Stimulus Salience as an Explanation for Imperfect Mimicry

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Summary

The theory of mimicry explains how a mimic species gains advantage by resembling a model species [1–3]. Selection for increased mimic-model similarity should then result in accurate mimicry, yet there are many surprising examples of poor mimicry in the natural world [4–8]. The existence of imperfect mimics remains a major unsolved conundrum. We propose and experimentally test a novel explanation of the phenomenon. We argue that predators perceive prey as having several traits, but that the traits differ in their importance for learning. When predators learn to discriminate prey, high-salience traits overshadow other traits, leaving them under little or no selection for similarity, and allowing imperfect mimicry to succeed. We tested this idea experimentally, using blue tits as predators and artificial prey with three prominent traits: color, pattern, and shape. We found that otherwise imperfect color mimics were avoided about as much as perfect mimics, whereas pattern and shape mimics did not gain from their similarity to the model. All traits could separately be perceived and learned by the predators, but the color trait was learned at a higher rate, implying that it had higher salience. We conclude that difference in salience between components of prey appearance is of major importance in explaining imperfect mimicry.

Results and Discussion

Mimicry is a textbook example of how natural selection acts on organisms, resulting in spectacular adaptations. Members of a mimic species gain selective advantages from identification mistakes by predators [1–3]. The mimics resemble another, unprofitable and avoided species in different components of appearance, such as color, pattern, and shape. Even though a high mimic-model similarity in all or nearly all components could be expected, there are many examples of poor mimicry in which only a few of the components of appearance are similar to the model [4–6]. Such imperfect mimicry is a major unsolved question and has been labeled a challenge to evolutionary theory [7, 8].

Here we introduce a new way of studying mimicry evolution, by investigating multitrait prey appearances, and identify the characteristics of predator psychology that make apparently poor mimicry possible. A common way of studying what predators perceive and learn about prey is to treat prey appearances as if they are one-dimensional. Consequently, there is an assumption that predators perceive a general likeness to the model when mimics are avoided. We argue that this approach is limiting and instead propose that predators only learn to use a few salient, higher-ranked traits of the prey appearance for discrimination between multitrait appearances. When predators generalize between models and mimics, they effectively ignore lower-ranked, less salient traits, and this allows imperfect mimicry to function. Our hypothesis is related to established mechanisms of associative learning, in particular the concepts of stimulus salience and overshadowing [9, 10], which can be represented using the Rescorla-Wagner model [11].

We have investigated the relative importance of color, pattern, shape components of prey appearance for multitrait model-mimic discrimination learning, using artificial prey that varied in these stimulus components. We then determined the salience of each component, in terms of how rapidly a discrimination of a difference in that component was learned, to see whether salience explained the ranking of traits in the multitrait discrimination.

In experiment 1, the model prey were distinct from the rewarded prey in all three stimulus components, and three different model variants were used (Figure 1A and Figure S1 available online). Wild-caught blue tits were trained to discriminate between rewarded prey and unrewarded model prey, and they readily learned the discrimination. The estimated learning curve from the best-fitting (lowest Akaike Information Criterion [AIC]) statistical model appears in Figure 2A. There was an increasing avoidance of the unrewarded model prey from trial 1 to trial 4, as shown by the right-turning slope of the mixed-model logistic regression (slope ± SE: 1.115 ± 0.095, p < 0.0001). This best-fitting model had only trial as fixed effect. For statistical models that also included the model variant as fixed effect, there were no statistically significant differences in the learning curves between model variants.

Subsequently, we conducted generalization tests with mimics that were similar to the model in all (a control) or only one of the components of appearance, in order to determine their relative importance for discrimination by the birds. By comparing different statistical models, we found that a model that only included the mimic variant as factor provided the best fit to the data (lowest AIC) and showed a statistically significant effect of the mimic variant (main effect: likelihood ratio [LR] chi-square = 49.8, degrees of freedom [df] = 3, p < 0.0001). The addition of the model variant used during discrimination learning as a factor did not result in any statistically significant effects (main effect: LR chi-square = 2.8, df = 2, p = 0.25; mimic-model variant interaction: LR chi-square = 7.1, df = 6, p = 0.31). For this reason, we present pooled data over the different model variants (Figure 2B).

The birds avoided the perfect mimics and the color mimics, whereas the pattern and shape mimics were attacked at approximately the same rate as the rewarded prey (Figure 2B). Tukey post hoc tests of the mimic variant main effect showed that there was no statistically significant difference in avoidance between the perfect and the color mimic variants (p = 0.66), nor between the pattern and shape variants (p = 1.0), whereas all comparisons between these groups were statistically significant (p < 0.003 for all four comparisons). Furthermore, the birds attacked the pattern and shape mimics nearly as much as the rewarded prey, in the
sense that the 95% confidence intervals in Figure 2B include the 0.5 proportion of attacks directed away from the mimic, which corresponds to random attacks. Thus, the imperfect color mimics were well protected by their similarity with the model, whereas the pattern and shape mimics received little or no protection. This was the case not just for one particular color-pattern-shape combination of model prey appearance, but for several different combinations.

In experiment 2, we examined the salience of the trait dimensions color, pattern, and shape. We measured the rate of discrimination learning for each dimension with rewarded and unrewarded prey that differed only in one of the components (Figure 1B). Our general hypothesis about imperfect mimicry is that high-salience traits overshadow other traits in a multitrait prey discrimination, so from the results of experiment 1, this hypothesis predicts that color difference should have a higher salience than the pattern and shape differences. We tested this prediction by comparing the intercepts (at midtrial) and slopes of the estimated learning curves for pattern and shape discrimination with that for color discrimination (Figure 3). These comparisons appear in Table 1 and show that both the intercepts and slopes for pattern and shape are lower than those for color, demonstrating that the color difference had higher salience than the pattern and shape differences. In a separate analysis of the learning curves for the different treatments, we verified that the birds did learn both the pattern (slope ± SE: 0.278 ± 0.079, p = 0.0004) and shape (slope ± SE: 0.363 ± 0.067, p < 0.0001) discriminations, in situations when the high-salience color difference was not present and therefore not overshadowing the other traits. Finally, to establish that the birds really used the color difference, and not a possible difference in brightness, to discriminate between rewarded (gray) and unrewarded (magenta) prey, we performed a brightness test. This showed that the birds used the color difference, rather than a brightness difference, for discrimination (see the Supplemental Experimental Procedures).

The results thus support our general hypothesis about how imperfect mimicry functions. In particular, the higher salience of the color component, compared to the pattern and shape components, explains the use of color for discrimination. Our hypothesis also agrees with established ideas in learning theory. Associative learning involves a change in an animal’s behavior as a result of an association between two or more events, and repeated pairings result in an increase in associative strength between these events. The phenomenon of overshadowing is observed during associative learning with compound stimuli [9–15]. When two or more stimuli are presented together and they predict an important event, they share the associative strength of that pairing so that more salient components of the compound gain higher strength. If the components differ markedly in salience, the animal learns to associate the most salient component with the reinforcement and the association with other components is overshadowed [9, 16]. In this context, a more salient stimulus is one that achieves a higher rate of associative learning and can, for instance, correspond to a louder, brighter, or otherwise more striking stimulus. In learning theory, the Rescorla-Wagner model is often used to represent the learning process. For this model, overshadowing and the related phenomenon of blocking are direct consequences of differences in the rate of learning between stimulus components [11].

Our hypothesis about imperfect mimicry thus entails that the most salient components of prey appearance will be learned primarily and will overshadow other components. The consequence is that when many trait differences occur simultaneously in a discrimination task (in our experiments, color, pattern, and shape), in which each of them in principle could provide reliable information, an imbalance in salience results in overshadowing. Hence, only one or a few components (in our case, color) are used for discrimination. The result of learning is as if the animal had ignored the other components.

A generally high salience of the color dimension for birds most likely lies behind the use of color for discrimination in our experiments, as well as in those by Aronsson and Gamberale-Stille [16, 17]. Color vision occurs in many groups of animals. Most mammals have dichromatic vision, whereas birds have tetrachromatic vision, which is phylogenetically more widespread in vertebrates. The adaptive function of color vision is to discriminate between objects based on differences in the relative amounts of different wavelengths of light, and bird vision is well developed for achieving this task [16]. Many birds have a lifestyle that is diurnal and involves flight, so they need to discriminate objects at a distance. A well-developed color vision improves this capacity. Thus, it is not surprising that color differences have high salience for bird predators. Even so, it is of course possible that other aspects than prey color sometimes dominate the discrimination of prey suitability. For instance, a striking pattern might have higher salience than a subtle difference in hue, and a “warning odor” could overshadow a color difference [19]. In general, experimental psychology has shown that high-intensity
stimulus properties or components tend to have high salience [9, 10].

A number of hypotheses have been put forward to explain imperfect mimicry [8]. For example, the multimodel hypothesis states that an imperfect mimic can benefit from simultaneously resembling several different model species, as a “jack of all trades” [4, 5]. Another influential hypothesis posits a relaxed selection pressure on the imperfect mimic, for instance because of a highly noxious model or a less nutritionally profitable mimic, making it less important for the predator to discriminate mimics from models [4, 5]. A speed-accuracy tradeoff in predator decision making could also permit imperfect mimicry [7]. Speed was, however, not a factor in our experiments, because the birds were not pressed for time when deciding about attacks. None of the suggestions provides a full explanation to most instances of imperfect mimicry [8, 20]. They also differ from our hypothesis by not explicitly referring to multitrait appearances.

Chittka and Osorio [7] suggested that “wholly dissimilar mimics may be protected, provided they share some common property with noxious prey,” through predator categorization behavior, and argued that predators need to categorize prey in order to handle a complex world. This idea was further developed by Balogh et al. [21] and Gamberale-Stille et al. [22]. Considering our current results, the effects of differences in salience and overshadowing between components of prey appearance provide a simple explanation for apparent categorization. This explanation is particularly likely to apply to mimicry of aposematic models, because high-salience traits are characteristic of aposematism [3]. Thus, high-salience, aposematic traits may well play a role in mimicry in the way we propose here. The idea can be applied to the evolutionary origin of mimicry, as studied using computer simulations of the evolutionary process [21–23], as well as to currently occurring imperfect mimicry.

In the case of Batesian mimicry, palatable prey mimic unprofitable models [1]. If the mimics become numerous, predators could benefit from learning to discriminate mimics from models. More components of prey appearance would then be required for discrimination. Even so, a relatively rare mimic sharing the most salient components of a model appearance could gain considerable protection.

Some examples of imperfect mimicry further illustrate our idea. There are many instances in which mimics differ from their models in the quantity and/or spatial arrangement of the colors in a pattern, and these differences may have low salience for bird predators. The butterfly Battus philenor occurs in North and Central America and is a probable model in a mimicry ring that includes the Batesian mimics Papilio polyxenes and Limenitis arthemis astyanax [24–26]. In B. philenor, the ventral hindwing surface has a row of orange spots placed centrally in a band of iridescent blue along the wing margin, set against the dark melanism of the background wing color [27]. The hindwing patterns of both Batesian mimics imperfectly resemble that of the model. They mimic the orange spots and blue color against a dark background, but the mimicry is imperfect in that the band in P. polyxenes has blue in the center, bordered by two rows of orange spots [27], and in L. a. astyanax the orange and blue patterns are even more deviant from that of B. philenor. The probable reason for the discrepancies is that the mimics have retained their ancestral positions of orange and blue markings on the hindwing and have acquired melanism to mimic B. philenor. Another
example of poor resemblance is found in coral snake mimicry. For instance, the eastern coral snake, Microslrus fulvius, has a color pattern consisting of a repetition of the sequence black-yellow-red along its body. Some of its Batesian mimics from the snake genus Lampropeltis have a pattern involving the same colors, but in different widths and arranged differently, by repeating the sequence black-yellow-black-red [8]. See [22] for a scenario of how these mimetic color patterns may have evolved.

A ranking of the components of a multitrait appearance according to their salience, and thus their importance for discrimination learning, could also help explain why mimics sometimes show similarity to models in more than one trait. This is expected if two or more traits have similar salience, and also if predators benefit substantially and have sufficient opportunity to learn to discriminate mimics from models using less salient traits.

Table 1. Statistical Analysis of the Salience Test

<table>
<thead>
<tr>
<th>Effect</th>
<th>Estimate</th>
<th>SE</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Color intercept</td>
<td>2.767</td>
<td>0.234</td>
<td></td>
</tr>
<tr>
<td>Pattern-color intercept contrast</td>
<td>-1.965</td>
<td>0.269</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Shape-color intercept contrast</td>
<td>-2.110</td>
<td>0.269</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Color slope</td>
<td>0.876</td>
<td>0.126</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Pattern-color slope contrast</td>
<td>-0.597</td>
<td>0.149</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Shape-color slope contrast</td>
<td>-0.506</td>
<td>0.149</td>
<td>0.0007</td>
</tr>
</tbody>
</table>

The logit-scale parameter estimates, SEs, and p values for the fixed effects from the mixed-model fitting are shown. In the model fitting, the trial number variable was centered at 3.5, so the intercept estimates refer to this value.

Conclusions

Based on our experiments, we have strong support for the idea that predators perceive prey as having several traits, but that traits differ in their importance for discrimination learning. High-salience traits can overshadow other traits, allowing imperfect mimicry to succeed. The general cognitive mechanisms of stimulus salience and overshadowing that our hypothesis builds on are likely to be of broad scope as explanations of mimicry, especially the seemingly baffling phenomenon of imperfect mimicry.

Experimental Procedures

We used blue tits (Cyanistes caeruleus) as predators, artificial prey items as stimuli, and pieces of mealworm as reward. The experiments were carried out in two rooms illuminated by fluorescent lamps with a spectral distribution similar to daylight. The artificial prey were presented on top of wells in experimental boards, placed on the floor. Depending on the prey type, the wells were either empty or contained a reward. After pretraining (day 1), the birds carried out trials (days 2–4) in which they learned to discriminate between rewarded and unrewarded prey. In experiment 1, the discrimination training was followed by a generalization trial with mimic variants. See the Supplemental Experimental Procedures for a detailed description.

We used generalized linear models to analyze the data from the experiments. The response variable was the number of attacks on palatable prey out of the first n attacks in a trial, where n = 8 for the discrimination learning, n = 4 for the generalization test, and n = 12 for the salience test. This response variable was modeled as having a binomial distribution, with logit link function, using the software package R 3.0.0 [28]. We used the glm function in R and the glmer function in the package lme4 [29]. See the Supplemental Experimental Procedures for details about the statistical analyses.

Accession Numbers

Data are available from the Dryad Digital Repository under DOI number http://dx.doi.org/10.5061/dryad.1415r.

Supplemental Information

Supplemental Information includes three figures, one table, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.02.061.

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