repeatedly performing a novel sequence of finger movements on a computer keyboard, and were subsequently cued by asterisk stimuli to perform a topographically similar or dissimilar sequence of finger movements. The participants' responses were faster when the cued sequence was topographically similar to that of the demonstrator (i.e., when their behavior was imitative), indicating that they had learned the novel sequence of finger movements by observation. However, the participants were not instructed to learn the sequence before observation, and, when the sequence was long, a range of postexperimental tests provided no evidence that they were consciously aware of what they had learned (Bird & Heyes, 2005; Bird et al., 2005).

Complex Imitation in Nonhumans

While research in cognitive science has been showing that human imitation can be surprisingly simple or “mindless”, research in comparative psychology has been suggesting that the imitative behavior of nonhuman animals can be surprisingly complex and deliberate.

For example, a recent study of marmosets suggests that they are capable of imitating actions with remarkably high fidelity (Voechl & Huber, 2007). The marmosets first learned to remove the lid from a film canister by observing a demonstrator perform this action (observers), or exclusively through their own efforts (non-observers). The lid removal behavior of both groups was then subjected to frame-by-frame motion analysis. This analysis indicated that the fractional head and mouth movement trajectories of the demonstrator were more like those of the observer than of the nonobserver marmosets.

Other studies suggest that birds are capable of goal-directed or R-S imitation—of imitating an action in order to obtain a desired outcome (Akins & Zentall, 1998; Dorrance & Zentall, 2001). Some of the strongest evidence of this kind was obtained using a devaluation procedure (Saggerson, George, & Honey, 2005, Experiment 3). In the first phase of this experiment, observer pigeons saw demonstrator pigeons pecking for food illuminated by one color and stepping for food illuminated by a different color; for example, pecking for red food and stepping for green food. In the second phase, they received experience designed to devalue one of the colors; for example, the observers were given free food to eat in the presence of the red light but were repeatedly presented with the green light in the absence of food. In the final phase of the experiment, the observers were given access to the response plate and, although neither color was present and neither pecking nor

stepping was rewarded, they performed the action for which the demonstrator had received the devalued outcome less frequently than the alternative action. This suggests that the observer pigeons wanted the color that had not been devalued, and chose to imitate the action used by the demonstrator to obtain this still valuable food.

In this section I have reviewed evidence that each type of social learning—stimulus enhancement, observational conditioning, and observational learning/imitation—occurs in diverse species, including humans. I have dwelt at some length on the third type of social learning, imitation, because it is in this case that recent evidence is most at odds with received wisdom. It has long been assumed that imitation is a complex, human- or ape-specific form of social learning (e.g., Thorndike, 1911), mediated by distinctive cognitive mechanisms. Challenging this view, recent research shows that both simple and complex imitation occur in both human and nonhuman animals. This evidence leaves open the possibility that human imitation is quantitatively different from imitation in nonhuman animals; for example, humans may be able to imitate longer action sequences or a wider range of action types than other animals. However, this evidence is not compatible with the view that the competence to imitate is mediated by qualitatively different cognitive mechanisms in human and nonhuman animals.

Footprints of Associative Learning

The previous sections reviewed research showing that social and asocial learning abilities covary, even solitary animals are capable of social learning, each type of social learning corresponds with a type of asocial learning, and each type of social learning occurs in taxonomically diverse species. These studies provide convergent evidence that social and asocial learning are mediated by the same learning mechanisms. But what is the nature of these mechanisms—how do they encode information? This section focuses on evidence that the mechanisms mediating both social and asocial learning are associative mechanisms—cognitive processes that encode information for long-term storage by forging excitatory and inhibitory links between event (stimulus and response) representations. Associative learning mechanisms are taxon- and domain-general. They have been found in a wide range of vertebrate and invertebrate species and in tasks relating to, for example, habitat selection, feeding, foraging, predator avoidance, and affiliative and sexual behavior (Pearce, 2008). These characteristics suggest that the mechanisms of associative learning are phylogenetically ancient adaptations for the detection of predictive relationships between events (Dickinson, 1980).

The three types of learning discussed above—S, S-S and S/R—were defined by research on associative processes (Rescorla, 1988). Therefore, the fact that social learning phenomena fall into the same three categories is itself an indicator that they are mediated by associative learning (Heyes, 1994). Further evidence comes from research examining examples of social learning for specific footprints, or characteristic features, of associative learning. Some of the earliest work of this kind focused on the social acquisition of snake fear by monkeys, and led to widespread use of the term *observational conditioning* (e.g., Cook et al., 1985; see also Olsson & Phelps, 2007). More recently, footprints of associative learning have been found in studies of the social enhance-

ment of food preferences in rats and in research on body movement imitation in humans.

Social Enhancement of Food Preferences

When rats encounter the odor of a distinctive diet on the breath of a conspecific they develop a preference for that diet (e.g., Galef & Stein, 1985). This effect is one of the most robust and carefully analyzed examples of social learning in the canon. To find out whether it is due to associative learning—to the formation of an excitatory link between internal representations of the food odor (conditioned stimulus, CS) and the attractive properties of rat breath (unconditioned stimulus, US)—Galef and Durlach (1993) tested for two footprints of associative learning: overshadowing and blocking.

Overshadowing refers to the finding that when one stimulus (CS1) is presented in compound with another stimulus (CS2) and followed by a US, CS1 acquires a weaker association with the US than when it is paired with the US in isolation. To test for overshadowing, Galef and Durlach compared, for example, the cinnamon diet consumption of rats that had interacted with demonstrators fed cinnamon only (CS1; control group) or cinnamon plus marjoram (CS1 and CS2; overshadowing group). *Blocking* refers to the finding that the interfering effect of CS2 on the conditioning of CS1 is greater when the animal has been preexposed to CS2 with the US (Kamin, 1969). To test for blocking, some rats were preexposed to a marjoram-fed demonstrator the day before they encountered both cinnamon and marjoram demonstrators and were given the cinnamon consumption test. In their original study, Galef and Durlach did not find overshadowing or blocking. However, confirming their suggestion that these negative results were due to insufficient stimulus preexposure, a subsequent study using Galef and Durlach's experimental design found evidence of both overshadowing and blocking when observers were preexposed on five occasions, rather than one occasion, to the interfering diet (e.g., marjoram) (Ray, 1997).

Human Body Movement Imitation

Another footprint of associative learning, a contingency effect, has been identified in research on body movement imitation in adult humans. A contingency effect occurs when the extent of learning about a relationship between two stimuli, or between a stimulus and a response, varies with the extent to which one of the events predicts the other; that is, the probability of the second event when the first event has occurred minus the probability of the second event when the first event has not occurred. For example, in an experiment where rats experienced a fixed number of pairings between a tone and a shock, the extent to which the animals learned to fear the tone declined with the number of additional unpaired presentations of the shock (Rescorla, 1968).

Cook, Press, Dickinson, and Heyes (2010) found a contingency effect in an experiment testing the associative sequence learning model of imitation (ASL; Heyes, 2001; Heyes & Ray, 2000; Ray & Heyes, 2011). This theory suggests that the capacity to imitate novel and familiar actions—to match the topography of observed body movements—depends on S/R associative learning. For example, it suggests that we are able to imitate a movement such as hand opening (splaying the fingers away from the palm) because,

in the course of normal development, as we watch our own hands in motion we associate a visual representation of hand opening (S) with a motor representation of hand opening (R). Human hands are alike, and therefore this S-R or visuomotor association, although learned via self-observation, is also activated by the sight of another person opening their hand.

A number of experiments have supported the ASL theory by showing that imitation can be “unlearned” through incompatible sensorimotor experience (Heyes, Bird, Johnson, & Haggard, 2005; Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Catmur, Walsh, & Heyes, 2007; Catmur, Mars, Rushworth, & Heyes, in press). For example, blind or automatic imitation of hand opening and closing is abolished by experience in which the sight of hand opening is paired with the performance of hand closing, and vice versa (Heyes et al., 2005). However, to check whether this unlearning—and, by implication, the original learning—is really due to associative processes, Cook et al. (2010) varied the contingency between the incompatible stimuli and the responses. All participants received an equal number of pairings of an opening-hand stimulus with a closing-hand response, and of a closing-hand stimulus with an opening-hand response. However, interdispersed with these pairings, half of the participants were given an equal number of additional trials in which opening and closing responses occurred in the absence of opening and closing stimuli. This group, in which the stimulus–response contingency was zero, showed significantly less learning than the other group, in which the stimulus–response contingency was 1.

Thus, recent research has found the footprints of associative learning on two important examples of social learning. There is evidence that the social enhancement of food preferences in rats—one of the most well-documented and robust examples of social learning in animals—is subject to overshadowing and blocking; and that human gesture imitation—an example of social learning that has long been assumed to involve complex, dedicated, cognitive processes—depends not only on contiguity (the pairing of stimuli and responses) but also on contingency. We need more research of this kind, involving tough tests for associative learning. However, in combination with the research in the previous sections, these studies provide strong evidence that social and asocial learning are mediated by a common set of associative processes.

Learning Mechanisms Versus Input Mechanisms

I have argued that evidence from a number of sources points to the conclusion that, across species and task domains, social and asocial learning depend on a common set of associative learning mechanisms. Learning mechanisms are cognitive processes that encode information for long-term storage. Therefore, this evidence implies that, across species and task domains, when information received via the observation of others is encoded for long-term storage (social learning), the encoding is achieved by the same cognitive processes that are responsible for the long-term storage of information received through other channels (asocial learning). Thus, from a cognitive science perspective, the term *social learning* is misleading. The learning (i.e., long-term encoding) mechanisms involved in social learning are not distinctively social. They are the very same mechanisms that mediate asocial learning. Therefore, social learning mechanisms (see Footnote 1) lack any

variation that could be attributed to adaptive specialization for social living.

In isolation, this conclusion seems to imply that there is nothing special about social learning. It suggests that social learning is merely a label we assign to some examples of learning. In these examples, it happens to be the case that the learned information is supplied through a social *channel* (Sterelny, 2009)—through the observation of others’ behavior—but the cognitive processes that encode this information are just the same as those that encode information received from other channels; they are not adaptively specialized in any way for the handling of socially channeled information. This may be true for some, perhaps many, cases of social learning. However, there is evidence that social learning is sometimes adaptively specialized. In the next section, I outline this evidence and argue briefly that it is due to the effects of social living, not on learning mechanisms, but on “input mechanisms”—perceptual, attentional, and motivational processes that supply information for learning.

The distinction between input mechanisms and learning mechanisms is analogous to the distinction between ingestive and digestive processes (Heyes, 2003). Ingestive processes, such as grasping and chewing, supply the body with materials that are broken down by digestive processes for long-term storage. Similarly, psychological input mechanisms supply the cognitive system with information that is encoded by learning mechanisms for long-term storage. Digestive processes sustain energy and growth, whereas learning processes support durable changes in behavior.

Adaptive Specialization of Input Mechanisms

There is remarkably little evidence for the adaptive specialization of social learning; that is, evidence that highly social animals are superior to less social animals in a social learning task but not in a comparable asocial learning task (Lefebvre & Giraldeau, 1996; Munger et al., 2010; Shettleworth, 1993). However, at least one study has provided such evidence. Templeton et al. (1999) tested two corvid species, Pinyon jays and Clark’s nutcrackers. These species have similar habitats, foraging ecologies, opportunistic foraging tendencies, and motor repertoires, but Pinyon jays are more social than Clark’s nutcrackers. The birds were given tasks in which they had to remove covers from food wells after observing a conspecific removing the covers (social learning) or exclusively through their own efforts (asocial learning). The jays’ performance in the social learning tasks was superior to their performance in the asocial learning tasks, whereas the nutcrackers were no better at social than at asocial learning.

This example of adaptive specialization can be explained in a straightforward way by assuming that Pinyon jays and Clark’s nutcrackers differ in the extent to which one or more of their input mechanisms are biased in favor of information carried by the behavior of other birds. The biased input mechanism could be perceptual, attentional, or motivational. For example, Pinyon jays may have a visual system that makes them better able to see the behavior of other birds, an attentional system that processes perceptual input from other birds more thoroughly, or a motivational system that makes them track the movements of other birds more closely and with less antagonism. Further research would be needed to distinguish these possibilities, and to find out whether the input bias (or *inflection*; Heyes, 2003) is specific to the forag-

ing context, to conspecifics, or even to certain familiar individuals (Scheid, Range & Bugnyar, 2007). Even without further study, it is clear that biased input mechanisms could produce the results reported by Templeton et al. (1999). In their social and asocial learning tasks, birds were given an equal opportunity to learn how to remove the covers by trial and error—by manipulating the covers themselves. In the social tasks the birds had, in addition, an opportunity to obtain information about the covers and the food beneath by observing conspecifics removing the covers and consuming the food. Therefore, even if the learning (long-term encoding) was done by identical mechanisms, observer birds that were better able to see what the demonstrators were doing—by virtue of perceptual, attentional, or motivational biases—would show superior performance in the social, but not in the asocial, learning tasks.

In principle, the adaptive specialization of input mechanisms could occur via genetic or developmental processes; it could be phylogenetic or ontogenetic. For example, natural selection may have endowed all Pinyon jays with socially biased attentional mechanisms (phylogenetic). Alternatively, individual jays may develop socially biased attentional mechanisms as a result of their experience with other birds (ontogenetic). More specifically, jays may become more attentive to the behavior of others through experience in which that behavior provides a safe and reliable source of information.

Another study of birds provides an example of this kind of ontogenetic adaptive specialization: Dolman, Templeton, and Lefebvre (1996) gave Zenaida doves the opportunity to learn the location of food by observing a conspecific or a Carib grackle feeding at that location. Observer doves from a “friendly” colony, in which conspecifics feed amicably together, learned preferentially from fellow doves. By contrast, doves from an “unfriendly” colony, in which they compete aggressively for food with conspecifics but feed alongside grackles, learned more readily from grackles than from doves. This difference suggests that the doves from the friendly colony were more attentive to the behavior of conspecifics than the doves from the unfriendly colony. Since the two colonies of doves were not genetically distinct, it is likely that the difference in attentiveness was due to the birds’ prior experience of interaction with conspecifics.

Further evidence that input mechanisms can be specialized ontogenetically rather than phylogenetically comes from studies showing that monkeys (Klein, Deaner, & Platt, 2008), rats (Miller & Dollard, 1941; Galef, 1981), budgerigars (Mui et al., 2007) honeybees (Dyer, Neumeyer, & Chittka, 2005), and humans (Behrens, Hunt, Woolrich, & Rushworth, 2008) become more attentive to social stimuli as a consequence of experience in which these stimuli provide reliable information about the availability and location of resources. The last of these studies is particularly interesting. Using functional MRI and computational modeling, Behrens et al. (2008) showed that humans learn to attend to social input via the same associative processes that modulate attention to nonsocial stimuli. Thus, associative processes may underwrite not only social learning—the encoding for long-term storage of information received via social interaction—but also the adaptive specialization of input mechanisms, making them especially receptive to information supplied by other agents.

Conclusions and Future Directions

So, returning to the title of this article, what’s social about social learning? At the purely descriptive level, social learning is defined by its channel (Sterelny, 2009). It is social by virtue of the fact that another individual, typically a conspecific, plays some role in supplying the learner with the information that is subsequently learned (see Footnote 1). Moving to the explanatory level—the level where we ask about cognitive processes—I have suggested in this article that some examples of social learning (descriptively defined) may be social in a deeper sense. They may be social by virtue of involving input mechanisms—perceptual, attentional, and/or motivational processes—that are adaptively specialized for the receipt of information from other agents. This adaptive specialization of input mechanisms can occur ontogenetically or phylogenetically. However, the primary message of this article is that social learning is not social by virtue of involving distinctively social learning mechanisms. The same associative processes do the learning—encode the information for long-term storage—when the information is received through social and asocial channels.

Some of the most interesting contemporary research on social learning asks about the conditions in which social learning evolves (e.g., Rendell et al., 2010). On the received view, this is understood to be an enquiry about the circumstances in which natural selection produces new cognitive processes that are adapted for the encoding and long-term storage of information received via other agents. On the view I am proposing, it is an enquiry about the conditions in which natural selection or learning act to bias perceptual, attentional, and motivational processes toward input received from other agents.

Related work on *social learning strategies* (e.g., Laland, 2004) examines the circumstances in which it is adaptive for individuals to base their behavior on information gained through a social channel (sometimes called *public information*, Giraldeau & Caraco, 2000). Drawing on theoretical modeling and empirical methods, researchers in this field suggest that human and nonhuman animals apply strategies such as *copy when uncertain*, *copy the majority*, and *copy successful individuals*. To the ear of a cognitive scientist, the term *strategy* implies a high-level executive process—the kind of cognitive process, typically implemented in human prefrontal cortex, that controls voluntary behavior using symbolically, and perhaps consciously, represented rules and plans. However, as far as I can tell, research on social learning strategies does not and need not assume such a cognitively rich interpretation of strategies. The purpose and significance of its findings are preserved when, consistent with the analysis presented in this paper, strategies are construed at the cognitive level as socially biased input mechanisms—perceptual, attentional, and motivational processes that privilege information received via one or more social channels. This construal is also consistent with the suggestion that associative learning plays a major role in biasing input mechanisms/producing social learning strategies. For example, associative learning is known to increase when outcomes are unpredictable (*copy when uncertain*), with the number of exposures to an event sequence (*copy the majority*), and when the event sequence occurs in conjunction with rewarding stimuli (*copy successful individuals*).

The perspective presented in this article is also consistent with the suggestion that, compared with chimpanzees, human children

have especially high *social motivation*, and this contributes to their greater tendency to *overimitate*—to copy more components of an adult's action sequence than is necessary to achieve a desired outcome, such as a toy or sticker (e.g., McGuigan, this issue, pp. 150–160; Over & Carpenter, this issue, pp. 182–192). Social motivation can be regarded as one or more socially biased input mechanisms. However, the evidence that input mechanisms can be biased ontogenetically (Dolman et al., 1996) and, even in adult humans, by associative learning (Behrens et al., 2008), reminds us that we should not assume that enhanced social motivation is a product of phylogenetic specialization—that it is innately human. We may endow children with heightened social motivation by rewarding them from earliest infancy for doing what we do (Ray & Heyes, 2011).

Obviously, the suggestion that social learning is mediated by associative processes does not imply that all learning is associative; that is, that the only learning processes available to human and nonhuman animals are the processes that produce Pavlovian and instrumental conditioning phenomena in the laboratory. Nor does it imply that all social cognition consists of social learning (see Footnote 1) and is therefore associative (for a broader review of social cognition, see Frith & Frith, in press). Less obviously, the suggestion that social learning is mediated by associative processes does not in any way undermine the view that social learning in general, or particular types of social learning, support an epigenetic or cultural inheritance system (e.g., Jablonka & Lamb, 2005; Richerson & Boyd, 2005). On the contrary, given that there is reason to believe that social learning supports epigenetic inheritance, and that this inheritance has important evolutionary consequences, the evidence reviewed in this article implies that associative learning can have a major impact on the rate and course of evolution.

The study of social learning has been isolated from cognitive science—it has been “behaviorist” —for too long. The analysis presented in this article suggests that investigation of the cognitive bases of social learning need not be isolated from research examining its contribution to the adaptiveness of behavior. An integrative program of research would ask a number of questions about each social learning phenomenon: 1) Is it due to a socially biased input mechanism? 2) If there is a social bias, what kind of input mechanism is involved (perceptual, attentional, motivational) and to exactly which social channel is it biased? 4) Is the source of bias phylogenetic or ontogenetic—was it produced by natural selection or by learning? 5) If the source was ontogenetic, what kind of learning process biases the input mechanism toward a social channel?

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