Forum: Invited Ideas

The challenges of mixing associational learning theory with information-based decision-making theory

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Behavioral ecologists frequently incorporate associational learning (AL) concepts into studies of choice behavior. Within behavioral ecology, AL is often considered a mechanism for information gathering. AL also provides alternative explanations of behavioral phenomena up to the level of motivational organization over the lifetime. AL assumes that all inputs to the learning system interact through a multistep process with feedbacks to control behavior and that cues are characterized by contingencies, whereas behavioral ecology assumes that learning inputs independently control responses, are in conflict, and convey information. Integrating the 2 perspectives is not straightforward and can lead to conflicting predictions or loss of predictive power. I examine 2 sets of case studies. First, I look at parallel research programs on mating in quail. Second, I consider how AL concepts have been integrated into foraging studies of nectarivores. The papers on quail mating demonstrate that to a large degree, the 2 approaches explain similar behaviors in compatible ways. The nectarivore papers show how the theories diverge, with AL predicting challenging results. Future studies should examine how much individuals select between sources of information and how much they respond to combinations of and interactions between cues within the process described by AL, using experimental designs that allow explicit cross-paradigm comparisons through the use of identical measurements of response. *Key words:* associational learning, *Coturnix japonica*, foraging, information, mate choice, nectarivore. *[Behav Ecol]*

INTRODUCTION

Behavioral ecologists frequently incorporate associational learning (AL) concepts into studies of choice behavior (e.g., Dukas and Duan 2000; Marsh et al. 2004; Fatouros et al. 2008; Siddall and Marples 2008; Witte and Godin 2010; Bacon et al. 2011). Within behavioral ecology, AL is often considered a mechanism by which abstract informational processes are achieved. However, AL also provides alternative explanations of behavioral phenomena up to the level of motivational organization over the lifetime (Timberlake 1993; Domjan 2005). Integrating the 2 approaches without forming hidden contradictions is essential for making accurate predictions.

In AL, cues are linked via temporal coincidence (Wasserman and Miller 1997). Coincidences between cues modify behavior through the association of responses (selected nonrandomly from the animal's repertoire; Timberlake 1993) with experienced outcomes (Dayan and Balleine 2002). The relative evaluation of cues takes place via feedback from the experience of the reward (Dayan and Balleine 2002). Experienced rewards control subsequent choices between behaviors, whereas the development of responses determines subsequent experienced rewards (Dayan and Balleine 2002; Berridge and Robinson 1998). Detailed overviews can be found in Niv et al. (2006), Domjan (2005), Dayan and Balleine (2002), Pearce and Bouton

(2001), Berridge and Robinson (2003), Wasserman and Miller (1997), Hollis (1997), and Timberlake (1993).

AL proposes that components of the learning process are combined in a multistep system with feedbacks rather than being selected between at a single decision point according to their informational quality or quantity (Figure 1). Cues are characterized by contingencies with other cues, rewards, and responses, not information content (Wasserman and Miller 1997). If big red seeds are more rewarding than small green seeds in AL, we say color and size predict or anticipate reward (Domjan 2005). When animals encounter stimuli associated with both anticipation and aversion, such as a big green seed, cues interact with one another via the same multistep process with feedbacks to achieve a modified response (see Figure 1). This is different from an information-based choice (IBC) approach, which assumes that the animal chooses the cue with highest informational content and responds to that cue alone.

IBC may be seen as operating at a higher (mathematizable) level of abstraction. Thus, "select the cue with better information" is an abstract rule, whereas "initiate response at the rewarded cue" is a detailed mechanistic rule. The mechanism can be subsumed under the abstraction (select better information by initiating foraging at the rewarded cue). Alternatively, select the cue with better information and initiate response at a rewarded cue may be mechanistic, with hidden conflicts: A cue associated with mate arrival may yield courtship rewards but poor information about partner fertility, whereas a cue informative about partner fertility may not facilitate anticipation of courtship. In practice, both views of the relationship between IBC and AL are adopted.

The relationship between AL and IBC is not straightforward. Here, I examine 2 sets of case studies. First, I look at parallel research programs on mating in quail. Second, I consider how
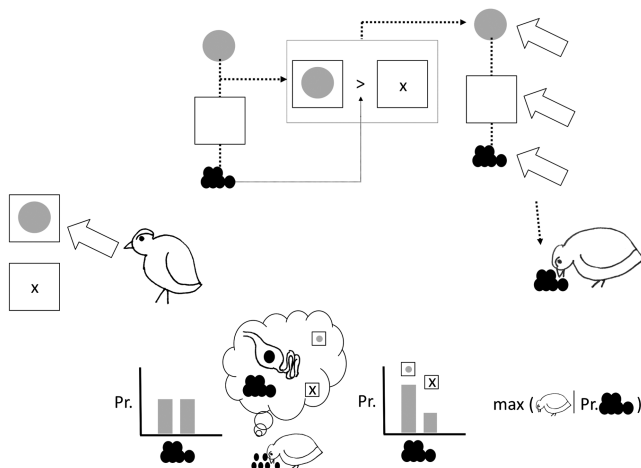
Figure 1

Two schema showing some differences between AL and IBC explanations of behavior. At left, a bird can forage for black oval pellets from behind 2 kinds of flaps. Gray circle flaps are rewarded, and x flaps are not. The bird learns to approach the rewarded flaps (large white arrow) and is then able to feed. Above, in AL, the gray circle is associated with the flap and the presence of food. These cues combine, or interact, during learning to jointly affect behavioral outcomes. After eating, feedback from the food reward leads to a relatively greater evaluation for the gray circle flap association. Subsequently, the bird can show an approach response to any of the elements of the higher valued association separately and in combination. The feeding response is then directed at the accessed food. Below, in IBC, the bird updates its probability distribution for access to food by gathering personal information from multiple sources, that is, visual cues, encounter rate, ingestive feedback, etc. The best information source (here, the design on the flap) is selected to adjust the probability distribution for access to food, and the bird then optimizes its foraging behavior given the expected food distribution, as shown by the information available in the environment. The AL mechanisms shown above may serve to clarify the selection process between information sources as shown in the IBC thought bubble below. However, AL also implies an explanation of the spatiotemporal distribution of behaviors (i.e., the 3 white approach arrows and the feeding response) different from optimization over expected probabilities, which in some cases leads to conflicting predictions.

AL concepts have been integrated into foraging studies of nectarivores. Finally, I suggest how behavioral ecologists could continue to engage productively with AL.

CASE STUDY: MATING IN JAPANESE QUAIL

IBC and AL have been used together to explain mate choice (Witte and Godin 2010). But the theories are also successful separately, as shown in parallel research programs on Japanese quail, *Coturnix japonica*.

When both male and female quail are signaled with a conditioned stimulus (CS) prior to the presentation of the partner of the opposite sex, copulatory efficiency, and fertility increase (Mahometa and Domjan 2005). Males who associate the location of a female with a CS outcompete naive males and copulate first (Gutiérrez and Domjan 1996). Males who see a demonstrator interact with a quail-shaped CS and then mate with a female quail (unconditioned stimulus [US]) spend more time at the CS at test (Köksal and Domjan 1998). Male quail respond to arbitrary CS's associated with females by approaching the CS, whereas female quail respond by squatting to a male quail CS (Gutiérrez and Domjan 1997). These results are consistent with the view that conditioned learning adaptively increases the effectiveness of interactions with the US, in this case a potential mate (Domjan et al. 2000; Domjan 2005).
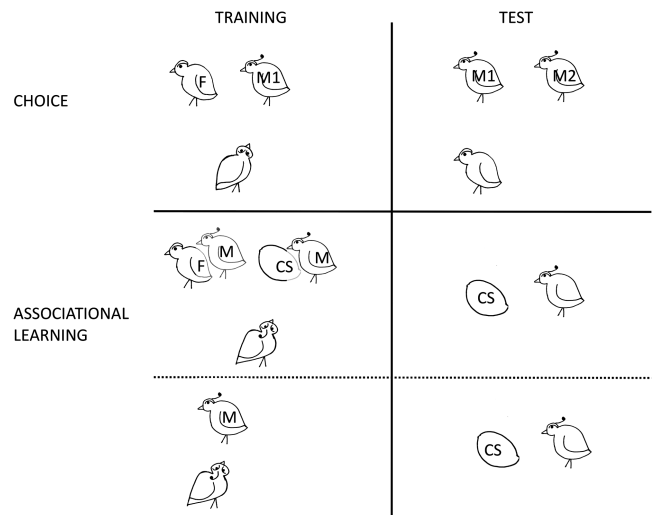

Figure 2

Top, a representation of a choice condition in Galef and While 1998; White and Galef 1999b. Bottom, 2 conditions in Experiment 1 of Köksal and Domjan (1998). In the choice experiment, during a single training session, the female subject sees a male M1 near a female F. At test, the female subject can spend time near the original male M1 or near another male M2. Preference is measured as the total time spent nearer each male. Females preferred M1. In the AL experiment, during training sessions, a male subject in the top condition observes a male M first mate with a female F and then mate with a quail-shaped CS (allowing mating behaviors). In the condition shown below, a different male subject observes only a male M. Both male subjects are tested by measuring the time spent near the CS, and responses are compared between conditions. Males spent more time near the CS in the top condition. To compare the experiments, note that 1) in the AL experiment, the lone male M in the lower condition is comparable to the second male M2 given as an option for response during the test in the choice experiment; 2) the AL experiment measures responses to a CS rather than the associated US (the opposite-sex conspecific); 3) the choice experiment makes within-subject comparisons, whereas the AL experiment makes between-subject comparisons.

In IBC experiments, Japanese quails' preferences for approaching opposite-sex quail correlate with mating choices (White and Galef 1999a), and females who mate with preferred males are more fertile (Persaud and Galef 2005). Female quail prefer to spend time near a male whom they have seen mating with or standing near another female (Galef and White 1998; White and Galef 1999b). Females also prefer the male in the location where the previously preferred male had been (White and Galef 1999b). Female quail preferred males with colored markings on their chests similar to markings on males they observed mating with another female (White and Galef 2000). Male quail preferred females whom they had not seen mate with another male, but a female and male standing together without mating did not affect the males' preferences (White and Galef 1999c).

The results are largely compatible. It is not clear how the results of Domjan et al. could be explained by choices between sources of information. However, the results of Galef and colleagues are consistent with AL, if male quail act as a US for females, and females act as US's for males, eliciting approach (appetitive) behavior, whereas same-sex individuals act as CS's for one another (see Westneat et al. 2000; Domjan 2005). For example, the observation of a male (US) with another female (CS) increased females' preferences for the male (Galef and While 1998; White and Galef 1999b). In a similar experiment, Köksal and Domjan (1998) found that a male quail demonstrator alone resulted in less responding by subject males to

the (previously not seen) female US at test than did a male demonstrator (CS) paired with both a female (US) and another CS (see Figure 2). In other choice experiments, females are CS's, paired with second CS's (CS2's), such as colored patches on males or locations.

AL has been described as the mechanism for obtaining information about mate quality (Westneat et al. 2000; Witte and Godin 2010). This is one possibility. Other possibilities suggested by this case study are that AL and IBC are parallel and equivalent or that AL explains all IBC results.

CASE STUDY: FORAGING IN NECTARIVORES

Many studies in behavioral ecology investigate how multimodal flower cues and nectar quality differences affect foraging decisions in nectarivores. Other studies come from an AL tradition (e.g., Cnaani et al. 2006; Arenas et al. 2007). Nectarivore foraging is thus useful for examining how to integrate the 2 perspectives.

Use of both paradigms together is often implicit. Baude et al. (2008) find that conspecifics can attract foraging bees to rewarded flower patches, a scenario which they introduce in terms of inadvertent social information, but then explain, in the discussion, in terms of associations between flower color and conspecific cues. The unstated assumption is that AL is the detailed mechanism by which the abstract explanation of IBC is achieved.

Illustrating the IBC perspective, Hill et al. (2001) state "Colour is a primary cue . . . used by foraging bees in an economical 'juggling' of the most pertinent information" (p. 730). In that study, they ask whether Italian honey bees, faithful to the color of the first rewarded flower they encounter, develop a color preference for yellow or blue flowers (easily distinguishable colors), and for white or blue flowers (hard to distinguish colors), when both have equal nectar rewards and whether they prefer the more rewarded color when rewards differ between hard to distinguish colors. Not surprisingly from an AL perspective, bees preferred the first color associated with reward when colors were easily distinguishable, but when colors were hard to distinguish, they discriminated only when one of the colors was more rewarded. The AL explanation would be that the flower color (CS) was associated with a US (nectar taste), and evaluative feedback from the reward led to an association with the response (approach and feed). However, when flower color was not salient to reward (rewards did not differ, and/or apparent colors did not differ), this association was not formed (Wasserman and Miller 1997). In contrast, the authors suggest that some flower color dimorphisms but not others constrain bees from optimizing nectar volume intake, depending on interflower distances (Hill et al. 2001). The AL explanation is simpler and is not the mechanism for the IBC interpretation.

Finally, in a recent paper, Bacon et al. (2011) ask how hummingbirds use current information about patch quality to modify expectations and update decisions about how often to visit patches. The introduction discusses hedonic value and incentive learning (terms from AL). However, their prediction that hummingbirds should use "more reliable" postingestive feedback rather than taste in adjusting patch visitation rates is not compatible with AL because 1) all cues had equal contingencies with reward and 2) taste and feedback are integrated (via "US devaluation"), not selected between, as the basis for behavior (Wasserman and Miller 1997; Dayan and Balleine 2002; Berridge and Robinson 2003).

Bacon et al. (2011) measure changes in volume of solution ingested (the behavioral response) at the first visit (feeding bout) to a single artificial flower under 2 conditions: a change from high to low sucrose intervals and a change from low to high sucrose intervals. Via AL, hummingbirds should associate tastes with ingestive rewards, which feedback to adjust responses (foraging rates). Learning about the 2 sucrose solutions would require feedback from multiple feeding bouts in each interval. The hummingbirds also need to learn that each sucrose concentration remains unchanging for intervals of 3 h in order to maintain optimal rates of feeding over these periods. The hummingbirds experienced only 4 transitions between intervals. Hummingbirds could show immediate adjustments in volume ingested at the first bout only after experiencing multiple (probably > 4) intervals. Consistent with these predictions, within-intervals adjustments in volume ingested did not reach optimality until after >5 feeding bouts. Between intervals, hummingbirds adjusted their rate of change in ingested volume faster for the second 2 transitions, compared with the first transition (Healy SD, personal communication), but without arriving at an immediate (first bout) adjustment.

The authors describe as "unexpected" the failure to immediately adjust volume ingested on any first bout, although this failure is predicted by AL. AL theory does not support their claim that "taste is not important in making decisions about meal sizes at least when foraging from fairly constant resources..." (p. 475). Rather, taste, as the cue that distinguishes between sucrose concentrations, is one component of the learning system that combines with other inputs to adjust foraging responses. It is likely that the hummingbirds needed more training to achieve the expected behavioral change.

CONCLUSION

I have concentrated on specific papers to show in some detail how AL could be most useful to IBC research. The 2 sets of papers on quail mating demonstrate that the 2 approaches explain similar behaviors in compatible ways. However, it is more obvious how to translate IBC experiments into AL terms than the reverse. This does not necessarily imply that AL is the mechanism filling in the abstractions of IBC—if this was the case, AL should not make alternative predictions to IBC. The nectarivore papers show how the theories diverge, with AL predicting and explaining results challenging for IBC. Nectarivore foraging may allow us to explicitly ask how much individuals choose between and how much they combine the cues/sources of information involved in directing foraging behavior. Experimental designs that allow explicit IBC-AL comparisons through the use of identical measurements of response would be welcome.

Incorporating theory from AL into behavioral ecology should be encouraged. Bacon et al. (2011) state " . . . detailed data about the amount and sorts of information animals require and prefer to use to make decisions may greatly improve the resolution with which we are able to model and interpret animal decision making . . . " (p. 476). I agree and propose that AL already provides much of that data. However, untested assumptions about how AL can be incorporated into IBC risk suboptimal experimental methods and hypotheses with unnecessarily low predictive power.

FUNDING

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