Research report

Socially acquired predator avoidance: Is it just classical conditioning?

Andrea S. Griffin *

School of Psychology, University of Newcastle, University Drive, Callaghan, NSW 2308, Australia

Abstract

Associative learning theories presume the existence of a general purpose learning process, the structure of which does not mirror the demands of any particular learning problem. In contrast, learning scientists working within an Evolutionary Biology tradition believe that learning processes have been shaped by ecological demands. One potential means of exploring how ecology may have modified properties of acquisition is to use associative learning theory as a framework within which to analyse a particular learning phenomenon. Recent work has used this approach to examine whether socially transmitted predator avoidance can be conceptualised as a classical conditioning process in which a novel predator stimulus acts as a conditioned stimulus (CS) and acquires control over an avoidance response after it has become associated with alarm signals of social companions, the unconditioned stimulus (US). I review here a series of studies examining the effect of CS/US presentation timing on the likelihood of acquisition. Results suggest that socially acquired predator avoidance may be less sensitive to forward relationships than traditional classical conditioning paradigms. I make the case that socially acquired predator avoidance is an exciting novel one-trial learning paradigm that could be studied along side fear conditioning. Comparisons between social and non-social learning of danger at both the behavioural and neural level may yield a better understanding of how ecology might shape properties and mechanisms of learning.
© 2008 Elsevier Inc. All rights reserved.

Keywords: Learning; Classical (Pavlovian) conditioning; Social learning; Ecological specialization; General process theory; Ecology; Predation; Backward conditioning

1. Classical conditioning: general process theory and adaptive specialization

In classical conditioning, also termed Pavlovian conditioning, animals acquire a response to a previously neutral stimulus (conditioned stimulus: CS; e.g. simple tone), if that stimulus predicts a biologically important event (unconditioned stimulus: US; e.g. food) [59]. The mechanism underpinning learning is considered to be the formation of an association between CS and US [60]. Over 100 years of behavioural research has lead to a good understanding of the parameters that affect the likelihood of acquisition. The primary impetus for this work has been the postulate that associative learning should follow one or a small number of laws valid across all species and all situations, a premise known as general process learning theory [62]. This postulate also forms the basis for intense efforts to build an all-inclusive mathematical model of learning that identifies the key environmental variables underpinning associative learning [29,42,54,60,67,76].

Yet it has long been recognised that learning should be adaptively specialised for the function it serves in nature [61]. Early work on adaptive specialization revealed that animals learn more readily about some stimuli than others [22,46]. Since then, preferential learning has been demonstrated in a wide range of taxa [26,43,51,65]. Recently, behavioural work has further revealed several instances in which the outcome of well-documented associative learning phenomena differs according to the nature of the stimuli involved [13,74]. Specialization may occur at various levels of the cascade of events that result in learning. For example, Gallistel and Gibbon [21] have proposed that while neural analyses may reveal phylogenetically shared mechanisms for storing and retrieving the values of variables involved in learning, a system's level analysis should lead to the discovery of circuits that are evolutionarily tailored to learn about particular categories of ecological stimuli.

One potentially fruitful approach to understanding how ecological demands may have fine-tuned mechanisms of learning is to use associative learning theory as a framework within

* Tel.: +61 2 4921 7161; fax: +61 2 4921 6980.
 E-mail address: andrea.griffin@newcastle.edu.au.

which to examine the properties of a particular learning phenomenon [63]. Such an analysis may reveal that although two instances of learning are mediated by the same mechanism (e.g. classical conditioning), they may be specialised in so far that some properties of learning, such as the speed of learning, or the duration of retention, have been evolutionarily modified to learn relationships between particular kinds of ecological stimuli. For instance, in taste aversion learning animals learn to avoid a novel food in one trial even if gastro-intestinal illness is experienced hours after the food is consumed [12].

2. Social learning

Social learning refers to instances of learning in which the behaviour of a 'demonstrator', or its by-products (e.g. scent marks), modify the subsequent behaviour of an 'observer'. Several varieties of social learning have been identified according to the role of the demonstrator [19,34]. For example, social companions may alter the probability of an observer interacting with a given stimulus (e.g. a stick), a phenomenon referred to as local enhancement [73]. Alternatively, they may alter the probability of an observer interacting with a given class of stimuli (e.g. sticks), an effect known as stimulus enhancement [66]. The focus of the present review will be on instances of social learning in which animals acquire a response to an initially neutral stimulus (e.g. a novel food), after they have experienced it together with the behaviour of a social companion (e.g. a companion eating the food). This form of social learning is referred to as socially transmitted recognition learning [69] or observational conditioning [9].

There have been several attempts to analyse social learning phenomena within an associative learning framework [34,63]. Work on socially enhanced food preferences in rats has been particularly revealing. After a Norway rat has detected a food odour on a recently fed demonstrator rat's breath, it exhibits an enhanced preference for that food. Such learning can be conceptualised as a classical conditioning process in which the food odour acts a CS and the demonstrator rat as a US. To explore the boundaries of this heuristic, Galef and Durlach [20] examined whether three well-documented phenomena – overshadowing, blocking and latent inhibition – known to interfere with classical conditioning similarly interfered with social transmission of food preferences.

First, they found no evidence that one flavour overshadowed the acquisition of a preference for another flavour if both flavours were experienced together during social conditioning. Observer rats given the opportunity to interact with a demonstrator fed a diet containing two flavours (CS1 and CS2), nevertheless showed a subsequent robust acquired preference for CS1. In contrast, when social interaction with a demonstrator fed a compound diet was followed by LiCl induced gastro-intestinal illness, CS2 overshadowed a learned aversion to CS1, demonstrating that the absence of overshadowing in socially acquired food preferences was not related to the nature of the overshadowing stimulus. Similarly, exposing each observer to a demonstrator fed a single flavoured diet (CS2) prior to exposing

it to a demonstrator fed a dual flavoured diet (CS1 and CS2), failed to block the acquisition of a preference for CS1.

Finally, prior habituation to a food also failed to interfere with the subsequent acquisition of a preference for that food via social learning. Although rats pre-exposed to a food before social training showed a lower preference for that food after social training, comparisons with control groups revealed that this effect was due to a tendency to shift to a novel food after consumption of a familiar food rather than any effect of food pre-exposure on the strength of social learning. The failure to find three effects well known to interfere with classical conditioning strongly suggests that social learning phenomena may exhibit different properties to those of classical conditioning.

Here, I describe work involving another attempt to analyse an instance of social learning within an associative learning framework, namely social learning of predator avoidance. My objective is to review the behavioural evidence that some properties of associative learning may have been modified to fulfil the needs of learning socially about predators. In doing so, I present some recent work examining the effects of CS/US presentation timing on learning. Temporal influences on likelihood of acquisition have been largely overlooked in comparisons of social learning and associative learning. Second, I make the case that social learning of predator avoidance could be an exciting, novel one-trial learning behavioural paradigm for exploring neural mechanisms of learning and memory. While several behavioural paradigms including olfactory learning [6], imprinting [4], taste aversion learning [77], fear conditioning [53], passive avoidance learning [23] and eye blink conditioning [36], are already the focus of intense study, socially acquired predator avoidance differs in so far that it is triggered by social communication signals. Many animal signals are now known to encode for events in the external perceptual world of the animal [7,15]. Socially acquired predator avoidance would therefore be the first paradigm to explore learning triggered by cognitive social stimuli, rather than hormonally mediated social behaviours, such as sexual interactions [6].

3. Socially acquired predator avoidance

Socially acquired predator avoidance is a taxonomically widespread phenomenon. It has been found in fish, birds and both eutherian and marsupial mammals. The pattern of acquisition is similar across groups. Although animals show initially little or no avoidance of a novel predator stimulus, once it has been presented together with the alarm signals of social companions, it evokes a fear response [24].

Efforts to understand whether socially acquired predator avoidance engages classical conditioning in which predator stimuli act as a CS and social alarm stimuli as a US have identified some similarities between the two learning phenomena. For example, in rhesus monkeys (*Macaca mulatta*) the level of fear exhibited by the observer during training is positively correlated with that of the demonstrator [52]. In addition, the acquired response measured after training is also positively correlated with the level of fear exhibited by the demonstrator during training [52]. These findings are consistent with the observation that

the strength of a classically conditioned response both during, and after, training tends to increase with that of the US and have lead to the view that socially acquired predator avoidance is mediated by Pavlovian conditioning [33,52,69].

However, a review of the properties of socially acquired predator avoidance reveals several differences from classical conditioning [24]. First, no relationships between demonstrator alarm levels and observer alarm levels either during, or after training, have been found in birds, contrasting with results obtained in monkeys [75]. Second, as has been found for social learning of food preferences, prior exposure to predator stimuli does not appear to interfere with subsequent acquisition of an avoidance response to that stimulus, suggesting that latent inhibition is absent from social learning about predators [10,52]. These differences raise the possibility that the similarities between socially acquired predator avoidance and classical conditioning may be more limited than once thought.

The effects of CS/US presentation timing on likelihood of acquisition is one property of classical conditioning that has been largely overlooked in comparisons with social learning. According to contemporary views on associative learning, relationships between two events are learned because the occurrence of one predicts that of the other [59]. A direct consequence of this view is that animals should learn to respond to stimuli that precede (forward conditioning), rather than follow (backward conditioning), a biologically important event. Although a small number of theoretical models propose that animals can learn backward relationships between USs and CSs [21,48,50] the vast majority predict that backward presentations of CS and US result in either no learning or inhibitory learning [29,42,54,60,71,76]. This view is supported by evidence that forward, but not backward, presentations of CS and US causes neural responsiveness to the CS presented later on its own to increase [32].

Functional considerations generate the prediction that, contrary to classical conditioning involving arbitrary stimuli as CSs (e.g. a light) and pain stimuli as USs (e.g. foot shock), social learning about predators should not be sensitive to forward relationships between CS and US. Indeed, in the wild, observers may detect the alarm signals of social companions either before, or after, they detect a predator stimulus. Both kinds of experience should trigger a robust acquired avoidance response to the predator stimulus. In an attempt to test this hypothesis, I conducted a series of studies designed to examine the effect of CS–US timing on socially acquired predator avoidance. Experiments were conducted in two separate avian systems, Carib grackles (*Quiscalus lugubris*) and Indian mynahs (*Acridotheres tristis*).

3.1. Socially acquired predator avoidance in Carib grackles

Carib grackles are common throughout the Carribean Lesser Antilles. They live in close association with humans and move around in small mobile flocks. Free-living grackles give broadband pulsatile alarm calls associated with the presence of a range of predators, such as mongooses (*Herpestes auropunctatus*), cats (*Felis catus*), dogs (*Canis familiaris*), vervet monkeys (*Chlorocebus aethiops*) and humans [28,35] (for a sonogram

of grackle alarm vocalisations, see [28]). Opportunistic observations revealed that wild-caught, individually held, captive grackles that are placed in acoustic, but not visual contact, of conspecifics give low levels of these vocalisations in the absence of any apparent disturbance. Initial work showed that baseline call rates decrease in response to a model predator (dog) presented inside the cage, but not outside the cage, a finding which is consistent with abundant evidence that individuals of many species modulate the rate at which they alarm call as a function of distance to predator [27]. For example, golden marmots (*Marmotta caudata*) decrease alarm call rates as a human approaches, then suppress alarm calling completely and run to their burrow when the human is very close [5]. In birds, individuals under immediate risk of a predator vocalise relatively little [31].

To study socially acquired predator avoidance, Griffin and Galef [27] used as a CS a novel predator stimulus, which consisted of a model bird the size and shape of a common urban pigeon with a 0.15 m long tail and painted black and yellow. This stimulus, which shared no resemblance with a natural predator of grackles, was selected to avoid the possibility that previous familiarity might interfere with subsequent learning. As a US, Griffin and Galef [27] used a playback of an alarm call sequence. The authors elected to use an acoustic stimulus rather than a live demonstrator because it allowed the careful control of US onset and offset relative to CS presentation. After experimentally evoking and recording the alarm calls of two wild-caught, individually held, captive grackles, the authors simulated the effects of multiple birds calling during learning experiments by playing back a series of continuous alarm calls through one loudspeaker and another series through a second loudspeaker placed at a certain distance (for more details, see [27]).

Each subject first received a pre-test during which its initial response to the model pigeon presented inside the subject's cage was quantified. Pre-tests were followed by a training trial in which subjects received model pigeon and the alarm call playback in either a forward, or a backward or unpaired presentation order (see below). After training, each subject received a posttest in which its response to the model pigeon was measured once again.

During training individuals in a forward conditioning treatment were presented with a 160-s presentation of the model pigeon that began 20 s before the onset of a 180-s alarm call playback and ended 40 s before the end of the acoustic stimulus. Birds in a backward treatment also received a 160-s pigeon presentation, but it began 20 s after the onset of a 180-s acoustic playback and ended simultaneously with the acoustic playback. Finally, grackles in an unpaired control group received both the 160-s pigeon presentation and the 180-s playback, but these two events were separated by a minimum of 40 min and a maximum of 2 h, and their order of presentation was randomised across subjects. Post-training comparisons between experimental treatments and the unpaired control group allowed for effects of associative learning to be isolated from those due to other factors, such as repeated exposure to CS and/or US.

To quantify responses to the pigeon mount during pre- and post-tests, Griffin and Galef [27] measured changes in alarm call rate from a pre-stimulus baseline time period. Given ear-
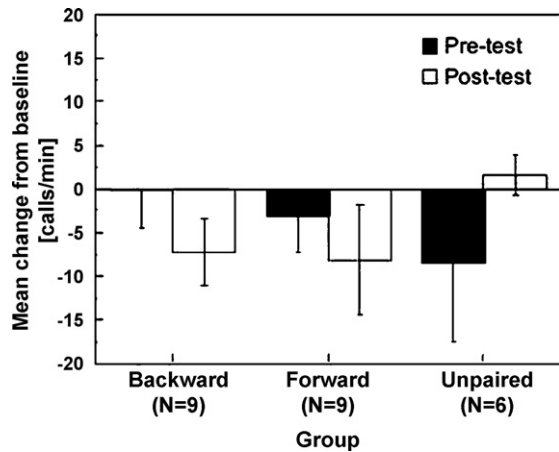
Fig. 1. Alarm call responses of Carib grackles evoked by a model pigeon both before (pre-test) and after (post-test) training. The mean (±S.E.M.) change from pre-stimulus baseline was averaged over a 1-min presentation period and three 1-min post-presentation time intervals for each group and each test. An analysis of variance revealed a significant group × test interaction ($F(2, 21) = 4.36$, $p = 0.026$). Planned pair-wise comparisons revealed that backward and forward treatments suppressed alarm call rate significantly more after training relative to the unpaired treatment. For more details see text and Ref. [27]. Copyright Elsevier (2005). Reprinted with permission.

lier evidence that grackles suppress baseline levels of calling in response to a predator presented inside their cage, the authors anticipated that acquisition of an alarm response to the novel predator stimulus would be reflected by a greater suppression of alarm calls after training relative to before training.

Results revealed that grackles that had received paired presentations of the pigeon and the alarm call sequence decreased alarm call rate more after training than before training in response to the model pigeon (Fig. 1). Response acquisition was not affected by the order in which the two stimuli were presented during training (Fig. 1). Grackles that had received the pigeon first (forward treatment) showed a similar acquired response to those that had received the social alarm stimulus first (backward treatment). In contrast, birds that had received unpaired presentations of pigeon and social alarm stimulus suppressed alarm calls less after training than before training in response to the model pigeon (Fig. 1).

Work on social conditioning in grackles hence revealed that acquisition of a response to a novel predator via social learning is not dependent upon a forward relationship between novel stimulus (CS) and social alarm signal (US). This finding is consistent with the functional prediction that in nature, individuals are just as likely to detect a predator stimulus after they have detected the alarm signals of social companions, as before. In contrast, it is inconsistent with the majority of learning models that predict that backward presentations of CS and US lead to no learning or inhibitory learning [29,42,54,60,68,71,76]. It is also inconsistent with a learning model that proposes that backward associations are learned, but that learning is not detectable using conventional anticipatory conditioning protocols [48,50]. These findings raise the possibility that temporal flexibility may be a property of learning socially about dangers. Indeed, backward occurrences of predator and fear are unlikely to be common in

individual interactions between predator and prey because prey would have to survive a surprise attack by a predator for fear or pain to be experienced before the predator stimulus.

3.2. Socially acquired predator avoidance in Indian mynahs

According to some definitions, but not others, training schedules in which a US is presented before the CS, but nevertheless overlaps with it, constitute a backward conditioning protocol. In work with Carib grackles, Griffin and Galef [27] selected this design for two reasons; first, it most closely resembled field observations that despite temporal flexibility between the appearance of a predator and production of alarm calls by groups of potential prey these events tend to overlap [3,5,30,39,78,79]; second, because it was consistent with definitions that classify as backward all designs in which US onset precedes CS onset. Nevertheless, given the discrepancy in definitions of what does, and does not constitute backward conditioning, I elected to conduct a second series of studies to examine whether social learning of predator avoidance could be obtained using a design in which an alarm signal (US) was presented before, and did not overlap with, a novel predator stimulus (CS). These experiments were conducted on Indian mynahs.

The Indian mynah was introduced to Australia in the mid-1800s. Since then, it has rapidly invaded large areas of the eastern coast where it competes with native species for breeding hollows, such that it is now the target of several pest control programs [55]. Just like Carib grackles, Indian mynahs live in close association with humans, are highly social and live in environments containing both terrestrial and aerial predators, even though the range of ground predators of Carib grackles is greater (e.g. includes vervet monkeys and mongooses). Accordingly, just like Carib grackles, Indian mynahs alarm vocalise when disturbed by predators such as cats, raptors or humans, making them an excellent system to study properties of socially acquired predator avoidance [57]. However, contrary to Carib grackles, which exhibit one characteristic high amplitude broad band vocalisation in response to predation threat, Indian mynahs give a broad array of alarm vocalisations ranging from low amplitude narrow frequency range peeps and medium amplitude broadband squawks produced by free-flying birds, to high amplitude distress calls produced by individuals when they are caught by a predator, or handled by a human (Griffin unpublished data [57]). Consequently, a first set of experiments aimed to identify an alarm vocalisation that triggered the acquisition of a response to a novel predator stimulus and to explore the nature of the acquired response [25]. Mynahs were wild-caught for the purposes of the experiments [25].

I used a taxidermic mount of a Reeve's pheasant (*Syrmaticus reevesii*) as a CS. This species is in no way similar to any predator of Indian mynahs. Furthermore, mynahs are highly unlikely to have encountered a Reeve's pheasant during their lifetime since this species is native to central China and only exists in captivity in Australia where it is bred by a few bird fanciers. As a US, I used recordings of Indian mynah distress calls, which were collected while birds were being handled for the purposes of

placing identification leg bands (for a sonogram, see [25]). Raw recordings of eight mynahs were edited to create eight distinct playback stimuli. Mean distress call rate was 6.7 ($\pm$1.2 S.E.M.) calls per min (for more details, see [25]). Distress calls convey high levels of alarm in the caller. As levels of acquisition in observers appear to be positively correlated with levels of alarm displayed by demonstrators during training [52,70], I anticipated that these calls would trigger robust avoidance learning in receivers.

Applying the same experimental design as in Griffin and Galef's [25,27] studies on Carib grackles, each mynah underwent a pre-test, followed by one training trial and a post-test. During training, subjects received either paired (synchronous) or unpaired (separated by 0.5–2 h) exposure to a 120-s pheasant presentation and a 120-s distress call sequence. Opportunistic observations had suggested that Indian mynahs increase locomotion and produce free-flight, broad-band alarm calls that are acoustically distinct from distress calls, in response to predatory threats [25,57]. Consequently, I anticipated that associative learning would be reflected by increases in these behaviours. In addition, I anticipated a change in the rate of head saccades, which facilitate distance judgments and/or visual exploration of objects in birds [1,11,41]. Saccades were quantified by counting any detectable movement of the head from experimental video recordings played back at low speed [25].

Unexpectedly, paired presentations of pheasant and distress calls produced a clear change in the rate at which the mynahs moved their head in response to the model pheasant, but no changes in locomotion or alarm call rates. Birds that had received paired presentations of pheasant and distress calls increased significantly the rate at which they moved their heads in response to the pheasant after training relative to before training, while birds that had received pheasant and distress calls separately decreased head saccade rates in response to pheasant after training relative to before training (Fig. 2).

It is well known that animals tend to go quiet, decrease locomotion or changes in locomotion, and increase vigilance in response to raptorial threats [2,16–18]. Responses acquired as a consequence of pairing pheasant with distress calls could
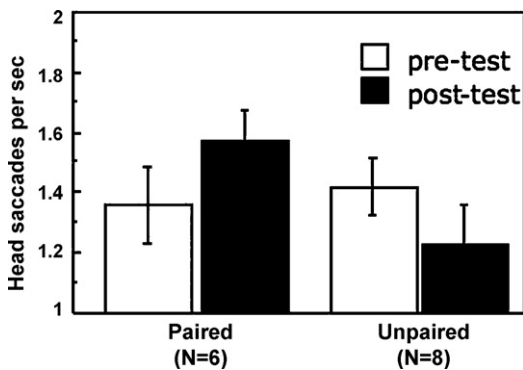

Fig. 3. Head movement responses of Indian mynahs evoked by a raptor mount, a pheasant mount and a blank control trial. The mean ($\pm$S.E.M., $N = 18$) head saccade rate was calculated for a 30-s time interval after stimulus onset for each stimulus. An analysis of variance revealed a significant main effect of stimulus ($F(1, 12) = 8.44$, $p = 0.001$). Planned pair-wise comparisons revealed that mynahs increased head saccade rate significantly more in response to both raptor and novel stimulus than to the blank control trial *$p < 0.05$; **$p < 0.001$. For more details see text and Ref. [25]. This figure was published in [27]. Copyright Elsevier (2005).

hence reflect an antipredator response specific to raptors. However, there is also evidence that head saccades can reflect efforts to extract more information about a stimulus, either by placing the stimulus on different parts of the retina or on different eyes, or by generating motion parallax or two sequential views of the same object to facilitate distance judgements [1,11,37,38,44,47,49,65]. In this case, acquired responses could reflect a visual exploratory response evoked by any stimulus of interest, in particular a novel one.

In order to understand the nature of the acquired response further, I presented a new sample of mynahs with a raptor mount, a novel stimulus (pheasant), and a blank control trial in which no stimulus appeared [25]. Results revealed that Indian mynahs increase head saccade rate in response to both a perched raptor and a novel stimulus (Fig. 3). However, they show an increase in flight rate and alarm call rate that is specific to the raptorial stimulus, suggesting that responses acquired as a consequence of pairing pheasant with distress calls most closely resembled a visual exploratory response rather then a response specifically evoked by a raptor [25].

Although this finding was unexpected, it might be attributable to the fact that distress calls are produced primarily by immature individuals. If juveniles are vulnerable to predation threats to which adults are no longer exposed, then it might be advantageous to pay more attention to a stimulus that has been experienced together with distress calls, but not to develop a full-blown antipredator response to it. This possibility is discussed in more detail elsewhere [25].

Having established that distress calls were an effective US for triggering social learning, work focused on examining the effect of CS/US timing on socially acquired predator avoidance in this avian system. Specifically, I aimed to address the question of whether a backward design in which the social alarm signal was presented before, but did not overlap with, the novel predator nevertheless triggered response acquisition.

Fig. 2. Head movement responses of Indian mynahs evoked by a pheasant mount both before (pre-test) and after (post-test) training. The mean ($\pm$S.E.M.) head saccade rate was calculated for a 30-s time interval after stimulus onset for each group and each test. An analysis of variance revealed a significant group $\times$ test interaction ($F(1, 12) = 7.92$ $p = 0.016$). For more details see text and Ref. [25]. Copyright Elsevier (2008). Reprinted with permission.
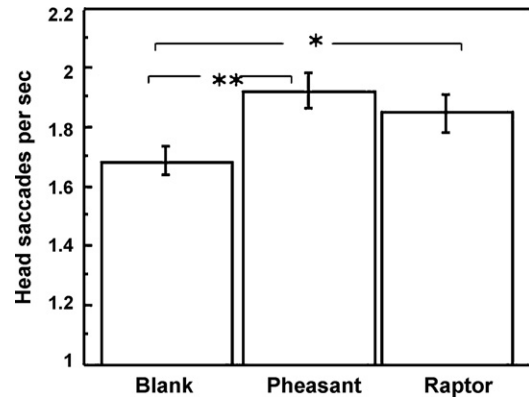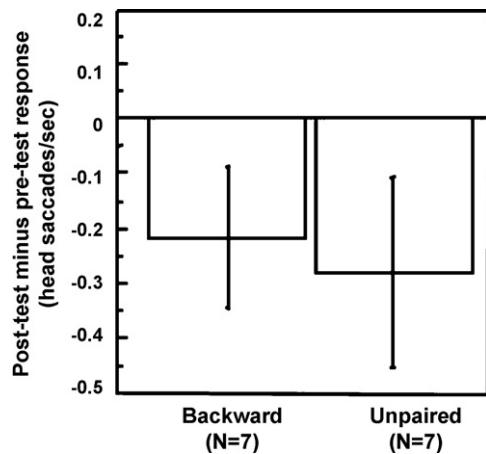
Fig. 4. Head movement responses of Indian mynahs evoked by a pheasant mount. The mean (±S.E.M.) difference between pre- and post-test was calculated for a 15-s time interval after stimulus onset for each treatment. For more details see text.

To this aim, I quantified the initial head saccade response of a new sample of Indian mynahs to the pheasant mount (pre-test). For subsequent training, subjects allocated to a backward treatment received a 120-s distress call playback followed immediately by a 110-s pheasant presentation, while mynahs allocated to an unpaired control group also received both stimuli, but temporally separated by 0.5–1.5 h and in an order that was randomised across subjects. Each subject's head saccade response to the pheasant was again measured after training (post-test). Results revealed no differential change in head saccade rate between birds in the backward treatment and birds in the unpaired treatment (Fig. 4), suggesting that a design in which social stimuli precede, but do not overlap with, novel predator does not inculcate an acquired response to the predator stimulus.

4. General discussion

Socially acquired predator avoidance is a learning paradigm in which animals acquire an avoidance response towards a novel predator stimulus that initially evokes a low or no response, after it has been experienced together with a social alarm signal. The work reviewed above aimed to explore the long held view that such learning engages a classical conditioning mechanism in which the predator stimulus acts as a CS and the social alarm signal as a US [34,52,69]. Specifically, I aimed to explore the effects of predator stimulus and alarm signal presentation timing on acquisition, a factor well known to influence the likelihood of a classically conditioned response. It is a widely held view that the function of classical conditioning is to learn about causal relationships [63]. In the physical world, causes most often precede their consequences, so acquiring a response to an event that precedes a biologically significant stimulus allows for an adaptive adjustment of behaviour in anticipation of that stimulus. In contrast, in the social world, detection of predators is just as likely to precede, as it is to follow, detection of social alarm calls. Based on these functional considerations, I reasoned that socially acquired predator avoidance should be temporally more flexible than conditioning paradigms involving arbitrary stimuli

(e.g. light) as predictors of biologically important events (e.g. foot shock) [24].

Overall, findings suggest that socially acquired predator avoidance is temporally flexible in so far as an avoidance response is acquired even if alarm signals are detected before the predator stimulus. As long as alarm signals and predator stimulus overlap to some, yet unknown, extent, learning takes place. This degree of temporal flexibility is consistent with observations in the wild showing that animals produce alarm calls when a predator is sighted and continue to call while it is present [3,5,30,39,78,79]. Consequently, observers are most likely to detect the caller's vocalisations first and then, alarm calls and predator simultaneously, rather than the predator on its own. Such temporal flexibility seems to be absent from single-trial appetitive associative learning; indeed, an electrophysiological study revealed that neurons that increased responsiveness to a CS odour after training in which CS onset preceded US onset, failed to change their firing rate after a training session in which the CS began after US onset, and completely overlapped with it [32]. Such differences suggest that social learning of predators might rely upon slightly different cellular or intracellular neural mechanisms. On the other hand, the finding that CS–US overlap is necessary for social learning to occur implies that according to authors who define backward conditioning as a technique in which US and CS do not overlap, socially acquired predator avoidance might be as sensitive to backward procedures as typical classical conditioning paradigms.

5. General conclusions

I argue that socially acquired predator avoidance presents an exciting and novel opportunity to explore mechanisms of learning and memory. By considering the function such learning plays in nature, one can formulate testable hypotheses regarding the way in which properties of acquisition may be evolutionarily tailored to solve this particular ecological problem, an approach I have illustrated above. Socially acquired predator avoidance learning is also a one-trial learning phenomenon, a feature that makes it appropriate for studying the temporal sequence of biochemical events that immediately follow learning. Social learning of predator avoidance would differ from all current conventional learning paradigms in that it would be the first to investigate a social acquisition process. Both behavioural and neural aspects of social learning of danger could be studied alongside behavioural and neural aspects of asocial learning of danger (i.e. fear conditioning) in order to understand whether these learning phenomena rely upon the same behavioural, cellular, and sub-cellular mechanisms. The integration of social and asocial learning of danger would parallel a recent attempt to compare taste aversion learning, an individual learning phenomenon, with socially acquired food preferences, in order to determine whether social and asocial learning of olfactory and gustatory stimuli engage the same neural structure, namely the amygdala [77]. The proposal that socially acquired predator avoidance should be used as a model system for studying mechanisms of learning and memory is strengthened by calls from other authors that there is a need to

broaden the range of current conventional learning paradigms to include those that involve learning about ecological, rather than arbitrary, stimuli, and those that involve learning about compound, rather than elemental, cues [13,74]. In both cases, there is evidence that laws of learning that have been exhaustively explored using arbitrary and elemental cues may not apply.

Birds are a particularly appropriate taxon for studying mechanisms of social learning. First, there is abundant evidence from both behavioural and ecological work that social companions are an important source of environmental information in a broad range of avian species. In fact, all systems in which tests of social learning have been attempted have reported positive results, contrary to findings from studies of social learning in mammals [40]. Second, a huge interest in social learning over the last three decades has generated a large range of well-studied social learning paradigms that can be of interest to learning researchers. Third, there is increasing awareness that birds show a level of behavioural sophistication that rivals that of mammals [8,14,15,45,56,64,72]. Underpinning such behaviour is the avian telencephalon, now widely recognised to be of similar embryonic origin to the mammalian neocortex and to play a similar role in higher cognitive tasks [58]. Finally, several powerful modern tools for identifying neuronal activity are now commonly used in avian brains, including early gene expression and electrophysiology, all of which could be incorporated into studies of learning and memory in this taxonomic group.

Conflict of interest

The material contained in the manuscript does not raise any conflict of interest.

Acknowledgements

References

[1] R.J. Andrew, Use of head position by birds to determine mode of analysis of what is seen, Acta Zool. Sin. 52 (2006) 388–391.

[2] J. Archer, Behavioural aspects of fear, in: W. Sluckin (Ed.), Fear in Animals and Man, Van Nostrand Reinhold Company, New York, 1979, pp. 56–85.

[3] M.C. Baker, A.M. Becker, Mobbing calls of black-capped Chickadees: effects of urgency on call production, Wilson Bull. 114 (2002) 510–516.

[4] P. Bateson, Models of memory: the case of imprinting, in: J. Bolhuis (Ed.), Brain, Perception and Memory: Advances in Cognitive Neuroscience, Oxford University Press, New York, 2000, pp. 267–278.

[5] D.T. Blumstein, Golden-marmot alarm calls. I. The production of situationally specific vocalisations, Ethology 100 (1995) 113–125.

[6] P.A. Brennan, E.B. Keverne, Neural mechanisms of olfactory recognition memory, in: J. Bolhuis (Ed.), Brain, Perception and Memory: Advances in Cognitive Neuroscience, Oxford University Press, New York, 2000, pp. 93–112.

[7] D.L. Cheney, R.M. Seyfarth, How Monkeys See the World, University of Chicago Press, Chicago, 1990.

[8] N.S. Clayton, A. Dickinson, Episodic-like memory during cache recovery by scrub jays, Nature 395 (1998) 272–274.

[9] M. Cook, S. Mineka, B. Wolkenstein, K. Laitsch, Observational conditioning of snake fear in unrelated rhesus monkeys, J. Abnorm. Psychol. 94 (1985) 591–610.

[10] E. Curio, U. Ernst, W. Vieth, The adaptive significance of avian mobbing. II. Cultural transmission of enemy recognition in blackbirds: effectiveness and some constraints, Z. Tierpsychol. 48 (1978) 184–202.

[11] M.S. Dawkins, What are birds looking at? Head movements and eye use in chickens, Anim. Behav. 63 (2002) 991–998.

[12] M. Domjan, Ingestional aversion learning: unique and general processes, Adv. Stud. Behav. 11 (1980) 275–336.

[13] M. Domjan, B. Cusato, M. Krause, Learning with arbitrary versus ecological conditioned stimuli: evidence from sexual conditioning, Psychon. Bull. Rev. 11 (2004) 232–246.

[14] N.J. Emery, N.S. Clayton, The mentality of crows: convergent evolution of intelligence in corvids and apes, Science 306 (2004) 1903–1907.

[15] C.S. Evans, Referential signals, Perspect. Ethol. 12 (1997) 99–143.

[16] C.S. Evans, J.M. Macedonia, P. Marler, Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerial predators, Anim. Behav. 46 (1993) 1–11.

[17] M.S. Fanselow, Neural organization of the defensive behavior system responsible for fear, Psychon. Bull. Rev. 1 (1994) 429–438.

[18] J.C. Fentress, Interrupted ongoing behaviour in two species of vole (*Microtus agrestis* and *Clethrionomys britannicus*). 1. Response as a function of preceding activity and the context of an apparently irrelevant motor pattern, Anim. Behav. 16 (1968) 135–153.

[19] B.G. Galef Jr., Imitation in animals: history, definition, and interpretation of data from the psychological laboratory, in: T.R. Zentall, B.G. Galef Jr. (Eds.), Social Learning: Psychological and Biological Perspectives, Lawrence Erlbaum Associates, Hillsdale, New Jersey, 1988, pp. 3–28.

[20] B.G. Galef Jr., P.J. Durlach, Absence of blocking, overshadowing, and latent inhibition in social enhancement of food preferences, Anim. Learn. Behav. 21 (1993) 214–220.

[21] C.R. Gallistel, J. Gibbon, Computational versus associative models of simple conditioning, Curr. Dir. Psychol. Sci. 10 (2001) 146–150.

[22] J. Garcia, R.A. Koelling, Relation of cue to consequence in avoidance learning, Psychon. Sci. 4 (1966) 123–124.

[23] M.E. Gibbs, R.J. Summers, Role of adrenoceptor subtypes in memory consolidation, Prog. Neurobiol. 67 (2002) 345–391.

[24] A.S. Griffin, Social learning about predators: a review and prospectus, Learn. Behav. 32 (2004) 131–140.

[25] A.S. Griffin, Social learning in Indian mynahs (*Acridotheres tristis*): the role of distress calls, Anim. Behav. 75 (2008) 79–89.

[26] A.S. Griffin, C.S. Evans, D.T. Blumstein, Learning specificity in acquired predator recognition, Anim. Behav. 62 (2001) 577–589.

[27] A.S. Griffin, B.G. Galef Jr., Social learning about predators: does timing matter? Anim. Behav. 69 (2005) 669–678.

[28] A.S. Griffin, R.S. Savani, K. Hausmanis, L. Lefebvre, Mixed species aggregations in birds: zenaida doves, *Zenaida aurita*, respond to the alarm calls of Carib grackles, *Quiscalus lugubris*, Anim. Behav. 70 (2005) 507–515.

[29] S. Grossberg, A neural network architecture for Pavlovian conditioning: reinforcement, attention, forgetting, timing, in: M.L. Commons, S. Grossberg, J.E.R. Staddon (Eds.), Neural Network Models of Conditioning and Action, Lawrence Erlbaum Associates, Hillsdale, New Jersey, 1991, pp. 69–122.

[30] S. Gursky, Predation experiments on infant spectral tarsiers (*Tarsius spectrum*), Folia Primatol. 74 (2003) 272–284.

[31] M. Gyger, P. Marler, R. Pickert, Semantics of an avian alarm call system: the male domestic fowl, *Gallus domesticus*, Behaviour 102 (1987) 15–40.

[32] M. Hammer, An identified neuron mediates the unconditioned stimuli in associative olfactory learning in honeybees, Nature 365 (1993) 59–63.

[33] C.M. Heyes, Imitation, culture and cognition, Anim. Behav. 46 (1993) 999–1010.

[34] C.M. Heyes, Social learning in animals: categories and mechanisms, Biol. Rev. 69 (1994) 207–231.

[35] A. Jaramillo, P. Burke, New World Blackbirds: The Icterids, Princeton University Press, Princeton, New Jersey, 1999.

[36] D.A.T. King, R.F. Thompson, Skill learning: the role of the cerebellum, in: J. Bolhuis (Ed.), Brain, Perception and Memory: Advances in Cognitive Neuroscience, Oxford University Press, New York, 2000, pp. 215–231.

[37] M.F. Land, The role of head movements in the search and capture strategy of a tern, J. Comp. Physiol. A 184 (1999) 265–272.

[38] M.F. Land, Motion and vision: why animals move their eyes, J. Comp. Physiol. A 185 (1999) 341–352.

[39] A.J. Leavesley, R.D. Magrath, Communicating about danger: urgency alarm calling in a bird, Anim. Behav. 70 (2005) 365–373.

[40] L. Lefebvre, J. Bouchard, Social learning about food in birds, in: D. Fragaszy, S. Perry (Eds.), The Biology of Traditions, Cambridge University Press, Cambridge/New York, 2003, pp. 94–126.

[41] S.L. Lima, P.A. Bednekoff, Back to the basics of antipredatory vigilance: can nonvigilant animals detect attack? Anim. Behav. 58 (1999) 537–543.

[42] N.J. Mackintosh, A theory of attention: variants in the associability of stimuli with reinforcements, Psychol. Rev. 82 (1975) 276–298.

[43] A.E. Magurran, Acquired recognition of predator odour in the European minnow (*Phoxinus phoxinus*), Ethology 82 (1989) 216–223.

[44] P.E. Maldonado, H. Maturana, F. Varela, Frontal and lateral visual system in birds, Brain. Behav. Evol. 32 (1988) 57–62.

[45] P. Marler, Bird song and speech development: could there be parallels? Am. Sci. 58 (1970) 669–673.

[46] P. Marler, S. Peters, Selective vocal learning in a sparrow, Science 198 (1977) 519–521.

[47] C. Martinoya, S. Rivaud, S. Bloch, Comparing frontal and lateral viewing in the pigeon. II. Velocity thresholds for movement discrimination, Behav. Brain Res. 8 (1983) 375–385.

[48] L.D. Matzel, F.P. Held, R.R. Miller, Information and expression of simultaneous and backward associations: implications for contiguity theory, Learn. Motiv. 19 (1988) 317–344.

[49] R. McKenzie, R.J. Andrew, R.B. Jones, Lateralization in chicks and hens: new evidence for control of response by the right eye system, Neuropsychologia 36 (1998) 51–58.

[50] R.R. Miller, R.C. Barnett, The role of time in elementary associations, Curr. Dir. Psychol. Sci. 2 (1993) 106–111.

[51] S. Mineka, M. Cook, Social learning and the acquisition of snake fear in monkeys, in: T.R. Zentall, B.G. Galef Jr. (Eds.), Social Learning: Psychological and Biological Perspectives, Lawrence Erlbaum Associates, Hillsdale, New Jersey, 1988, pp. 51–73.

[52] S. Mineka, M. Cook, Mechanisms involved in the observational conditioning of fear, J. Exp. Psychol. Gen. 122 (1993) 23–38.

[53] K. Nader, J. LeDoux, How the brain learns about danger, in: J. Bolhuis (Ed.), Brain, Perception And Memory: Advances in Cognitive Neuroscience, Oxford University Press, New York, 2000, pp. 267–278.

[54] J.M. Pearce, G. Hall, A model of Pavlovian learning: variations in the effectiveness of conditioned but not of unconditioned stimuli, Psychol. Rev. 87 (1980) 532–552.

[55] A.S. Pell, C.R. Tidemann, The impact of two exotic hollow-nesting birds on two native parrots in savannah and woodland in eastern Australia, Biol. Conserv. 79 (1997) 145–153.

[56] I.M. Pepperberg, In search of King Solomon's ring: cognitive and communicative studies of grey parrots (*Psittacus erithacus*), Brain. Behav. Evol. 59 (2002) 54–67.

[57] G. Pizzey, F. Knight, The Graham Pizzey and Frank Knight field guide to the birds of Australia, HarperCollins, Sydney, 1998.

[58] A. Reiner, D.J. Perkel, C.V. Mello, E.D. Jarvis, Songbirds and the revised avian brain nomenclature, Ann. NY Acad. Sci. 1016 (2004) 77–108.

[59] R.A. Rescorla, Pavlovian conditioning: it's not what you think it is, Am. Psychol. 43 (1988) 151–160.

[60] R.A. Rescorla, A.R. Wagner, A theory of Pavlovian conditioning: variations in the effectiveness of reinforcement and nonreinforcement, in: A.H. Black (Ed.), Classical Conditioning. II. Current Research and Theory, Appleton-Century-Crofts, New York, 1972, pp. 64–99.

[61] P. Rozin, J.W. Kalat, Specific hungers and poison avoidance as adaptive specializations of learning, Psychol. Rev. 78 (1971) 459–486.

[62] M.E.P. Seligman, On the generality of the laws of learning, Psychol. Rev. 77 (1970) 406–418.

[63] S.J. Shettleworth, Cognition, Evolution and Behavior, Oxford University Press, New York, 1998.

[64] S.J. Shettleworth, Rank inferred by reason, Nature 430 (2004) 732–733.

[65] J.A. Soha, P. Marler, A species-specific acoustic cue for selective song learning in the white-crowned sparrow, Anim. Behav. 60 (2000) 297–306.

[66] K.W. Spence, Experimental studies of learning and higher mental processes in infra-human primates, Psychol. Bull. 34 (1937) 806–850.

[67] J.E.R. Staddon, J.J. Higa, Time and memory: towards a pacemaker-free theory of interval timing, J. Exp. Anal. Behav. 71 (1999) 215–284.

[68] S.C. Stout, R. Chang, R.R. Miller, Trial spacing as a determinant of cue competition, J. Exp. Psychol. Anim. B 29 (2003) 23–38.

[69] M.D. Suboski, Releaser-induced recognition learning, Psychol. Rev. 97 (1990) 271–284.

[70] M.D. Suboski, S. Bain, A.E. Carty, L.M. McQuoid, M.I. Seelen, M. Seifert, Alarm reaction in acquisition and social transmission of simulated-predator recognition by zebra danio fish, J. Comp. Psychol. 104 (1990) 101–112.

[71] R.S. Sutton, A.G. Barto, Time-derivative models of Pavlovian reinforcement, in: M. Gabriel, J. Moore (Eds.), Learning and Computational Neuroscience: Foundations of Adaptative Networks, MIT Press, Cambridge, MA, 1990, pp. 497–537.

[72] W.H. Thorpe, The learning abilities of birds, Ibis 93 (1–52) (1951) 252–296.

[73] W.H. Thorpe, Learning and Instinct in Animals, Methuen, London, 1956.

[74] K. Urushihara, S.C. Stout, R.R. Miller, The basic laws of conditioning differ for elemental cues and cues trained in compound, Psychol. Sci. 15 (2004) 268–271.

[75] W. Vieth, E. Curio, U. Ernst, The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds: cross-species tutoring and properties of learning, Anim. Behav. 28 (1980) 1217–1229.

[76] A.R. Wagner, SOP: a model of automatic memory processing in animal behavior, in: N.E. Spear, R.R. Miller (Eds.), Information Processing in Animals: Memory Mechanisms, Lawrence Erlbaum Associates, New Jersey, 1981, pp. 5–47.

[77] Y. Wang, A. Fontanini, D.B. Katz, Temporary basolateral amygdala lesions disrupt acquisition of socially transmitted food preferences in rats, Learn. Memory 13 (2006) 794–800.

[78] S.A. Wich, E.H.M. Sterck, Possible audience effect in Thomas Langurs (Primates; *Presbytis thomasi*): an experimental study on male loud calls in response to a tiger model, Am. J. Primatol. 60 (2003) 155–159.

[79] K. Zuberbühler, R. Noe, R.M. Seyfarth, Diana monkey long-distance calls: messages for conspecifics and predators, Anim. Behav. 53 (1997) 589–604.