

Cognitive dimensions of predator responses to imperfect mimicry?

Lars Chittka¹ & Daniel Osorio²

1. School of Biological and Chemical Sciences; Queen Mary; University of London, Mile End Road, London E1 4NS

2. University of Sussex; School of Life Sciences; Falmer; Brighton BN1 9QG

Summary

Many palatable insects, for example hoverflies, deter predators by mimicking well-defended insects such as wasps. However, for human observers, these flies often seem to be little better than caricatures of wasps – their visual appearance and behaviour are easily distinguishable. This **imperfect mimicry** baffles evolutionary biologists, because one might expect natural selection to do a more thorough job. Here we discuss two types of **cognitive processes** that might explain why mimics distinguishable mimics might enjoy increased protection from predation. **Speed accuracy tradeoffs** in predator decision making might give imperfect mimics sufficient time to escape, and predators under time constraint might avoid time-consuming discriminations between well-defended models and inaccurate edible mimics, and instead adopt a “safety first” policy of avoiding insects with similar appearance. **Categorization** of prey types by predators could mean that wholly dissimilar mimics may be protected, provided they share some common property with noxious prey.

Introduction

Mimicry provides examples of adaptive evolution so striking that they should convince even staunch sceptics of the principles of evolution. Perfectly harmless caterpillars look like venomous snakes, while angler fish display lures that resemble small fish. In many other cases, however, the match between the mimic and its model is almost disappointingly sloppy. Take many of the familiar hoverflies: their yellow and black stripes might resemble a stinging wasp to an inexperienced observer – but the body shape, flight behaviour and colour pattern of many species easily identify them as defenceless flies (Figure 1). Yet, the strategy works: the flies' coloration pattern must provide protection that they would not enjoy if they were, say, plain brown.

Insert figure 1 about here

A simple explanation for predator responses to poor mimics could be that predators innately avoid any stripy pattern. Such innate biases do exist [1], but typically they are weak, and can easily be overwritten by learning [2-4]. Therefore, current explanations of imperfect mimicry refer to predators' *individual experience* with unpleasant mimics, and responses to mimics that are guided by such experience. Previous explanations of imperfect mimicry include: *a*) the possibility that differences in visual systems between humans and insectivores (typically avian predators) might mean that what constitutes a poor match for human observers might in fact be perfect mimicry for some predators [5]; *b*) that, in the presence of multiple aposematic models, mimics attempt to find a compromise by appearing intermediate to all of them [4,6]; and *c*) that generalisation of predators to distinguishable but similar prey might give sufficient protection for poor mimics [3,7,8]. These explanations remain controversial [4], but we do not question their validity in some cases. However, the predator learning processes that have been discussed in the context of mimicry are essentially Pavlovian, in that they

invoke only simple processes of information storage, generalization and forgetting [9] and thus do not fully capture the complexity of cognitive abilities that predators might use. Here we discuss two cognitive abilities that allow predators to make effective decisions about whether or not to attack while maintaining a low level of risk of confusing a nutritious mimic from its noxious model. These processes may be exploited by imperfect mimics.

Speed accuracy tradeoffs in animal decision making?

Everyday experience shows that difficult perceptual tasks require more time than easy tasks. If time is limited for difficult judgments, you are more likely to make mistakes. Consider a hypothetical football match where one team wears red and the other orange. The two colours are easily distinguished, but as players continuously change position and mingle with one another, the time for classifying them as members of one or the other team will be limited. The result is confusion of red and orange that will make the match substantially less enjoyable. Conversely, when it is essential to avoid mistakes, more time is needed. A mushroom collector has to make triply sure not to mistake a death cap (*Amanita phalloides*) for the similar and edible false death cap (*Amanita citrina*). If, after extensive inspection, there is any uncertainty, a *false alarm* is preferable to a fatal error! Understanding such speed-accuracy tradeoffs is an essential part of contemporary decision theory [10].

In bees and mice, just as in humans, sensory discrimination typically improves with the time allowed for a decision, and difficult discrimination tasks require more time to be solved with high accuracy [10-13]. Such speed-accuracy tradeoffs result from the need to sample information over time in noisy conditions, so that evidence for competing options accumulates until a decision threshold is reached [11,14-16]. Such tradeoffs should be of fundamental importance to animal decision making in the economy of

nature, but their relevance in the natural lives of animals has only recently been considered [12,17-19]. There are obvious implications for predators, when similar mimics must be discriminated from noxious models; especially in time-constrained situations, such as scramble competition or when the prey might escape. Data on speed-accuracy tradeoffs for avian predators are still outstanding, but we suggest possible avenues of future research below.

Testing the role of speed accuracy tradeoffs in predators judging inaccurate mimics

An appropriate test of the interaction between choice time and precision of choice needs to involve prey items that are only briefly on display, or moving, rather than stationary and with no time limitations. Because there are ethical concerns with experimental designs where birds might be stung by insects, live prey cannot be used; instead penalties might consist of food rendered unpalatable with bitter quinine solution [12]. Two types of experimental setups seem feasible. Either, prey items can be displayed (for a limited time, or moving at a given speed) to birds pecking at a monitor (with food or penalties being subsequently given depending on choice accuracy) [12]; or, food items may be attached to printed displays of an aposematic insect, or a mimic that can be varied in similarity [20]. Such items could be moved through a flight cage being pulled by transparent strings at predetermined speed; this scenario is more realistic than computer screen setups because the visual stimulus is effectively the actual prey item, as in nature. It will be essential to vary the display time or movement speed, as well as the number (and perhaps direction of movement) of palatable and unpalatable prey, to mimic the crowded conditions that predators might encounter in nature. Both sequential and simultaneous choice should be tested.

It will first be necessary to quantify the speed-accuracy trade-off depending on the similarity between unpalatable models and palatable mimics. Emphasis can be placed

either on accuracy (by varying the severity of punishment for errors) or speed (by limiting the time available for an attack). Once such baseline data are established, two predictions are especially worth testing. One is that if discrimination between a model and a mimic costs appreciably more time, even relatively inaccurate mimics might gain time to escape [21]. Consider your own response to a yellow-and-black hoverfly approaching you on a summer day: the first reaction might be that you are temporarily alarmed, even though close (but time-costly) inspection might identify it as harmless. The second prediction is that a predator, under time constraint, will avoid time-costly discriminations between defended models and inaccurate edible mimics, and instead adopt a “safety first” policy of avoiding all insects with similar appearance. This could be tested by offering three types of prey that vary in colour and palatability, for example: A (red, unpalatable – the aposematic model), B (red-orange – a "mimic" similar to A, but palatable), and F (blue, palatable but distinct from A). An optimal forager should choose B and F, but there is of course the risk of errors (“confusing” A with B). Thus, in a situation when time is limited, predators should go for safe option F. However, this would involve *false alarm* errors, avoiding the profitable B, and halving the intake rate. These experiments should identify the range of similarity in which speed accuracy tradeoffs mean that inaccurate mimics might not only enjoy improved protection from predators relative to palatable insects without aposematic colouration, but also, critically, the a further increase in similarity to the model might confer no further fitness benefits.

Insert Figure 2 about here

Categorization of food types by animals

Categorization allow us to classify stimuli in meaningful way (e.g. as dogs, cats, chairs, tables etc.), and independently of their individual shape and colour. Note that

categorization differs from generalization. Generalization allows animals to attribute common properties to distinguishable objects; however, the level of similarity can vary in a continuous fashion, as when one sees a greater similarity of yellow to orange than to red, and likewise of yellow to lime than to green. On a continuous sensory dimension, such as the visible spectrum, the extent of generalization from a given stimulus value (e.g. wavelength of light) typically has a Gaussian or exponentially shaped function centred on that value [7,22,23]. By comparison, categories have definite boundaries – an object is either a member of a category or not – and they can include diverse or entirely dissimilar items, such as dogs or fruit, but a category has some defining feature that is common to all its members. Categorization may also be understood as a strategy for being economic with memory – by extracting the cues that define a class of objects, rather than just a single object, an animal might circumvent having to memorise the appearance of dozens of salient objects [24].

A predator *without* categorisation might make almost inconceivably inappropriate judgments: consider an animal that, after being stung in the tongue by a black-and-red bumblebee, treats a black/yellow/white striped bumblebee as potentially palatable. Hence, categorisation is adaptive, but there is a risk of “false alarm” errors, where palatable mimics (even if they bear no direct similarity to aposematic prey) fall within an avoided category. Pigeons and chicks have been shown to be able to form categories [23,24]; for example, Cerella [25] made a good case that pigeons recognise oak leaves as a natural category. In particular, after learning a single oak leaf shape, they did not discriminate between a wide range of oak leaves, but reliably distinguished oaks from leaves of other species. As with tree leaves, aposematic insects such as wasps, bumblebees and shield-bugs (Pentatomidae) have a characteristic shape that birds might recognise as natural kinds; alternatively, they might classify patterns according to

whether or not they contain more than one colour (independently of the particular combinations of colours) etc.

Testing the role of prey categorization in insectivores

Rather than just associating one colour pattern with an unpleasant experience, do predators learn the rules for classifying patterns, such as those that are displayed by toxic insects, to predict whether an unfamiliar species of insect is safe to eat? In human education a successful strategy is first to learn the rules, then the exceptions. If birds first learn the basic principles of warning coloration, then even poor mimics might enjoy protection, especially when predators have to make rapid judgements (see above). For example, after a predator has had unpleasant encounters with two distinct bumblebee species, it might categorise by prey shape and not colour, and subsequently avoid all bumblebees irrespective of colour banding pattern. An especially interesting question concerns the way in which animals establish categories after learning about a number of distinct stimuli that share common properties. It is widely thought that groups of similar but discriminable prey species form so-called 'mimicry-rings' [3,4,26] (Figure 2), and there is experimental evidence that birds can establish well-defined color categories from multiple examples [22]. In nature, after being exposed to two or more different wasp species that differ in shape and colour but share a high contrast stripe pattern, birds might categorise by pattern and irrespective of shape, therefore including some hoverflies despite their difference in body shape. These questions should be straightforward to address experimentally, using sequential exposure to different prey items either on computer screens, or printed patterns with food attached (see above). Understanding how avian predators classify the range of patterns that are displayed by hymenopterans and their mimics, depending on individual experience, and the cues that they extract to form categories will give valuable insights into the evolution of mimicry, and also provide a

naturalistic context in which to address wider questions about the cognitive processes that underlying object recognition in non-human species [27]. The differences between responses following training to single and multiple examples will give important information about the natural history of mimicry rings, and the underlying cognitive processes. An important (and untested) prediction is that if predators use experience with multiple prey types to learn rules rather than just memorising the appearance of individual prey types, it follows that different individual predators should form different categories, each including separate types of novel prey – depending on individual experience.

Conclusion

Mimicry - the phenomenon where organisms converge in appearance on one another, often to warn or deceive predators – is one of the most venerable and at the same time most dynamic areas in whole organism biology. Recent developments in animal cognition now make it possible to understand not only how animals perceive mimicry systems [5,28,29], but also how they store information about such systems, how such information consolidates and changes with experience and with time [30-32], and how animals might extract the general rules by which animal colouration and palatability are linked. Incorporating realistic time constraints into experiment designs, and the visual information processing speed of predators, should help identify the conditions under which the cognitive processes of predators, which will be adaptive under most conditions, will sometimes create quirks that produce space for inaccurate mimics to live.

Acknowledgments

We wish to thank I.C. Cuthill, A. G. Dyer and J. Mallet for discussions.

Competing interests. The authors declare that no competing interests exist.

References

1. Rowe C, Guilford T (1996) Hidden colour aversions in domestic chicks triggered by pyrazine odours of insect warning displays. *Nature* 383: 520-522.
2. Mostler G (1935) Beobachtungen zur Frage der Wespenmimikry. *Zeitschrift für Morphologie und Ökologie der Tiere* 29: 381-454.
3. Ruxton GD, Sherratt TN, Speed MP (2004) *Avoiding attack*. Oxford: Oxford University Press. 249 p.
4. Gilbert F (2005) The evolution of imperfect mimicry. In: Fellowes M, Holloway G, Rolff J, editors. *Insect Evolutionary Ecology*. Wallingford: CABI Publishing. pp. 231-288.
5. Dittrich W, Gilbert F, Green P, McGregor P, Grewcock D (1993) Imperfect mimicry: a pigeon's perspective. *Proc R Soc Lond B* 251: 195-200.
6. Sherratt TN (2002) The evolution of imperfect mimicry. *Behavioral Ecology* 13: 821-826.
7. Ham AD, Ihalaenen E, Lindstrom L, Mappes J (2006) Does colour matter? The importance of colour in avoidance learning, memorability and generalisation. *Behav Ecol Sociobiol* 60: 482-491.
8. Johnstone RA (2002) The evolution of inaccurate mimics. *Nature* 418: 524-526.
9. Speed MP (2000) Warning signals, receiver psychology and predator memory. *Animal Behaviour* 60: 269-278.
10. Wolfe J (2000) Visual attention. In: DeValois KK, editor. *Seeing*. San Diego: Academic Press.
11. Abraham NM, Spors H, Carleton A, Margrie TW, Kuner T, et al. (2004) Maintaining accuracy at the expense of speed: Stimulus similarity defines odor discrimination time in mice. *Neuron* 44: 865-876.
12. Chittka L, Dyer AG, Bock F, Dornhaus A (2003) Bees trade off foraging speed for accuracy. *Nature* 424: 388-388.
13. Dyer AG, Chittka L (2004) Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. *J Comp Physiol A* 190: 759-763.
14. Ditterich J, Mazurek ME, Shadlen MN (2003) Microstimulation of visual cortex affects the speed of perceptual decisions. *Nature Neuroscience* 6: 891-898.
15. Heekeren HR, Marrett S, Bandettini PA, Ungerleider LG (2004) A general mechanism for perceptual decision-making in the human brain. *Nature* 431: 859-862.
16. Chittka L, Spaethe J (2007) Visual search and the importance of time

- in complex decision making by bees. *Arthropod Plant Interactions* 1: 37-44.
17. Chittka L, Raine NE (2006) Recognition of flowers by pollinators. *Current Opinion in Plant Biology* 9: 428-435.
 18. Passino KM, Seeley TD (2006) Modeling and analysis of nest-site selection by honeybee swarms: the speed and accuracy trade-off. *Behavioral Ecology and Sociobiology* 59: 427-442.
 19. Franks NR, Dornhaus A, Fitzsimmons JP, Stevens M (2003) Speed versus accuracy in collective decision making. *Proceedings of the Royal Society of London Series B-Biological Sciences* 270: 2457-2463.
 20. Cuthill IC, Stevens M, Sheppard J, Maddocks T, Parraga CA, et al. (2005) Disruptive coloration and background pattern matching. *Nature* 434: 72-74.
 21. Howse PE, Allen JA (1994) Satyric mimicry: the evolution of apparent imperfection. *Proc R Soc B* 257: 111-114.
 22. Baddeley RJ, Osorio D, Jones CD (2007) Generalization of color by chickens: Experimental observations and a Bayesian model. *American Naturalist* 169: S27-S41.
 23. Jones CD, Osorio A, Baddeley RJ (2001) Colour categorization by domestic chicks. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268: 2077-2084.
 24. Huber L, Troje NF, Loidolt M, Aust U, Grass D (2000) Natural categorization through multiple feature learning in pigeons. *Quarterly Journal of Experimental Psychology Section B-Comparative and Physiological Psychology* 53: 341-357.
 25. Cerella J (1979) Visual Classes and Natural Categories in the Pigeon. *Journal of Experimental Psychology-Human Perception and Performance* 5: 68-77.
 26. Plowright RC, Owen RE (1980) The evolutionary significance of bumble bee color patterns: a mimetic interpretation. *Evol* 34: 622-637.
 27. Bain RS, Rashed A, Cowper VJ, Gilbert FS, Sherratt TN (2007) The key mimetic features of hoverflies through avian eyes. *Proc R Soc B* 274: 1949-1954.
 28. Cuthill IC, Bennett ATD (1993) Mimicry and the eye of the beholder. *Proc R Soc Lond B* 253: 203-204.
 29. Stevens M (2007) Predator perception and the interrelation between different forms of protective coloration. *Proceedings of the Royal Society B-Biological Sciences* 274: 1457-1464.
 30. Darst CR, Cummings ME (2006) Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature* 440: 208-211.
 31. Ruxton GD, Speed MP (2005) A taste for mimicry. *Nature* 433: 205-207.
 32. Skelhorn J, Rowe C (2005) Tasting the difference: do multiple defence chemicals interact in Mullerian mimicry? *Proceedings of the Royal Society B-Biological Sciences* 272: 339-345.

Figures



a



b



c



d



e



f

Figure 1: Two wasp species and four less-than perfect and palatable mimics. a) *Dolichovespula media*; b) *Polistes* spec.; c) *Eupeodes* spec.; d) *Syrphus* spec; e) *Helophilus pendulus*; f) *Clytus arietes* (all species European). Note that species c-f) do not look closely similar to *any* wasp species. The three hoverfly species differ in wing and body shape, antennal length, flight behaviour and striping pattern from European wasps. One fly species (e) even has longitudinal stripes which wasps typically don't. The harmless wasp beetle does not normally display wings, and its legs do not resemble those of any wasps. Photos a,c,e and f by Rob Knell; photos b and d by Tom Ings.



Figure 2. Colour coats of European bumblebees, and a stingless mimic. a) *Bombus lapidaries*; b) *B. terrestris*; c) *B. pascuorum* and d) the fly *Volucella bombylans*. Note that b) and d) are considered part of the same mimicry ring [26], even though they are clearly distinct – but a predator categorizing by shape might respond equally to both, as to the highly distinct *B. lapidaries* (a), and the individual of the fly *V. bombylans* (d) that looks like no particular Central European bumblebee species, but captures the overall essence of a bumblebee-like appearance (body shape, and hair coat, and some form of stripes. Photos a) and b) by Tom Ings; photo c) by Mike Edwards and d) by Rob Knell.