Sound improves visual discrimination learning in avian predators

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Aposematic insects use warning colours to deter predators, but many also produce odours or sounds when attacked by a predator. One possible role for these additional components is that they promote the association between the warning colour and the non-profitability it signals, thus reducing the chance of future attacks from visually hunting predators. This experiment explicitly tests this idea by looking at the effects of sound on a visual discrimination task. Young domestic chicks were trained to look for food rewards under coloured paper cones scattered in an experimental arena. In a subsequent visual discrimination task, they learned to discriminate between rewarded and non-rewarded hats on the basis of colour. Half the chicks performed this task in silence, whilst the other half had a tone played when they attacked non-rewarded hats. The presence of the tone improved the speed of colour discrimination learning. This demonstrates that there could be a selective advantage for aposematic coloured insects to emit sounds when attacked, since avian predators will learn to avoid their coloration more quickly. The role of psychological interactions between signal components in receivers is discussed in relation to the evolution of multimodal displays.

Keywords: evolution; aposematism; multimodal signals; domestic chick

1. INTRODUCTION

Aposematic insects use bright coloration to advertise their non-profitability or unpalatability to would-be predators. Conspicuous coloration is particularly effective as a warning signal, as avian predators learn to avoid unpalatable prey faster if they are conspicuously coloured rather than if they are cryptic (Gittleman & Harvey 1980; Roper & Redston 1987), and there is also evidence that birds may instinctively avoid food that has colour typical of aposematic prey (Schuler 1982; Schuler & Hesse 1985; Roper & Cook 1989; Gamberale-Stille & Tullberg 2001). However, many aposematic insects do not just use colourful signals, but also often emit odours or sounds when they are approached or attacked by a predator (Cott 1940; Rothschild 1961; Rothschild & Haskell 1966; Edmunds 1974). These warning displays, consisting of components in more than one sensory modality, have been called ‘multimodal’ signals (Partan & Marler 1999; Rowe 1999). The question is, given that conspicuous colour patterns are effective warning signals against avian predators, why have aposematic insects also evolved these additional signal components?

Recent experiments have investigated the signalling significance of pyrazine, an odour commonly found in multimodal insect warning displays (Rothschild 1961; Moore et al. 1990; Marples et al. 1994; Marples & Roper 1996; Rowe & Guilford 1996, 1999; Roper & Marples 1997; Jetz et al. 2001; Lindström et al. 2001). Birds can detect pyrazine, and learn to avoid unpalatable prey by odour alone (Guilford et al. 1987; see Roper (1999) for a review of birds’ olfactory capabilities), but pyrazine can also evoke unlearned colour biases in naive avian predators. Pyrazine odour causes naive domestic chicks (Gallus gallus domesticus) to reduce their intake of prey that share visual characteristics typical of aposematic insects, such as prey that are red or yellow (Rowe & Guilford 1996, 1999), conspicuously against the background (Lindström et al. 2001), or novel in appearance (Jetz et al. 2001). Further results show that such biases are not elicited by pyrazine alone and that other odours, and even sounds, can elicit these unlearned biases (Jetz et al. 2001; Rowe & Guilford 2001).

Therefore, there is evidence that non-visual components could enhance prey survival through eliciting unlearned visual biases in naive avian predators, but it is also possible that they could enhance the learning process. Claridge (1974), and later Rothschild et al. (1984), proposed that sounds and odours could promote the association between the colour pattern of the prey and its unpalatability, thus avian predators would learn to avoid aposematic prey more quickly. Kaye et al. (1989) showed that pyrazine odour could enhance the association between visual environmental cues and water palatability in rats (Rattus norvegicus). For birds, Roper & Marples (1997) showed that chicks learned to avoid unpalatable water that was a familiar colour if a novel odour (almond) was presented alongside. Although one interpretation is that the odour enhanced the colour avoidance learning, an alternative interpretation is that the learning proceeded more quickly because the chicks associated the novel odour with the unpalatability; there is as yet no conclusive evidence supporting the idea that a non-visual component can promote the learning of prey coloration in avian predators.

This experiment is, to my knowledge, the first to explore how a sound produced upon attack can enhance the speed of discrimination learning in avian predators. I used sound rather than odour since it is easier to use in a laboratory setting, but more importantly, it also allowed me to control the order of presentation of visual and auditory components. In previous experiments using pyrazine, the odour was detected before any attack to the prey had been made: in this experiment sound is only produced when an unrewarded prey item is actually attacked, mimicking natural insect warning displays. Naive predators had to
learn to discriminate between two colours of prey, one that was rewarded and one that was not. For half the birds, a simple tone was played when they mistakenly attacked the unrewarded prey, in order to investigate the effect on the speed of learning. Throughout the experiment I used colours and sounds that are not typically associated with warning signals, to prevent any unlearned aversive reactions to the stimuli. This experiment is concerned with whether there are any general psychological mechanisms that could help explain the evolution of auditory (and possibly also olfactory) components of aposematic displays.

2. MATERIAL AND METHODS

(a) Subjects and housing

Seven batches of mixed-sex domestic chicks (*Gallus gallus domesticus*, Goldline strain) hatched in the laboratory between 8 August 2000 and 15 May 2001. The chicks were kept in cages measuring ca. 100 cm × 50 cm × 50 cm, and maintained at 20–22 °C using heat lamps. They were subject to a 14 L:10 D cycle. Water was provided *ad libitum*, as were chick starter crumbs when the chicks were not being food deprived during the experiment (all food deprivation was in accordance with ethical guidelines issued by the Home Office). Chicks were kept for 10–14 days and were subsequently donated to free-range farms.

(b) Training

Each week, I trained chicks using the same general procedure. On days 1 and 2 post-hatch, I trained single chicks to eat brown chick starter crumbs scattered on the white floor of a walled circular arena (ca. 1 m in diameter). Chicks were food deprived, initially, for 1–2 h before being given a series of training sessions. They were allowed to eat to satiation in the arena in each session before being returned to the home cage. By the end of day 2, all chicks were eating from the arena on their own.

On day 3, I gave individual chicks three sessions with the first type of training stimuli. These were discs of coloured paper, 2 cm in diameter, under which I placed a small pile of chick crumbs (ca. 10–15 crumbs under each disc). There were six discs in each session, three each of two different colours, which were changed between sessions so that chicks became accustomed to the presence of novel colours. The colours I used were merely selected to look different since I was not training the chicks to any particular set of colours, but attempting to eliminate any neophobic responses that might occur towards the novel experimental colours when they were presented. Colours were selected from a panel of 14, ranging from violet (peak reflectance measured with a PR650 spectrosan was 420 nm) to red (peak reflectance was 600 nm). There was no ultraviolet component to these colours due to the lighting in the experimental room. Chicks rapidly learned to find food under the paper discs, and also to attack them regardless of novel coloration.

After a further training session with these discs on day 4, I gave chicks three sessions with shallow cones or ‘hats’ under which food could now be hidden (these were the circles that had been made into ‘hat’–like shapes). Although I left the food visible underneath these hats at first, by the end of day 5 and a further four to five training sessions, I could hide the food completely and chicks flipped them over to look for food underneath.

(c) Experiment

On day 6, I gave chicks a visual discrimination-learning task. They were given six hats of two different colours (i.e. 12 in total) arranged randomly in the arena where only hats of one colour had three chick crumbs hidden underneath. I used two novel colours, purple and green, which were selected in order to reduce any colour biases that chicks might show: these colours are not commonly associated with warning signals, and chicks show no biases against them (Rowe & Guilford 2001). Chicks were given eight sessions; in each session they were allowed to attack six hats before they were removed from the arena, and the colours of these hats were recorded. An attack was defined as a chick pecking a hat, whether they were rewarded or not. There were 30–50 min between each session (depending upon the number of chicks being tested), except for a break halfway through the trials, when the chicks were fed chick crumbs and left for ca. 1 h.

On day 7, all chicks were given two further sessions to make a total of 10. I considered chicks to have learned the task if they attacked only the six rewarded hats in a given session, and by the end of these 10 sessions, nearly all the chicks (77 out of 81) had achieved this learning criterion. These chicks were then given an extinction session to ensure that they had learned the colours of the hats, and had not used any other visual or olfactory cues to find the food. In this session, three chick crumbs were put under all 12 hats, regardless of colour, and the colour choices of the chicks were recorded. Any chick that had not achieved the learning criterion was given further trials spaced 30 min apart until it attacked only the rewarded hats in a session (no chick needed more than four further sessions). These chicks were then also given an extinction trial.

Eighty-five chicks were trained in total. In each week, chicks were assigned to four groups before the start of the experiment. For approximately half the chicks, food was placed under the purple hats, whilst for the other half it was under the green hats. Within each colour treatment, chicks were divided into two further groups, one that heard a tone when they attacked an unrewarded hat, whilst the other performed the task in silence. It was impossible to have equal numbers in each group since different numbers were hatched and trained each week, and some chicks were excluded; three chicks refused to attack six hats in a given session on the first day, whilst the other had an extreme preference for green hats and attacked only these in the very first session. However, across all seven weeks, the number of chicks in each experimental group was virtually equal: rewarded purple hats, no sound, *n* = 21; rewarded purple hats, sound, *n* = 20; green hats rewarded, no sound, *n* = 20; green hats rewarded, sound, *n* = 20.

The sound played was a simple alert beep, played at maximum volume, from a Macintosh CS1400 laptop situated adjacent to the arena. I used this instead of a warning buzz or rattle to reduce the likelihood of eliciting an aversive reaction, and during this experiment (and others using sound: C. Rowe, unpublished data; Rowe & Guilford 2001), chicks did not avertly react to the novel sound. Groups where food was hidden under the purple hats were always tested first before the two groups where it was under the green hats. Within each colour treatment, in weeks 1–4 the groups that had a sound played were tested first, whilst in weeks 5–7 this order was reversed and these groups were tested second.

3. RESULTS

Although green and purple were selected to reduce the chance of a colour bias in this experiment, chicks showed an initial preference for green hats. Looking at the first
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4. DISCUSSION

These results clearly demonstrate that sound can improve the speed of visual discrimination learning in birds. This occurs regardless of the direction of the colour discrimination, despite a bias for the first hat colour to be attacked to be green. This colour bias could be unlearned (Roper & Cook 1989; Gamberale-Stille & Tullberg 2001), or have been caused by the colours used in the training set; fewer colours occurred at shorter wavelengths around the purple stimuli than at longer wavelengths around the green. This may have made purple test stimuli relatively more novel when they were initially presented, thus creating a bias for green.

However, regardless of the initial colour bias, there is no significant effect on the speed of learning between the two colour treatments, and the only main effect is that of sound. But how does sound enhance colour discrimination learning? What is not known from this experiment, or from observations of wild birds, is whether the sound functions as a conditioned or an unconditioned stimulus in the learning process. The coloration is a conditioned stimulus, in that it becomes associated with a valued outcome (the unconditioned stimulus), which in this case is the reward, or lack of it. The role of sound in this process is more ambiguous, and it could be working in one of two ways.

The first is that it is perceived as an additional unconditioned stimulus, with learning proceeding faster because those groups with sound have additional negative reinforcement. However, tones are regularly used in psychological experiments (Mackintosh 1974; Pearce 1997), including those investigating compound learning (Keohoe et al. 1994), and no aversive behaviour towards the tone was evident (see also Rowe & Guilford 2001).

Alternatively, it could be acting as an additional conditioned stimulus, which promotes the strength of colour aversion learning. Such a mechanism would be similar to that of 'potentiation', which occurs when two conditioned stimuli predict an outcome and where one conditioned stimulus promotes the association between the other conditioned stimulus and the outcome (Durlach & Rescorla 1980; Honey & Bolhuis 1997). For example, in the context of multimodal warning signals, rats make a stronger association between visual environmental cues and water palatability if the warning odour, pyrazine, is also present in the environment (Kaye et al. 1989). In a different context, visual filial imprinting in chicks can be improved by the presence of a simultaneous auditory signal, as can auditory imprinting by a visual stimulus (Van Kampen & Bolhuis 1991, 1993). In my experiment, although learning about the colour may be promoted by the sound, this is not potentiation in the strict sense, as the two conditioned stimuli are not presented together, with the sound being presented after the coloration. In some attacks, the coloured hats remained upright rather than being flipped over, and in these cases perhaps the sound and the coloration could be said to have occurred together. However, in most cases, the sound would have been perceived after a hat had been flipped over (all hats were white underneath), and possibly even after the lack of reward had been realized. Further experiments, under more controlled presentation conditions, will be required to determine the importance of the order and timing of the stimulus presentations.

Sound has also been shown to help animals in discrimination tasks, where it is played during a long delay between the presentation of a visual stimulus and the reward or punishment that it predicts (Spence 1947;
Table 1. Results of three-way ANOVA performed on the standardized data.

<table>
<thead>
<tr>
<th>source</th>
<th>sum of squares</th>
<th>d.f.</th>
<th>mean square</th>
<th>F-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>sound</td>
<td>4.923</td>
<td>1</td>
<td>4.923</td>
<td>6.154</td>
<td>0.015</td>
</tr>
<tr>
<td>colour</td>
<td>1.932</td>
<td>1</td>
<td>1.932</td>
<td>2.415</td>
<td>0.124</td>
</tr>
<tr>
<td>order</td>
<td>0.299</td>
<td>1</td>
<td>0.299</td>
<td>0.374</td>
<td>0.543</td>
</tr>
<tr>
<td>sound × colour</td>
<td>0.115</td>
<td>1</td>
<td>0.115</td>
<td>0.144</td>
<td>0.705</td>
</tr>
<tr>
<td>sound × order</td>
<td>0.009</td>
<td>1</td>
<td>0.009</td>
<td>0.011</td>
<td>0.916</td>
</tr>
<tr>
<td>colour × order</td>
<td>0.245</td>
<td>1</td>
<td>0.245</td>
<td>0.306</td>
<td>0.582</td>
</tr>
<tr>
<td>sound × colour × order</td>
<td>0.218</td>
<td>1</td>
<td>0.218</td>
<td>0.272</td>
<td>0.604</td>
</tr>
<tr>
<td>error</td>
<td>58.39</td>
<td>73</td>
<td>0.800</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 2. The standardized (by week) number of sessions needed to achieve learning criterion. Open bars are the scores for two groups where food was hidden under purple hats, and shaded bars are where food was rewarded under green hats. Sample sizes for each group are as follows: rewarded purple hats, no sound, n = 21; rewarded purple hats, sound, n = 20; green hats rewarded, no sound, n = 20; green hats rewarded, sound, n = 20.

Regardless of the specifics of the psychological mechanism, this effect will have important implications for insects in the wild. What is important for multimodal warning signals is that the speed of learning is improved by the sound being played after an attack. Therefore, sound is not being used by the birds to discriminate between differently coloured prey before an attack, but instead enhances the avoidance of unrewarded prey types, purely on the basis of their visual signals. This mimics the natural situation where insects produce sounds and odours when approached or attacked by a predator. Therefore, aposematic insects that produce sounds could improve birds’ abilities to learn their colour patterns, thus enhancing their survival prospects (Claridge 1974). This intersensory interaction could be more general and work between other sensory modalities, and it is possible that odours that are produced after attack will also enhance colour discrimination learning (Rothschild et al. 1984).

Multimodal displays are common in nature, and yet we are still at an early stage of understanding how signal receivers process multiple components. In some instances, auditory and visual signal components may simultaneously transmit redundant information (Møller & Pomiankowski 1993; Johnstone 1996), as in the case of signals of need in reed warbler chicks (Acrocephalus scirpaceus) (Kilner et al. 1999). However, not all signal components need be informative, and psychological interactions between signal components in different sensory modalities could enhance signal efficacy (Guilford & Dawkins 1991; Rowe 1999). These results demonstrate how an auditory signal component can enhance the efficacy of a visual warning signal through enhanced discrimination learning. Of course, it is also possible that sounds could increase the detection and discrimination of visual signals (see Rowe (1999) for a review). Therefore, signal components need not necessarily evolve solely to transmit information, but instead could be under selection to promote the perception of an informative signal component in signal receivers.

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Thomas et al. (1987, 1991). However, in this experiment, the delay between pecking the colour and its profitability was almost instantaneous. One proposed mechanism for this effect is that the sound alerts the animal to pay more attention to the visual stimulus, and thus the association with the delayed punishment would be made more readily (Rothschild et al. 1984). Hultsch et al. (1999) highlighted the potential importance of the role of attention in signal learning by showing that a synchronous flashing light was sufficient to enhance song learning in nightingales (Luscinia megarhynchos). However, other operant experiments with zebra finches (Taeniopygia guttata) have not found any evidence that the presentation of a visual stimulus improves song learning (Bolhuis et al. 1999; Houx & ten Cate 1999), although this could possibly be due to the nature of the visual stimulus. It is possible that in this experiment sound is alerting the birds to the association between the visual stimulus and the lack of reward and making it more salient in the birds’ memories, but further experiments will be needed to fully identify the mechanism behind this intersensory interaction.

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