

Theoretical and Empirical Approaches to Understanding When Animals Use Socially Acquired Information and from Whom They Acquire It

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Abstract

Introduction

Integration of Social Information with Other Sources of Information When Making Decisions

Internal State

Affective Responses

Preparedness

Characteristics of Demonstrators

Success

Reliability

Proficiency

Frequency

Social and Individual Learning

Individual Experience and Subsequent Social Acquisition of Behaviour

Familiarity

Familiarity of Demonstrators

Familiarity of Stimuli

Social Learning and Subsequent Independent Acquisition and Performance of Behaviour

Acquisition

Performance

Effects of Individual Learning on Subsequent Acquisition and Performance

of Socially Learned Behaviours

Acquisition

Performance

Acquisition and Performance

Conclusion

Acknowledgments

References

Abstract

I review empirical studies of the integration of individually and socially acquired information by animals faced with a choice between alternative

courses of action. Focus on results of empirical studies is intended as a compliment to recent reviews of similar material that have focused on predictions from formal models. In introduction and conclusion, I consider both the relationship between empirical and theoretical approaches to the study of social learning and implications of the material reviewed for future work in the area.

Introduction

Many of the biologically important decisions that animals make can be biased by interaction with conspecifics making similar decisions. However, even when information acquired socially affects behaviour, socially acquired information does not act in a vacuum. Before an individual chooses to act, it integrates information extracted from the social environment with: (1) information acquired during previous experience with the asocial environment, (2) affective responses to alternative potential goal objects, and (3) information as to its own internal state.

Great progress has been made in both identifying behavioural domains where social learning is important and understanding behavioural processes that underlie social influences on behaviour. However, we still know relatively little about how socially acquired and other sources of information are integrated before action is initiated.

There are two quite different approaches to understanding how animals achieve such integration. The first is a theoretical approach admirably presented in Laland's (2004) review of formal models of social learning. Laland's paper discusses predictions, derived from both game theory and evolutionary models, as to when animals might be expected to use social cues to guide their behaviour ("when strategies"), and whose behaviour social learners might be expected to copy ("who strategies"), as well as tests of some of those predictions.

The alternative approach to the theoretical one is empirical. It involves direct investigation of variables that might determine whether animals use available social information when making decisions. Often, variables are selected for examination because they are known to be important in determining whether animals acquire and perform behaviours when no social learning is involved. Such extrapolation from asocial to social learning is reasonable because although exposition is made simpler by categorising learning as either "social" or "asocial," the dichotomy is not so real as the terminology implies.

As Heyes (1993) pointed out some years ago, with the exception of learning by imitation (that appears to be relatively rare in animals), animal social learning does not involve learning directly about the *behaviour* of others. Rather, socially acquired information directs an individual's behaviour

towards objects in the environment with which the "social learner" then interacts directly. Consequently, most social learning in animals is, in fact, socially biased individual learning (Galef 1995), and variables that affect individual learning might be expected to influence social learning as well.

To synthesise and organise information, general theories of social learning have had to ignore much of the detail of learning processes and social interactions. Such detail, although of relatively little obvious theoretical significance, can place boundary conditions on theories and determine whether predictions from theory are confirmed in particular instances.

Empirical approaches exploring variables that affect the probability of social learning will invariably be more intuitive and less integrative than theoretical approaches. Still, empirical approaches result in discovery of phenomena that theory does not predict and reveal the impact of variables that general models have yet to consider. For example, as Laland (2004) indicates in his review, functional considerations lead to the conclusion that animals should copy the behaviour of others when: (1) their ongoing behaviour is relatively unproductive, (2) asocial learning is costly, and (3) asocial learning is uncertain. However, as indicated later, lack of productivity, uncertainty, and costliness can each have many causes, and not all need have similar effects on the probability that social learning will occur.

Here, I review empirical studies that contribute to our understanding of how socially acquired information interacts with other sources of information to determine the decisions animals reach and suggest ways in which the interplay between theory and data might guide future research. The chapter is organised first in terms of the type of information that is being integrated with socially acquired information and, second, with respect to whether effects of socially acquired information are on the acquisition of behaviour or its subsequent performance.

Integration of Social Information with Other Sources of Information When Making Decisions

Internal State

It has been predicted on functional grounds that an animal doing poorly will be more likely to adopt the behaviour of others than an individual that has independently acquired behaviour leading to success (Laland 2004). However, it is not clear from general theory just how an animal might determine whether it is succeeding or failing. A possibility considered here is that an individual might gauge its success by monitoring its internal state. For example, an animal experiencing hunger or deficiency in some necessary nutrient (e.g., protein, sodium) might be more likely than a well-fed animal to

consider itself unsuccessful, to abandon its individually acquired foraging patterns or food choices and adopt those of others.

Theory suggests further that if a relatively unsuccessful animal could identify successful conspecifics, it should be more likely to affiliate with, attend to, and adopt the behaviour of successful rather than of unsuccessful individuals. However, and obviously, for relatively unsuccessful individuals to be able to copy the behaviour of the relatively successful, relatively unsuccessful individuals must both assess their own relative success and identify the more successful.

Ward and Zahavi's (1973) information-centre hypothesis implicitly assumed that unsuccessful avian foragers can both recognise their own failure and detect successful individuals so that the unsuccessful can follow the successful when the latter leave a roost to forage. Thirty years of observation and experiment in natural circumstances have provided little data consistent with the information-centre hypothesis regarding the function of avian roosts (Mock *et al.* 1988). Even if, in some species, unsuccessful foragers do follow successful foragers from aggregation to foraging sites (e.g., Sonerud *et al.* 2001; Wilkinson 1992), considerable empirical work will be required to understand why the phenomenon is not observed in other central-place foraging avian species, as theory suggests it should be. Are central-place foragers whose aggregation sites do not function as information centres insensitive to their own relative success? Are they unable to detect or unable to follow successful individuals, or is there some other reason why they fail to exploit useful social information that appears to be available to them?

Laboratory studies undertaken to look for effects of deprivation states on social learning of food preferences in Norway rats have provided a partial picture of the influence of lack of success on reliance on social learning, as well as information on the ability of rats to discriminate successful from unsuccessful conspecifics. Galef and colleagues (1991) presented individual protein-deprived and protein-replete Norway rats with a cafeteria of four distinctively flavoured, protein-deficient foods and found no differences in their food choices. However, when both protein-deprived and protein-replete rats were presented with the same cafeteria of four foods in the presence of a "demonstrator" rat trained to eat only the least palatable of the foods in the cafeteria, protein-deprived observers ate far more of that food than did protein-replete observers. The findings are consistent with theory in that a state of protein deprivation, a sign of lack of success, increased reliance on socially acquired information (Beck & Galef 1989).

However, further evidence suggested: (1) that not all deprivation states affected reliance on social information in the same way, and (2) that a particular deprivation state may have different effects in different species. For example, and as theory predicts, food-deprived juvenile Norway rats prefer a food bowl where a conspecific adult is feeding to a food bowl where no adult

is present. However, water-deprived juvenile rats do not prefer to drink from a water bowl where an adult rat is drinking (Galef 1978).

Unlike food-deprived rats, which are more strongly influenced by social stimuli than their replete fellows, food-deprived banded killifish (*Fundulus diaphanous*) spend more time alone and less time shoaling than do well-fed killifish (Hensor *et al.* 2003). Perhaps competition for food is more severe in killifish than in rats. Perhaps there is some other cause for their differing responses to food deprivation.

A focal individual's deprivation state can also affect its choice between replete and deprived conspecifics as companions (Galef & Whiskin 2001). Food- or sodium-deprived Norway rats choosing to affiliate with either food-deprived or food-replete rats preferred to remain near well-fed individuals. However, both sodium-deprived and food-deprived rats were indifferent as to whether potential partners were sodium-deprived.

In sum, as formal models predict, internal states indicative of a lack of success sometimes increase an animal's probability of using social information. However, theory does not yet predict which internal states indicative of lack of success affect use of social information, and gives no indication of which species might be expected to increase affiliation or social learning when unsuccessful. Indeed, "successful" and "unsuccessful" are probably not sufficient descriptors of either potential social learners or their potential models. What is needed, but not available, is programmatic examination of the effects of various sorts of lack of success on susceptibility to various types of social learning. When are deficient animals more likely to affiliate with conspecifics than healthy animals? What types of social learning are affected by lack of success: are deficient animals more susceptible to local enhancement, more likely to follow conspecifics to food, or to copy conspecifics' food choices? Do different deprivation states affect differently which potential models deprived animals choose to copy? Theory does not yet provide much guidance in asking or answering such mechanistic questions.

Affective Responses

Whether an animal chooses to adopt another's behaviour can depend not only on its internal state, but also on its affective response to the outcomes of alternative behaviours in which others are engaged. Such "direct bias" (Boyd & Richerson 1985) can have important effects on the probability of socially acquired information affecting behaviour. For example, Dugatkin (1996) set in opposition the tendency of female guppies to affiliate with physically attractive males (those with large orange-coloured areas on their bodies; Houde 1988) and with males that they had been previously seen courting other females (Dugatkin 1992; Dugatkin & Godin 1992). He found that a

female guppy that had watched the less-orange-coloured of two males court subsequently preferred to affiliate with him, but only if his areas of orange colouration were slightly smaller (4% to 24%) than those of his competitor (Dugatkin 1996). If two males differed 40% or more in orange colouration, then females preferred the male with larger orange patches even after seeing the male with smaller orange patches court another female.

In analogous fashion, observer rats that interacted with demonstrator rats that were fed a diet flavoured with unpalatable cayenne pepper before choosing between a standard diet and a diet flavoured with varying concentrations of cayenne pepper showed less social influence on their diet choice the greater the concentration of cayenne pepper in the flavoured diet offered to them (Galef & Whiskin 1998). When the relative palatability of two diets offered to observer rats was manipulated by increasing rather than by decreasing the palatability of the food that demonstrators ate, once again, as the difference in palatability of the diets offered to demonstrators increased, the effects of demonstrators on their observers' food choices decreased (Galef & Whiskin 1998).

In general, as theory predicts, the greater the difference in affective response of naïve individuals to two stimuli, the less the impact of demonstrators on their observers' subsequent choices between those stimuli.

Preparedness

In a classic series of studies of social learning of predator avoidance, Cook and Mineka (1989, 1990) demonstrated that laboratory-reared, juvenile rhesus monkeys learn to respond fearfully to snakes or snake-like objects by watching adults of their species exhibit fearful responses to such stimuli. However, such social learning of avoidance was limited to specific stimuli. After watching video sequences of conspecifics appearing to behave fearfully towards either a toy rabbit or flowers, rhesus monkeys failed to acquire fear responses to them. However, similar video presentations were sufficient to induce fear of snake-like stimuli (Cook & Mineka 1989, 1990).

Similar preferential social learning to certain stimuli has also been found in birds, although it is of lesser degree (Griffin 2004). Curio and colleagues (1978) found that socially learned antipredator responses to a stuffed bird were stronger than similar responses learned to a plastic bottle. Initial responses of naïve birds were greater to presentation of a stuffed bird than a plastic bottle, and may have been responsible for the different strengths of subsequent social learning. Thus, empirical investigations suggest the need for theoretical developments to extend the notion of "preparedness" (Seligman 1970), "cue to consequence specificity" (Garcia & Koelling 1966), or "adaptive specialisation of learning" (Rozin & Kalat 1971) from individual learning to social learning.

Characteristics of Demonstrators

Boyd and Richerson (1985) have discussed the effects on social learning not only of affective responses to outcomes of alternative actions (direct bias), but also of the characteristics of models on the probability that their behaviour will be adopted (indirect bias). Effects of a number of different attributes of potential models on the probability that the naïve will adopt their behaviour have been explored.

Success

Both common sense and theory suggest that observers should be more likely to adopt the behaviour of successful than of unsuccessful demonstrators (Laland 2004). Surprisingly, observers do not always make the predicted discrimination. For example, although Norway rats can readily distinguish poisoned from unpoisoned conspecifics, they are no more likely to adopt the food choices of the healthy than of the ill (Galef *et al.* 1990; Galef *et al.* 1983). Perhaps similarly, domestic hens are no more likely to learn socially from previously highly successful than from the less successful foragers (Nicol & Pope 1994, 1999). Norway rats and domestic fowl appear to lack the behavioural machinery needed to learn differentially from successful and unsuccessful potential demonstrators, though functional considerations lead to the prediction that they should.

Reliability

Norway rats are also unable to distinguish reliable from unreliable demonstrators. Galef and colleagues (1999) poisoned observer rats on several occasions after the rats ate whatever foods one demonstrator had eaten and never poisoned the rats after they ate the foods that a second demonstrator had eaten. The observers were subsequently equally likely to copy the food choices of the two demonstrators.

Proficiency

Both theory and common sense also suggest that individuals should be more likely to adopt the behaviour of proficient than of ineffective conspecifics (Laland 2004), but this is often not the case. Swaney and colleagues (2001) found that guppies were more likely to use socially acquired information to learn a path to concealed food when conspecific demonstrators were poorly trained than when they were well trained. Well-trained demonstrators appeared to move too quickly for naïve individuals to join them en route to food (van Bergen *et al.* 2004).

Similar superiority of nonproficient to proficient demonstrators as tutors has been reported in two sets of experiments in which birds watched proficient and less proficient tutors perform arbitrary operant responses (Beauchamp & Kacelnik 1991; Biederman & Vanayan 1988). Beauchamp and Kacelnik (1991) interpreted the superiority of nonproficient to proficient demonstrators, both in their own experiment and that of Biederman and Vanayan (1988), to proficient demonstrators providing a reliable cue for the opportunity to forage that interfered with learning about any other cues that predicted food availability. Studies of asocial learning have shown repeatedly that learning to respond to a reliable cue of the occurrence of a rewarding event interferes with subsequent learning to respond to a second cue that predicts occurrence of the same event.

Although theory led to the posing of interesting questions about the relationship of demonstrator proficiency to demonstrator effectiveness, the observed relationship between proficiency and effectiveness depended on details of mechanisms of little current interest from an evolutionary perspective. The importance of such mechanistic detail in determining behavioural outcomes suggests the need for further integration of mechanistic and functional perspectives in theory building.

Frequency

Some theory has been developed to reflect social learners' sensitivity to the frequency with which other individuals engage in each of two or more alternative behaviours (Boyd & Richerson 1985; Chou & Richerson 1992). Both, Chou and Richerson (1992) and Galef and Whiskin (1995b) found that observer rats offered a choice between two diets after interacting with groups of demonstrator rats, some of whose members had eaten each of the two diets, showed diet choices reflecting the proportion of group members that had eaten each diet. For example, observer rats offered a choice of cinnamon- and cocoa-flavoured diets after interacting with a group of four demonstrators, three of which had eaten cocoa-flavoured diet and one cinnamon-flavoured diet, ate more cocoa-flavoured diet than observer rats that had interacted with a group of four demonstrators, three of which had eaten cinnamon-flavoured diet and one cocoa-flavoured diet.

Social and Individual Learning

Individual experiences of various kinds can affect the probability that an observer will subsequently copy the behaviour of others. Conversely, social learning can affect both the probability that subsequent individual learning will occur and the stimuli towards which individual learning will be directed.

Individual Experience and Subsequent Social Acquisition of Behaviour

Several types of individual experience (e.g., simple exposure, Pavlovian conditioning, operant conditioning) can affect the probability that an individual's subsequent acquisition of behaviour will be influenced by interaction with others.

Familiarity

Familiarity of Demonstrators

Coussi-Korbel and Fragaszy (1995: 1444) have distinguished between instances of social learning where the relationship between a demonstrator and its observer affects the strength of social learning ("directed social learning") and those where the relationship between demonstrator and observer is irrelevant ("nonspecific social learning"). The distinction is similar to an earlier one proposed by Boyd and Richerson (1985) between indirectly biased and unbiased social learning.

Several laboratories have looked for and found effects of a prior relationship between an observer and its demonstrator on subsequent social learning. The general finding, as Coussi-Korbel and Fragaszy (1995) observed, is that naïve individuals are more likely to learn from interaction with familiar rather than with unfamiliar conspecifics, though there are both exceptions to that rule and no obvious functional reason why familiar individuals should be preferred to nonpreferred individuals as sources of information.

In a very early study of local enhancement, Chesler (1969) found that kittens that had watched their mothers press a lever for a food reward subsequently learned the same behaviour faster than did kittens that had watched an unfamiliar cat engage in the same behaviour. More recently, Lupfer and colleagues (2003) reported that young golden hamsters exhibit enhanced preference for novel foods eaten by their dam, but not for those eaten by an unfamiliar adult. Moreover, Benskin and colleagues (2002) showed that the probability that young zebra finches will copy the food choice of a male model increases when he is familiar with his observers. Swaney and colleagues (2001) provide data indicating, similarly, that naïve guppies learned a path to a concealed food source more rapidly when a demonstrator shoal consisted of familiar rather than of unfamiliar individuals.

Cadiou and Cadiou (2002, 2004) compared effects of parents and unfamiliar conspecific adult demonstrators on ingestion of a novel food by young canaries and found that parents were more effective in inducing feeding on novel food. Juveniles' manipulation of unfamiliar seed was more frequent in the presence of fathers than of unfamiliar males, and juveniles ingested more

seed in the presence of a parent of either sex than in the presence of an unfamiliar adult. Cadieu and Cadieu (2004) suggested that the greater efficacy of fathers than of unfamiliar male canaries as demonstrators resulted from fathers exhibiting the relevant behaviour more often in the presence of their own offspring than in the presence of others' young.

Kaveliers and colleagues (2005) report that naïve, laboratory-bred deer-mice (*Peromyscus maniculatus*) show greater social learning of defensive responses to biting flies after observing siblings or familiar non-kin than after observing unfamiliar individuals respond defensively to biting flies. Further, within familiar pairs, social status affected acquisition, with subordinate observers displaying better social learning than dominants.

In a possible exception to the rule that increasing familiarity of demonstrators increases their effectiveness as demonstrators, Hatch and Lefebvre (1997) reported that juvenile ring doves tend to learn a novel foraging technique better from unrelated but familiar adults than from their fathers, possibly because parental tolerance permits scrounging of food that inhibits social learning.

Valsecchi and colleagues (1996) reported striking differences in social enhancement of food preferences in Mongolian gerbils exposed to either familiar or unfamiliar demonstrators, a somewhat unexpected finding given that Galef and colleagues (1984) had previously reported no effect of familiarity between demonstrator and observer Norway rats on social learning of food preferences. Subsequent analysis (Galef *et al.* 1998) suggested that whether familiarity of demonstrator and observer affected social learning of food preferences depended not on species differences, but on the strength of the cues that demonstrators provided for their observers. When demonstrators were fed immediately before interacting with observers, and were therefore presumably emitting relatively strong diet-identifying cues for their observers to learn about, both familiar and unfamiliar demonstrator rats and gerbils had equivalent effects on conspecific observers' subsequent food choices. When demonstrators ate some hours before they interacted with observers, and presumably therefore provided weaker diet-identifying cues than demonstrators fed immediately before they interacted with their observers, familiarity of demonstrators had a significant effect on observers' food preferences.

In general, there is a need for further experimental work to determine the conditions under which familiarity influences the strength of social learning and, for further theoretical work exploring possible functional implications of the apparent greater effectiveness of familiar than of unfamiliar demonstrators. Coussi-Korbel and Frigaszy (1995) suggested that individual differences in the efficacy of demonstrators result from differences in the salience of their behaviour to their observers, though, obviously, differences in salience are only one of many possible causes of differences in the effectiveness of familiar and unfamiliar demonstrators in altering the behaviour of their observers.

Familiarity of Stimuli

Galef (1993) and Galef and Whiskin (1994) found that rats maintained on a single type of food for several days did not show an enhanced preference for that food after interacting with a demonstrator rat that had eaten it; however, rats that were unfamiliar with the food that a demonstrator ate exhibited a marked enhancement of their preference for that food. Because the effect of personal experience of a food on subsequent social learning of a preference for it is to restrict socially learned food preferences to foods not eaten in the recent past, Galef (1993) interpreted this familiarity-induced inhibition of social learning as indicating that social learning about foods evolved to facilitate individuals increasing or maintaining dietary breadth. However, subsequent findings suggest that it is probably incorrect to infer that effects of diet familiarity on social learning are adaptations related to social learning about foods.

Recent work indicates that maintenance on a single food causes a surprisingly powerful, though relatively short-lived (24 to 48 hours), reduction in Norway rats' (and golden hamsters') subsequent preference for that food (DiBattista 2002; Galef & Whiskin 2003, 2005). Consequently, an observer rat that has eaten a food for 3 days before encountering a conspecific demonstrator that has eaten the same food experiences social induction of preference for a food to which it has already developed an aversion (Galef & Whiskin 2003). As discussed earlier, animals' affective responses towards stimuli to which socially acquired information directs them can affect the probability that social learning will occur.

Aversion to a maintenance diet may also underlie Forkman's (1991) finding that Mongolian gerbils resume eating novel but not familiar foods when a hungry, feeding conspecific is placed with them. Whether Mongolian gerbils, like Norway rats and golden hamsters, develop an aversion to a food after eating it for several days in succession is not known. However, if they do, then the difference that Forkman found in social facilitation of gerbils eating familiar and unfamiliar foods might reflect a difference in social facilitation of ingestion of relatively palatable and unpalatable foods.

Social Learning and Subsequent Independent Acquisition and Performance of Behaviour

Students of individual learning have discovered that variables can have rather different effects on the acquisition of behaviour and on the performance of previously acquired behaviours (Staddon & Simmelhag 1971). The same distinction can be applied to social learning (Galef 1995). In the following sections, I discuss issues relevant to the acquisition and performance of behaviour separately, though the distinction is seldom made in the literature on social learning.

Acquisition

Whether social influences on acquisition of behaviour lead to optimal or sub-optimal performance is situation-dependent. In particular, social learning in relatively stable environments tends to promote adaptive interactions between social and individual learning, whereas social learning in more variable environments can result in delayed acquisition of novel adaptive responses (Boyd & Richerson 1985).

Studies of social influence on the acquisition of aversions by Norway rats provide examples of possibly adaptive effects of prior social learning on individual learning. For example, an observer rat that: (1) interacts with a conspecific demonstrator eating an unfamiliar food, (2) then eats the food that its demonstrator ate and becomes ill, is relatively unlikely to learn an aversion to the food that it ate before experiencing illness (Galef 1989). Similarly, if an observer rat: (1) interacts with a conspecific demonstrator that has eaten a food; (2) then eats two foods for the first time, one of which is the food its demonstrator ate; and (3) is poisoned, the observer learns an aversion to whichever food it ate that its demonstrator had not eaten (Galef 1989). Such social influence on acquisition might increase the probability that ill rats would avoid the lost opportunity costs of learning an aversion to a food when illness experienced in the hours following ingestion of a novel food results from some cause other than food poisoning.

Laland and Williams (1998) provide evidence of circumstances in which social learning appears to reduce the probability of later adaptive individual learning. Guppies tested while members of shoals that were taking the longer of two routes to food learned an alternative, more efficient route to food more slowly than did naïve guppies tested individually. Testing of the trained guppies in shoals and of the naïve animals individually, though appropriate from a functional perspective, makes it difficult to determine the relative contribution of social learning and a tendency to remain in a shoal to slowed acquisition of a novel, adaptive response.

Pongracz and colleagues (2003) also discuss a situation where social learning interferes with subsequent individual acquisition of more efficient behaviours. They found that dogs that had learned socially to make a detour around a fence were subsequently less likely than naïve dogs to use an open door in the fence to access reward. The greater the number of demonstrations of detouring around the fence a dog had received, the slower it was to learn the direct route. Whether social learning itself or experience of rewards after social learning occurred was responsible for retardation of individual acquisition of the more efficient route to food remains to be determined.

Performance

Interaction with conspecifics can influence not only acquisition of behaviour, but also how long a previously independently learned behaviour is expressed.

For example, after a focal animal, a rat (Galef 1986) or a hyena (Yoerg 1991), learns independently to avoid a food because ingestion of that food preceded experience of illness, the focal animal will abandon its learned aversion after interacting with one or more conspecifics that have recently eaten the food that the focal animal had learned independently to avoid. In a conceptually similar study, Pongracz and colleagues (2003) trained dogs to go through an open door to reach food or a favourite toy. When the door was closed, the dogs' perseverance was substantially reduced if a human demonstrated a detour around the fence.

Effects of Individual Learning on Subsequent Acquisition and Performance of Socially Learned Behaviours

Following, I now consider the inverse relationship to that discussed in the preceding section, reviewing evidence of effects of individual learning on subsequent acquisition and performance of socially learned behaviours.

Acquisition

Theory suggests that individuals should “copy when uncertain,” and prior individual experience in an environment should affect judgement as to its predictability. For example, as theory suggests, maintaining rats in constantly changing conditions, a circumstance that should increase uncertainty, increased their dependence on information acquired from others. For 12 days, Galef and Whiskin (2004) fed rats a different food, at a different hour, for different lengths of time, and found a small, but statistically reliable increase in subjects' subsequent use of social information in food choice relative to rats fed on predictable schedules.

On the other hand, feeding observer rats two foods for a week (which should have reduced their uncertainty concerning those foods) and then allowing them to interact with demonstrators that had eaten one of the two foods did not reduce demonstrators' influence on their observers' preferences for those foods (Galef & Whiskin 2001). As discussed earlier, although maintenance on a single food temporarily blocks subsequent social induction of preference for that food, such inhibition results from exposure-induced aversion and probably does not involve reduced uncertainty (Galef 1993; Galef & Whiskin 2005).

Individual learning can determine the attractiveness of the stimuli encountered as a result of copying the behaviour of another, and as discussed in a preceding section, affective responses to behavioural outcomes can alter the probability that an individual will adopt the behaviour of another individual. For example, Galef (1985) varied the strength of toxin used to induce an

aversion to a palatable food in observer rats and then examined the effect of interaction with a demonstrator rat eating that food on observer rats' subsequent choice of it. The greater the pharmacological insult used to induce an aversion to the palatable food, and consequently the greater the strength of the aversion learned, the smaller the effect of interaction with a demonstrator rat fed the palatable diet on its observers' intake of the food that they had previously learned to avoid.

Galef and colleagues (1987) found, similarly, that the probability that a hungry Norway rat would follow a trained leader rat through a maze to food was affected by potential followers' information regarding the safety of the food that a potential leader had eaten. Galef and colleagues (1987) either poisoned or did not poison rats immediately after they ate a palatable food. When a trained leader rat was fed the same palatable food that its potential followers had learned to avoid, the poisoned rats failed to follow the leader, although the poisoned rats readily followed leader rats that had eaten other foods.

Performance

A number of experiments have been undertaken to examine factors that affect the longevity of a socially learned behaviour when a superior alternative becomes available. The general method of such studies has been similar. An observer learns socially to perform some behaviour that is less rewarding than an alternative subsequently made available to it, and the number of trials or time taken under various conditions for the observer to adopt the superior behaviour is measured. As might be expected, strength of initial social learning (determined by the number of demonstrators, the number of demonstrations, or the temporal distribution of demonstrations) affects the longevity of performance of a socially learned behaviour (Galef & Whiskin 1998), as does the opportunity to evaluate consequences of engaging in alternative courses of action (Galef 1999; Galef & Allen 1995; Galef & Whiskin 1997, 2001). For example, longevity of rats' socially enhanced food preferences, when choosing between a food that demonstrators had eaten and an alternative, decreased with an increase in either the time available to sample foods or the palatability of an alternative food (Galef & Allen 1995; Galef & Whiskin 1997, 2001).

Results of such experiments suggest that socially learned behaviours, similar to behaviours learned individually, are not maintained when they lead to insufficient reward. For example, McQuoid and Galef (1992) found that observer Burmese jungle fowl that watched conspecific demonstrators fed from a visually distinctive bowl on television were equally likely to initiate pecking at a similar bowl when it was presented in a choice situation, whether food was present in the bowl or it was empty. When food was present in the

bowl that looked like the one from which demonstrators had fed, observers continued to peck at that bowl for many minutes. However, when that bowl was empty, pecking by observers ceased in seconds. Effects of individual experience were clearly on performance of a socially learned behaviour, not on its acquisition.

The little evidence available suggests that socially learned behaviours are abandoned as rapidly as individually learned behaviours by those discovering alternative behaviours that produce either greater reward or equal reward at less cost (Mason *et al.* 1984; Galef & Whiskin 1995a). Mason and colleagues (1984) trained red-winged blackbirds to avoid distinctively coloured food cups either directly, by poisoning them after they ate from those cups, or socially, by watching conspecifics who became ill after eating from those cups. They then offered the birds a choice between two food cups containing the same food. One cup was the colour associated with illness, and the other a different colour. Mason and colleagues (1984) found that birds that had learned directly and birds that had learned socially continued to avoid the food cup associated with illness for the same length of time. If, as seems to be the case, socially learned behaviours extinguish rapidly without differential reward, the probability of a suboptimal behaviour becoming fixed in a population diminishes and perseverance of "maladaptive" traditions (Laland 1996) becomes less likely (Galef 1995, 1996).

Acquisition and Performance

Giraldeau and Lefebvre (1987) examined effects of the opportunity to "scrounge" seeds produced by another's foraging on the frequency with which pigeons acquired a behaviour that resulted in access to seeds by observing others engage in that behaviour. Scrounging food produced by a demonstrator that removed a stopper from an inverted test tube and released seed that both producer and observer could eat reduced the probability that observers would both learn and perform the behaviour that they had observed. Naïve observers that scrounged some of the food that their demonstrators produced while demonstrating were less likely to open tubes when subsequently tested alone than were observers assigned to a control group that watched demonstrators open tubes, but had no access to the food that their demonstrators produced.

When observers that had learned socially to open tubes foraged together with a bird trained to produce, the observers stopped opening tubes and scrounged seeds released by producers. When producers were removed, observers produced. Thus, scrounging interfered with performance of a socially learned behaviour as well as with its acquisition. No subsequent study has provided such clear evidence of social effects on both learning and

performance, and results of some studies have failed to provide evidence that scrounging interferes with social learning (McQuoid & Galef 1994; Giraldeau & Templeton 1991: experiment 2; Mason & Reidinger 1981).

Conclusion

Theoretically and empirically based approaches to the study of variables affecting the probability of social learning are clearly complementary. Formal models reveal unexpected order in previously unconnected observations and serve as heuristics to identify areas in need of empirical exploration. Empirical studies, undertaken to explore mechanisms of social learning, often reveal effects that formal models have not, and perhaps, given the current state of our knowledge, cannot predict. For example, and as discussed earlier, theory predicts that animals should be more likely to adopt the behaviour of successful than unsuccessful potential models. Yet, naïve Norway rats show as great an enhancement of their preferences for those foods eaten by healthy demonstrators as for those eaten by unconscious demonstrators or retching demonstrators with uncontrollable diarrhoea.

The reasons for the failure of observation to confirm theory are unclear. For example, although the potential benefits of copying food choices of healthy individuals seem obvious, there may be hidden costs of responding differently to successful and unsuccessful demonstrators that have resulted in the failure of rats to evolve that ability. Perhaps, in natural circumstances, ill or unconscious rats are only rarely incapacitated by ingesting toxic substances. If so, lost opportunity costs of ignoring information about foods that unhealthy potential demonstrators have eaten may be greater than the benefits of ignoring such information. Alternatively, costs of maintaining neural structures needed to inhibit acquiring a preference for foods eaten by unhealthy demonstrators may be greater than benefits resulting from ignoring information extracted from the unwell. Whatever the ultimate cause of the inability of rats to inhibit acquisition of preferences for foods eaten by ill demonstrators, empirical investigations suggest boundary conditions on theoretical predictions that point the way for the next generation of theories.

It might be argued that variables that influence the acquisition and performance of socially learned behaviours are simply specific examples of factors identified in formal models as determinants of when animals should rely on socially acquired information in decision making. For instance, theorists tell us that animals should copy when their established behaviour is unproductive. Suffering protein deficiency or hunger might indicate to an animal that its current behaviour is unproductive. If so, experiencing either protein or caloric deprivation should increase the probability that animals will adopt the behaviour of others. Of course, at a mechanistic level, there is

no guarantee that experiencing caloric deficiency and protein deficiency will have similar effects on the probability of social learning, and the evidence to date suggests that they may not.

In closing his review of formal models of social learning, Laland (2004) calls for empirical research that explicitly evaluates predictions derived from such models. As this chapter makes clear, there is also a need for theoretical models to take into account the rich empirical literature demonstrating boundary conditions that appear to restrict the generality of current theoretical formulations. Dewar (2004) developed a formal model of the effects of previous experience on social learning using as a starting point previously reported differences among species in both willingness to ingest unfamiliar foods and responsiveness to social influences on food choice. Such integration of theoretical and empirical approaches in modelling is clearly necessary.

Perhaps both the most interesting and, at the same time the most challenging, feature of social learning as a field of inquiry is the requirement to integrate work undertaken from divergent perspectives. In isolation, neither theoretical nor empirical approaches are sufficient to provide a full understanding of the role of social learning in the development of behavioural repertoires of animals. The future of the field lies in integration of two quite different approaches.

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