# How cognitive biases select for imperfect mimicry: a study of asymmetry in learning with bumblebees

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Imperfect mimicry presents a paradox of incomplete adaptation — intuitively, closer resemblance should improve performance. Receiver psychology can often explain why mimetic signals do not always evolve to match those of their models. Here, we explored the influence of a pervasive and powerful cognitive bias where associative learning depends upon an asymmetric interaction between the cue (stimulus) and consequence (reinforcer), such as in rats, which will associate light and tone with shock, and taste with nausea, but not the converse. Can such biases alter selection for mimicry? We designed an artificial mimicry system where bees foraged on artificial flowers, so that colours could be switched between rewarding or aversive. We found that when the colour blue was paired with a sucrose reward, other cues were ignored, but not when blue was paired with aversive compounds. We also tested the hypothesis that costs of errors affect how receivers sample imperfect mimics. However, costs of errors did not affect bee visits to imperfect mimics in our study. We propose a novel hypothesis for imperfect mimicry, in which the pairing between specific cues and reinforcers allows an imperfect mimic to resemble multiple models simultaneously. Generally, our results emphasize the importance of receiver psychology for the evolution of signal complexity and specificity.

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Mimicry is a classic example of adaptation in which one organism (the mimic) evolves to resemble another (the model) because selection favours displaying the same signal to shared receivers (Bates, 1862; Johnson & Schiestl, 2016; Müller, 1879; Ruxton, Sherratt, & Speed, 2004). Across mimicry as a whole, there is a spectrum of mimetic perfection that stretches from the exquisitely precise to the barely plausible (Fig. 1) (Chittka & Osorio, 2007; Dittrich, Gilbert, Green, McGregor, & Grewcock, 1993; Gilbert, 2005; Johnson & Schiestl, 2016; Sherratt & Peet-Paré, 2017). When mimicry is imperfect, it is surprising: either our intuition about the nature of the signals is incorrect, or additional constraints or selective forces need to be taken into account (Kikuchi & Pfennig, 2013; Ruxton et al., 2004). Mimicry is a rare instance in which a reasonable hypothesis can be formulated about a potential adaptive optimum (Maynard Smith, 1978), as its evolution is explicitly predicated upon an observable phenotype. To ask why imperfect mimics occur is to explicitly study constraints, trade-offs and other forces that, in combination with selection, determine the form of adaptations.

Receiver psychology is a selective force with extensive scope for explaining the evolution of communication (Endler & Basolo, 1998; Guilford & Dawkins, 1991; Rowe, 2013; Schiestl & Johnson, 2013; Speed, 2001). Indeed, a recent major review identified it as an area in need of research (Endler & Mappes, 2017). It includes simple biases for preferring (or avoiding) features before any learning has occurred, which can make imperfect mimicry viable, such as when innate aversions to certain traits cause avoidance (Kikuchi & Pfennig, 2010; Smith, 1975, 1977). It also includes biases that only manifest themselves during learning, such as cue competition, in which a receiver learns to associate one feature of a model's signal with its reward or punishment at the expense of other features that could also be associated with the reward (Mackintosh, 1976; Pavlov, 1927; Rescorla & Wagner, 1972). Cue competition thus reduces the number of features in which mimics must evolve to resemble their models (Kazemi, Gamberale-Stille, Tullberg, & Leimar, 2014; Sherratt, Whissell, Webster, & Kikuchi, 2015). Conversely, in the absence of cue competition, multiple features of the mimic may fall under selection to resemble the model (Kazemi, Gamberale-Stille, & Leimar, 2015; Kikuchi, Mappes, Sherratt, & Valkonen, 2016). Properties of cues such as their salience (how quickly receivers learn to associate them with unconditioned stimuli, sensu Kazemi et al., 2014) or relative validity (accuracy in predicting an

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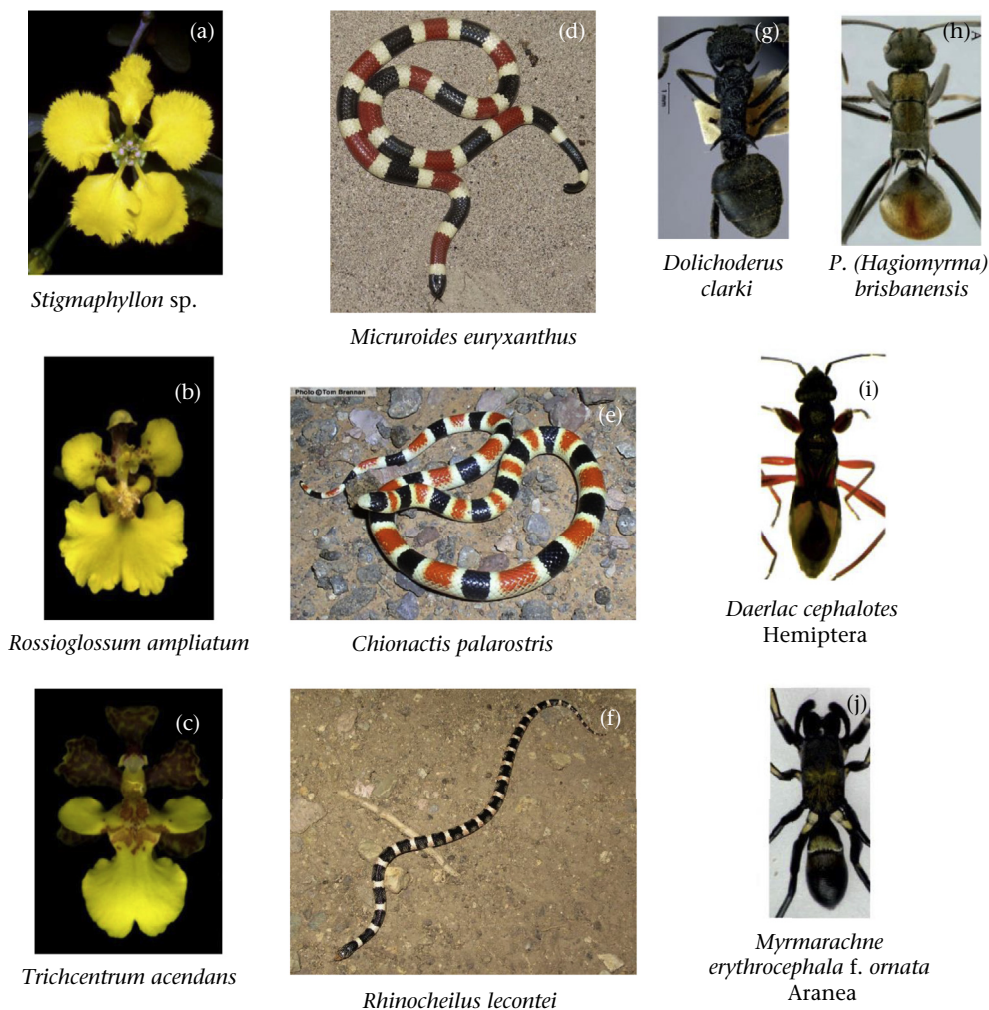   *E-mail address:* dkikuchi@email.arizona.edu (D. W. Kikuchi).

**Figure 1.** The range of mimetic precision across different mimicry complexes. The top row contains model species, the middle row contains relatively good mimics and the bottom row contains poor mimics. (a−c) A floral mimicry complex where a Malpighiaceae is mimicked by orchids (from Papadapulos et al., 2013, with permission). (d−f) The Arizona coral snake is mimicked by two nonvenomous colubrid snakes (photos: D. W. Kikuchi, Tom Brennan and David Pfennig, respectively, with permission). (g−j) In Australia, defended ants are models for other members of the so-called 'golden mimicry complex', typified by ant-like appearance and golden abdomens (from Pekár, Petráková, Bulbert, Whiting, & Herberstein, 2017, with permission). In this particular golden mimicry ring, these mimics appear intermediate in phenotype between two species of models.

unconditioned stimulus) can determine which ones outcompete others (Oberling, Bristol, Matute, & Miller, 2000; Shettleworth, 2010). Here, we aim to expand our understanding of how cognitive biases can explain the form of mimetic signals.

Cognitive biases can be beneficial for signal receivers because they reduce the burden of exploration that receivers must undertake in complex, potentially dangerous and changeable environments (Bradbury & Vehrencamp, 2011; Dunlap & Stephens, 2009). One powerful, pervasive type of bias occurs when one cue outcompetes others only when it is paired with a particular unconditioned stimulus (Dunlap & Stephens, 2014; Garcia & Koelling, 1966; Oberling et al., 2000; Schindler & Weiss, 1982). In these biases, some pairs of conditioned and unconditioned stimuli can be easily learned, but others cannot. The classic example occurs in rats, which can associate the audiovisual stimulus of light and tone with shock, and taste with nausea, but not light and tone with nausea or taste with shock, which is likely due to an evolutionary history of association between stimuli that are similar to the first two pairings of stimuli but not the latter two (Garcia & Koelling, 1966). In this manuscript, because we do not use the classical experimental design that defines stimulus−reinforcer interactions, many cognitive psychologists seek to explain (wherein animals are trained to compound stimuli, such as light and tone + taste, which are then tested separately; Powell, Honey, & Symbaluk, 2013), we call the phenomenon that we investigate 'asymmetric learning'. We do so because this classical design is less directly relevant to mimicry. Asymmetric learning may impinge on the features that models and mimics include in their signals, because some features (i.e. stimuli) are more easily associated with particular reinforcers than others. It is especially important to study these biases, since they are expected to at least some degree across many combinations of stimulus−reinforcer pairings, making them the norm rather than the exception (Schindler & Weiss, 1982). To fill this gap, we examine how the relationship between cues (i.e. stimuli) and their consequences (i.e. reinforcers) affects selection on imperfect mimics.

Another potentially important selective force acting on mimics is rational economic foraging behaviour by signal receivers (Berger, 1985; Dayan & Daw, 2008; Kacelnik & Bateson, 1996; McNamara & Houston, 1980). A widespread assumption of optimality models for receiver behaviour in mimicry systems is that receivers should be sensitive to the costs of errors (Getty, 1985; Kikuchi & Sherratt, 2015; Oaten, Pearce, & Smyth, 1975). Costs of errors are predicted to influence both the degree of mimetic imperfection that informed receivers will tolerate (Sherratt, 2002) and how much uninformed

receivers will invest in learning about imperfect mimics (Kikuchi & Sherratt, 2015). Such costs may include toxins (Irwin, Cook, Richardson, Manson, & Gardner, 2014), envenomation (Smith, 1975) or time wasted (Getty & Krebs, 1985). In addition to exploring cognitive biases, we also asked whether costs influence how willing receivers are to sample unfamiliar imperfect mimics. This hypothesis predicts that, rather than exhibiting invariant cognitive biases, receivers will visit fewer imperfect mimics as the potential costs of errors increase.

We conducted two experiments with bumblebees (*Bombus impatiens*) trained to forage in an artificial floral mimicry system. The flowers had multiple signal dimensions (two orthogonal pairs of colours − blue versus grey and cyan versus green). The first experiment tested whether one dimension of stimulus outcompeted the other. It also tested the prediction that cost influences how willing receivers are to sample imperfect mimics. The second experiment was designed to test for asymmetric learning. Specifically, we tested the hypothesis that blue outcompetes other cues only when it is paired with reward. We use the results of these experiments to propose a novel hypothesis for the evolution of imperfect mimicry that is founded upon asymmetric learning.

## METHODS

### Experiment 1

We conducted experiments with *B. impatiens*. *Bombus* spp. are generalist foragers that collect both nectar and pollen from flowers and readily learn floral preferences based on the rewards they receive (Goulson, 2010; Heinrich, 1979; Muth, Papaj, & Leonard, 2015). Furthermore, bees can be important participants in floral mimicry systems (e.g. de Avila, Oleques, Marciniak, & Ribeiro, 2017). We obtained four colonies from Koppert Biological Systems (Howell, MI, U.S.A.) and maintained them in wooden nestboxes with pine wood pellets (cat litter) as a substrate. Each nestbox was connected to a flight arena (74 × 58 cm and 38 cm tall) where bees were trained to forage for 2 M sucrose. At first, sucrose was delivered in a glass feeder, but once bees were acclimated to their foraging arenas, we trained them to forage from 0.1 ml PCR tubes embedded in plain, circular wooden pegs 19 mm in diameter and 75 mm tall. These pegs formed the structure of our artificial flowers. They were approximately 10 cm apart from one another.

We printed coloured patterns on paper and glued them on top of the wooden pegs before sealing them with clear polyurethane. Each pattern had two colours. We used four different colours in our experiment: blue, cyan, grey and green. The spectral reflectances of the finished flowers and their coordinates in bee colour space are shown in Fig. A1, and colour distances and achromatic contrasts between them are shown in Table A1. We used four different colour combinations on our flowers: blue−cyan, blue−green, grey−cyan and grey−green, producing a 2 × 2 design of blue versus grey and cyan versus green (Fig. 2).

Our experiment had two stages: training and testing. In the training stage, only two of the four kinds of flowers were present: grey−cyan and blue−green. One kind was rewarding, offering 8 μl of 2 M sucrose (i.e. it was a 'model' in our artificial mimicry complex), and the other was aversive, in one treatment group providing 8 μl of water, and in the other, 8 μl of 0.01 M quinine (making it a nonrewarding 'nonmimic', as it shared no colours in common with the rewarding flower). Water and quinine were chosen to create two treatments that differed in their levels of cost for making errors, because quinine is thought to be more aversive to bees than water alone (Chittka, Dyer, Bock, & Dornhaus, 2003) and has a lower LD50 (Tiedeken, Stout, Stevenson, & Wright, 2014). Bees were pseudorandomly assigned to the water or quinine treatment,
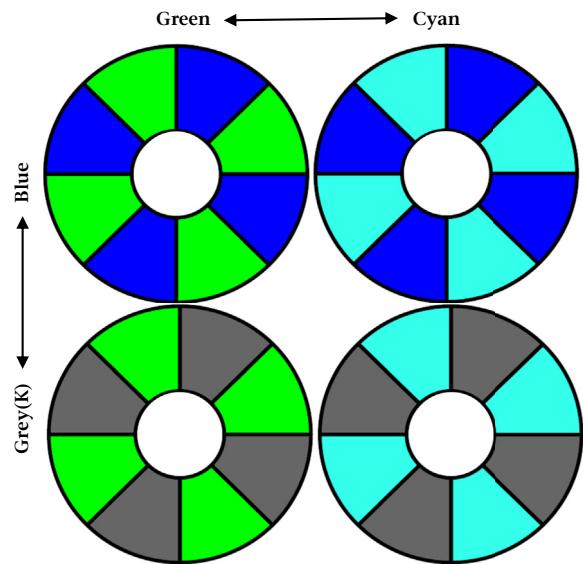
and we also randomized whether grey−cyan or blue−green was rewarding to examine potential effects of colour biases. We gave bees four trials of training in which they were allowed to forage on randomized arrangements of 16 rewarding flowers and 16 aversive flowers. A trial began when a worker entered the arena and ended when she returned to the colony to empty her honey crop.

Once a bee had completed four training trials, we gave her a test trial where eight of each of the four kinds of flowers were available: the rewarding flower, the aversive flower and two ambiguous flowers that had one previously rewarding and one previously aversive colour each (i.e. ambiguous flowers were imperfect mimics of rewarding flowers). This design forced bees to make a choice when confronting ambiguous flowers: they could treat them as rewarding or aversive, or unknown. All flowers in the test trial contained sucrose. After a bee finished her test trial, we removed her from the colony so that she would not interfere with future trials. We sampled 49 bees during experiment 1: 13 bees were trained to prefer blue−green flowers over grey−cyan flowers with quinine (blue−green+/grey−cyan quinine); 12 bees each were trained to prefer blue−green flowers over grey−cyan flowers with water (blue−green+/grey−cyan water), grey−cyan flowers over blue−green flowers with quinine (grey−cyan+/blue−green quinine) and grey−cyan flowers over blue−green flowers with water (grey−cyan+/blue−green water).

### Experiment 2

In experiment 1, it is possible that bees learned to respond only to colours paired with reward and ignored punishment. This would make any apparent asymmetry in learning that depended upon a stimulus−reinforcer pairing irrelevant. Therefore, it was critical to our study to show that bees did not respond only to the colours paired with reward in experiment 1 (Giurfa, Nunez, Chittka, & Menzel, 1995), but also that learning required colours to be paired with punishment. To determine the importance of punishment, we designed experiment 2 so that bees were trained on an absolute conditioning schedule, rather than differential conditioning. Absolute conditioning means that during training, only rewarding flowers of a single kind are present. Thus, procedures for



**Figure 2.** The four flower types used in our experiment. We chose this 2 × 2 design so that flowers would be defined by two orthogonal axes: blue versus grey and cyan versus green.

experiment 2 were similar to those for experiment 1, with two modifications. First, bees were trained to drink from wooden flowers that already bore the rewarding colours (grey–cyan), so that they never experienced rewards on any other kind of feeder (i.e. plain wooden flowers). We made this change to avoid teaching bees that flower colour is irrelevant. Second, we did not train bees with anything aversive; only rewarding grey–cyan flowers were present through the four training trials. The number of rewarding flowers available per trial was the same as it was in experiment 1 (i.e. 16 flowers in each training trial). We used a total of 15 bees from three different colonies for experiment 2.

All data generated in both experiments is available as Supplementary Material.

*Analysis*

We analysed how bees learned to discriminate between rewarding and unrewarding flowers across their four training trials of experiment 1 to see if the level of cost affected how quickly they learned. We also analysed the colours of the flowers that were paired with reward or punishment among our predictors to detect any biases in learning rate during training. The response variable was the proportion of rewarding flowers visited out of all flowers visited in each trial. We used logistic regression with the identity of each bee as a random effect. We considered five potential structures of fixed effects, and selected among them using Akaike's information criterion (AIC). We used the difference in AIC between the best-fit model and other models to assess how well one model fit versus another (ΔAIC). The parameters that we considered as fixed effects were the aversive flower type (factor), trial number (continuous) and cost level (factor). We used analysis of deviance to test our best-fit model against the next simplest possible model to confirm the significance of model fit (likelihood ratio test, LRT).

We then analysed the test trial. To maximize the rewards:costs ratio, one would expect that higher costs would cause bees to visit imperfect mimics at a lower rate. To see whether this was the case, we tested whether the cost treatment affected flower choices by bees (number of flowers landed on as a function of their type; i.e. rewarding models, nonmimics or imperfect mimics) during the test trial in experiment 1. In terms of the statistical model, we tested whether the number of flowers visited (response) was predicted by the interaction of flower type with the level of cost the bees were trained on. We used Poisson errors with a log link to perform a log-linear analysis of these contingency table data and included bee identity as a random intercept. In R pseudocode: number visited ~ cost × flower type + (1|bee).

We tested for a significant interaction with cost by using an analysis of deviance (which returns a *P* value) and also evaluated ΔAIC scores (Akaike, 1974; Bolker, 2008; Burnham & Anderson, 2004). Only the first five flowers visited by each bee were used for this analysis, which was a compromise between analysing the behaviour of bees before extinction had occurred and taking into account multiple choices of flowers for each bee. Five was the average number of visits each bee made before visiting a flower that was previously paired with punishment; however, our results are not sensitive to this specific number.

In addition to testing whether simply being a model, nonmimic or imperfect mimic influenced visiting rates, we also analysed the effect of colour dimensions on visits (i.e. we desegregated flowers into their colour combinations, rather than using the three factor levels model, mimic and imperfect mimic). This was essential for determining whether cognitive biases such as cue competition affected bee behaviour. Although the traditional way of demonstrating cue competition phenomena (e.g. blocking, over-shadowing; Kruschke, 2008) is to train animals on compounds and

test them with separate elements of the compounds, modern statistical model-fitting methods make it possible to infer the marginal contributions of elements. We compared four models for predicting the characteristics of the first five flowers visited: (1) an additive model that included both whether flowers were blue versus grey and cyan versus green; (2) a single-factor model that only included blue versus grey; (3) a single factor model that only included cyan versus green; and (4) an intercept-only model. The response variable was the number of flowers of each colour combination visited. All models were GLMMs with Poisson errors, log links and bee identity included as a random intercept. In R pseudocode: number visited ~ blue versus grey + green versus cyan + (1|bee); number visited ~ green versus cyan + (1|bee); number visited ~ blue versus grey + (1|bee); number visited ~ 1 + (1|bee).

We ran these models separately for blue–green (+) and grey–cyan (+) treatments so that if biases existed, they would be readily interpretable. Again, we used analysis of deviance to test our best-fit model against the next-simplest possible model (if there were two, we used the one with the smallest ΔAIC for comparison).

In experiment 2, we wanted to determine whether absolute conditioning could produce the same pattern of colour categorization as differential conditioning did, as this could tell us whether the outcome of cue competition by blue depended on pairing it with reward rather than punishment. To contrast the results with those of experiment 1, we used the same four models described in the preceding paragraph to predict visiting to the first five flowers of the test trial. As above, the ΔAIC scores were used to identify the models that fit the data best, as well as analysis of deviance.

## RESULTS

The best model of learning rate had an interaction between trial number and the type of flower that was aversive, but not the level of cost (ΔAIC = 2.14; Fig. 3). The next best-fit model featured only
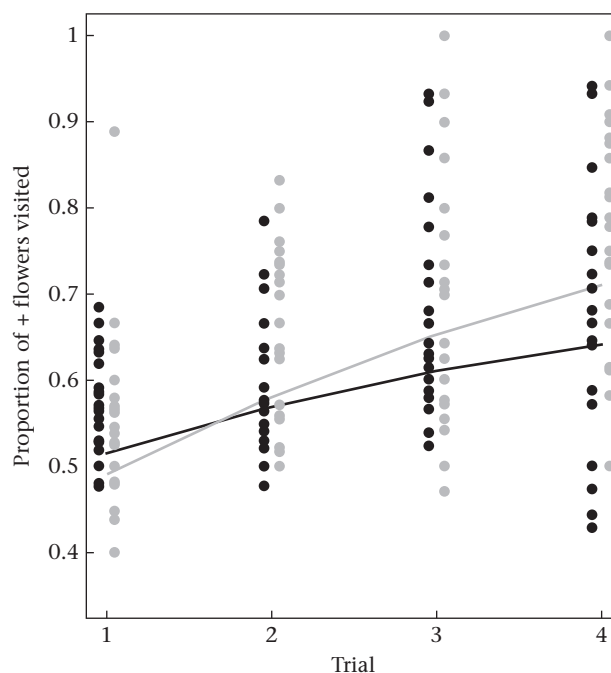


**Figure 3.** The proportion of rewarding flowers visited (out of both rewarding and aversive flowers visited) across the four training trials of experiment 1. Grey symbols: blue–green rewarding; black symbols: cyan–grey rewarding.

trial as a fixed effect. Analysis of deviance revealed that the former model with the lower AIC fit the data significantly better than the next-best model (LRT: $\chi^2_1 = 5.18$, $P = 0.023$). Thus, we found no evidence that bees learned to discriminate at different rates when aversive flowers contained water or quinine.

In the test trial of experiment 1, including an interaction between flower type (model, nonmimic, imperfect mimic) and punishment (water, quinine) did not improve model fit over a simpler model without the interaction ($\Delta AIC = 3.64$ in favour of simpler model; LRT: $\chi^2_2 = 0.36$, $P = 0.84$). This result was inconsistent with the hypothesis that costs influence visits to imperfect mimics.

In experiment 1, we also found evidence that the blue versus grey dimension outcompeted the green versus cyan dimension, but this depended upon whether blue–green or grey–cyan combination was paired with reward (Fig. 4). When grey–cyan was rewarding, bees used both dimensions make decisions, so that the probability of a response was influenced by all of the colours on each flower ($\Delta AIC = 7.93$ for the additive model including both colour axes; LRT: $\chi^2_1 = 9.93$, $P = 0.002$). For example, if a flower had both grey and cyan, it was visited at approximately twice the rate as flowers that had only one of those two colours (compared to the baseline probability of visiting the aversive blue–green flowers; Fig. 4a). Thus, there was no one cue that outcompeted the others. On the other hand, when blue–green was rewarding, bees used only the presence of blue versus grey to make their foraging decisions, so this colour axis outcompeted green versus cyan (Fig. 4a). We demonstrated this by showing two things: first, that the blue versus grey model fit better than the intercept-only model (so bees were not guessing randomly; $\Delta AIC = 17.75$; LRT: $\chi^2_1 = 19.75$, $P < 10^{-4}$). Second, the more complex, additive model did not explain the data significantly better than the simpler, blue versus grey model (so bees did not pay attention to green versus cyan; $\Delta AIC = 2.00$; LRT: $\chi^2_1 = 0$, $P = 1$; coincidentally, bees visited exactly the same number of green and cyan flowers, resulting in this anomalous statistic).

Experiment 2 tested whether punishment was necessary for discrimination learning. In the test trial, the best-fit model was the intercept-only model ($\Delta AIC = 0.89$ LRT: $\chi^2_1 = 1.11$, $P = 0.29$). In other words, because we failed to reject the intercept-only model in favour of more complicated ones, there was no evidence to suggest that bees discriminated among flowers at all (Fig. 5, Fig. A2). Bees
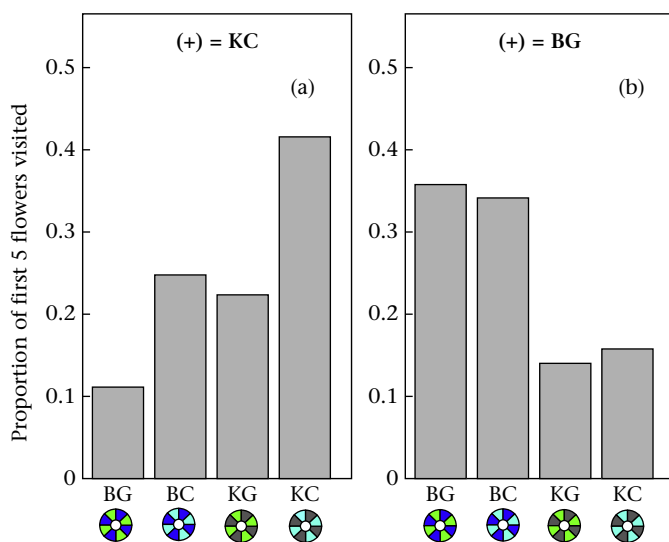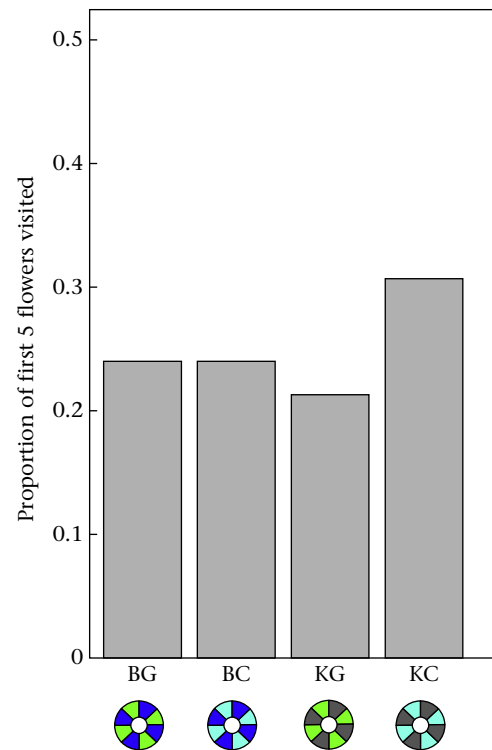


**Figure 5.** Relative visiting rates to each type of flower among the first five flowers visited during the test trial of experiment 2. B = blue; C = cyan; G = green; K = grey.

only learned to discriminate in experiment 1, where both reward and punishment were used.

## DISCUSSION

We performed two experiments in this study. The first experiment tested the hypothesis that costs influence the rate at which bees visit flowers that resemble, but do not perfectly match, training stimuli ('imperfect mimics'); this was not supported. It also suggested that some colours could outcompete others during associative learning, but that this effect depends on which reinforcers are paired with which colours. Imperfect mimics that had blue were visited at the same rate as the flower that was paired with rewards during training (i.e. the model) if the model had blue (Fig. 4a), but both imperfect mimics were visited at lower rates if the model did not have blue (Fig. 4a). The second experiment showed no discrimination based on colour, confirming what experiment 1 suggested: that the outcome of cue competition depended on the interaction of colour with both reward and punishment.

Blue is often preferred by bumblebees over other colours (Cakmak et al., 2010; Gumbert, 2000; Ings, Raine, & Chittka, 2009). Whether bees use it to the exclusion of other cues for learning therefore seems to depend on it occurring in its ecologically expected role – as an indicator of rewarding flowers (Raine & Chittka, 2007). It is likely that asymmetric learning of blue colours and nectar has evolved because bumblebees have a long evolutionary history with rewarding flowers whose most reliable visual signal is blue (or violet) coloration (Raine & Chittka, 2007). Colours that feature transitions in reflectance at 400 nm and 500 nm may also be particularly salient to bees, acting as so-called 'marker points' (Bukovac et al., 2017; Chittka & Menzel, 1992).

Asymmetric learning has implications for the design of visual signals, particularly mimicry (Johnson & Schiestl, 2016). Our work



**Figure 4.** Relative visiting rates to each type of flower among the first five flowers visited during the test trial of experiment 1. (a) Grey–cyan rewarding. (b) Blue–green rewarding. B = blue; C = cyan; G = green; K = grey.

reveals that unrewarding floral mimics can be imperfect if they mimic blue flowers, because a feature that outcompetes others relaxes selection on the dimensions that are excluded (Kazemi et al., 2014; Sherratt et al., 2015). Blue coloration would not be a handicap to mimicking rewarding flowers without blue, however, because blue does not outcompete those other colours when it is unrewarding. This means that if a partially blue flower imperfectly mimics another that does not have blue, it may also be an effective mimic of blue-containing flowers. This sort of imperfect mimic would receive visits from receivers that respond to either type of model flower (Fig. 6). Thus, it would have greater fitness than imperfect mimics not containing blue, as well as perfect mimics of either model (Fig. 6). We emphasize that our hypothesis means that imperfect mimics can have greater fitness than perfect ones, whereas other hypotheses involving overshadowing are of the 'relaxed selection' type where imperfect mimics are simply as good as perfect ones. Of course, any other trait besides blue coloration could also do the same if its role in associative learning depended on its interaction with different reinforcers.

The hypothesis for imperfect mimicry that we describe above is a psychological twist on the multiple models hypothesis for the evolution of imperfect mimicry (Darst, Cummings, & Cannatella, 2006; Edmunds, 2000), formalized in continuous trait space by Sherratt (2002). This hypothesis generally proposes that imperfect mimics are imperfect because they receive the benefits of simultaneously resembling multiple models. Our hypothesis is similar to signal detection theories for mimicry of multiple models, but differs in the following ways: it operates on discrete traits, makes no prediction about how the phenotypes of imperfect mimics will vary with the relative abundance of models and mimics, and it predicts that imperfect mimics and one of their models should share a trait that is subject to asymmetric learning. It may be especially helpful in understanding mimicry complexes that feature multicomponent signals (Bradbury & Vehrencamp, 2011; Dalziell & Welbergen, 2016; Hebets & Papaj, 2005). For example, in Mexico, a defensive mimic (*Pliocercus* spp.) has a mixture of features from the signals of two models, *Micrurus diastema* and *Micrurus elegans* (Greene & McDiarmid, 1981). In addition, rewardless flowers are often difficult classify as Batesian mimics because they can resemble many model species ('generalized floral deception'; Johnson & Schiestl, 2016; Papadopulos et al., 2013; Schaefer & Ruxton, 2009). We suggest that in some cases, rewardless flowers that are difficult to assign to a single model species may be reaping the benefits of asymmetric learning to resemble more than one model. Specific floral assemblages to test the predictions of our hypothesis could be identified using large data sets of floral phenotypes and floral rewards (e.g. Ollerton et al., 2009; Papadopulos et al., 2013), and then targeted with behavioural experiments in the field and laboratory.

An important point to make regarding any of the hypotheses for how receiver psychology affects mimicry is that selection will only reflect a receiver's cognitive biases to the degree to which it is represented in the community of receivers. The selective surface
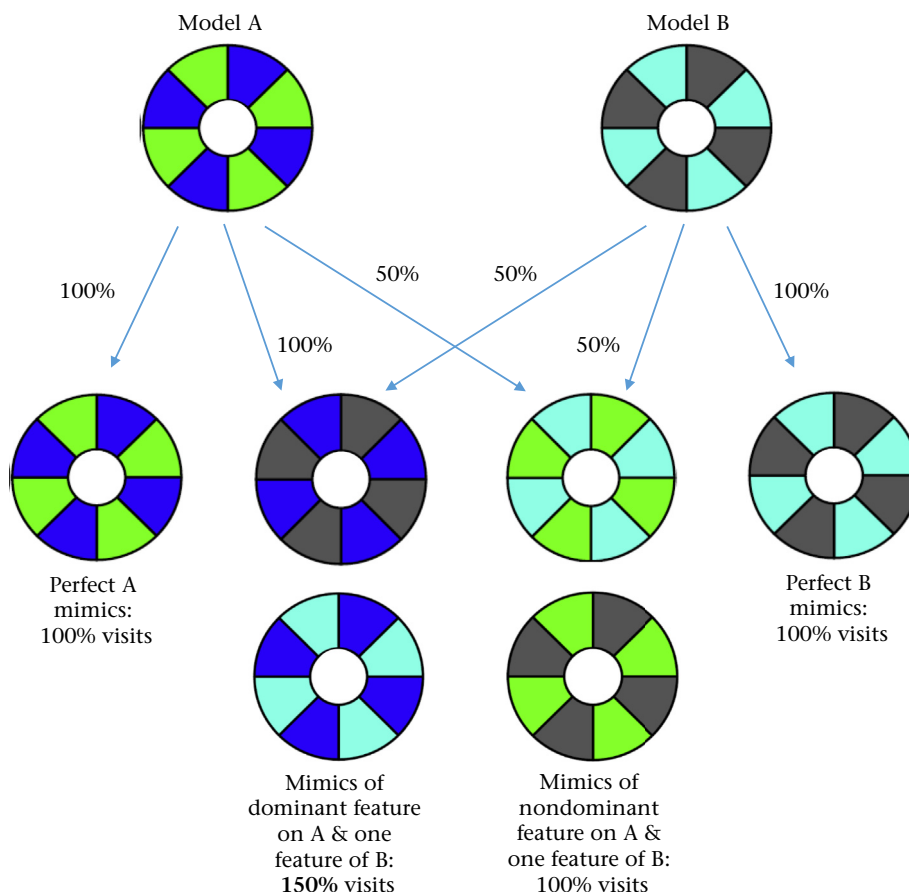


**Figure 6.** An illustration of how asymmetric learning could lead to imperfect mimics that have higher fitness than perfect mimics of either of two models (A or B) or imperfect mimics that do not have a feature that is subject to asymmetric learning. In this illustration, imperfect mimics with blue get the full benefit of mimicking model A, due to blue having an advantage in cue competition. However, blue does not outcompete other colours when paired with punishment, so it does not completely prevent the mimic from being partially associated with model B. This leads to an elevated rate of response to the mimic's signal. Percentages listed on the arrows are arbitrary and could be substituted for others that have the same relative ordering.

over which mimicry evolves will represent the aggregate behaviour of all the receivers in a community (Endler & Mappes, 2004; Kikuchi et al., 2016). For example, the effect of a pollinator guild on a flower might be determined by the summed visit rates of each pollinator species, multiplied by the pollination efficacy of each species. Consequently, studies that apply receiver psychology to empirical mimicry systems should consider which receiver species are the most important for selection, and the combined effects of their biases.

We did not find that the cost we implemented of visiting aversive flowers had an effect on bee learning rates (Fig. 3) or behaviour in the test trial. Instead, bees appeared to quickly learn to minimize their costs of sampling flowers of both water and quinine types by minimally dipping the tips of their tongues into either the solution, leaving behind the majority (D. W. Kikuchi, personal observation). It was surprising to find no effect of cost, because Chittka et al. (2003) found that *Bombus terrestris* did decrease its error rate when foraging among flowers with quinine versus water, and Tiedeken et al. (2014) found that *B. terrestris* avoided quinine more than any other toxic compound they added to nectar. Our results may reflect a species-specific difference in how *B. terrestris* and *B. impatiens* respond to toxins in nectar (Adler, 2000; Irwin et al., 2014), or our design may have favoured time minimization rather than cost minimization during foraging (Maynard Smith, 1978).

We must also comment on the lack of colour discrimination by bees on an absolute conditioning schedule where all flowers are rewarding, as this differs from what has been found by other researchers. In other studies, bees learned to discriminate colours under absolute conditioning when colours were easy to distinguish, but not when they were very similar (Dyer & Chittka, 2004; Giurfa, 2004). The colours we used were easy for bees to distinguish — most were separated by at least the number of hexagon units in bee colour space as the stimuli that allowed bumblebees to discriminate with absolute conditioning in Dyer and Chittka (2004) (cyan and grey, which were closer together than other colour pairs, were separated by a large achromatic distance). However, in both Dyer and Chittka (2004) and Giurfa (2004), bees foraged on coloured disks that were presented to them on flat backgrounds, making colour the only cue the bees could use to locate nectar wells. Likely, in our experiment, the physical shape of the wooden flowers created an ancillary set of cues that the bees could use to locate nectar, although seeing the colour of the flowers surrounding the nectar was also unavoidable for bees.

In summary, we found that asymmetric learning governed how bees responded to imperfect mimics. Features subject to such cognitive biases may make imperfect mimics fitter than perfect mimics if multiple models are present. We did not find an effect of punishment cost on visits to imperfect mimics, which is assumed by many models but has received inconsistent support (Kikuchi et al., 2016; Kikuchi, Malick, Webster, Whissell, & Sherratt, 2015; Lindström, Alatalo, & Mappes, 1997; McGuire, Van Gossum, Beirinckx, & Sherratt, 2006).

## Declaration of Interest

We have no conflicts of interest to declare.

## Acknowledgments

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## Supplementary Data

## Appendix

**Table A1**
The six possible comparisons that can be made between colours in our study

| Colours contrasted | Chromatic contrast | Achromatic contrast |
|---|---|---|
| Blue–Cyan | 0.153134 | −0.27893 |
| Blue–Grey | 0.124358 | −0.01192 |
| Blue–Green | 0.340679 | −0.21334 |
| Cyan–Grey | 0.079964 | 0.267005 |
| Cyan–Green | 0.216074 | 0.06559 |
| Grey–Green | 0.295471 | −0.20142 |

Chromatic distance between colours is relatively large for all combinations except for cyan–grey, which show high achromatic contrast.
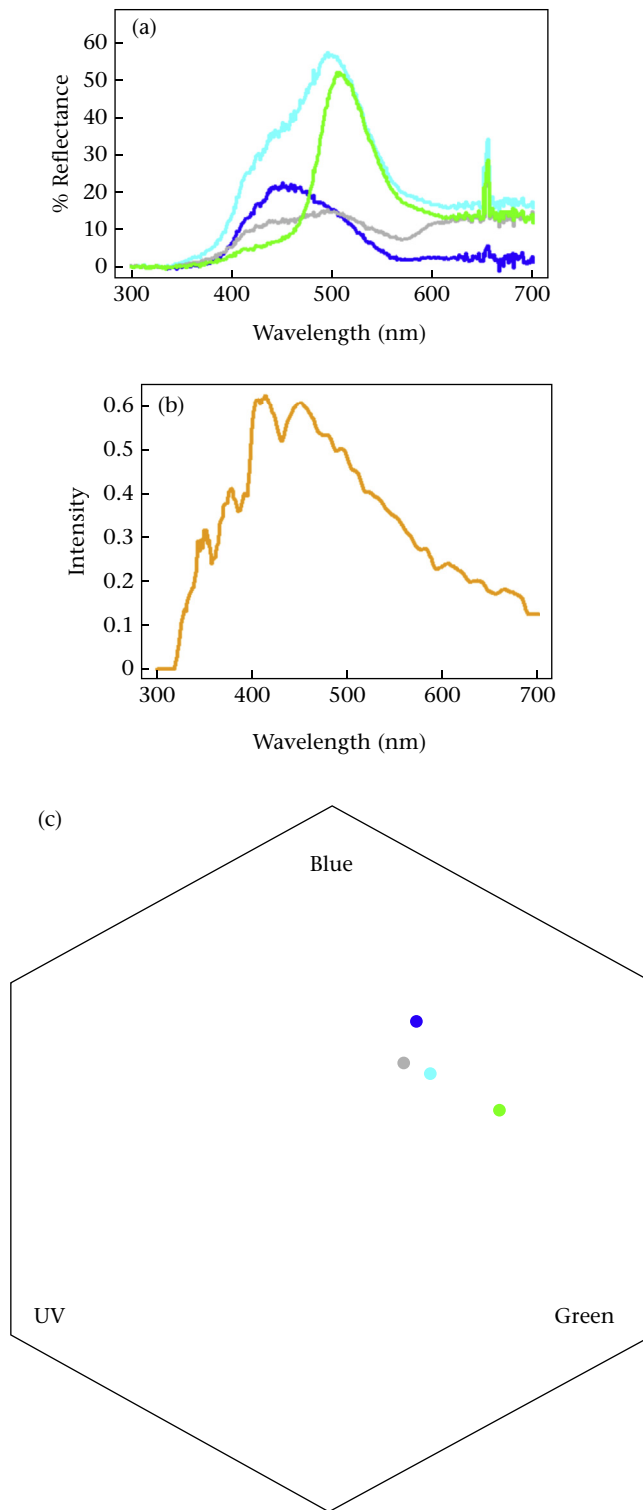
**Figure A1.** (a) Spectral reflectance curves of colours used in this study. (b) The ambient light source (default in Avicol v.6, Gomez, 2006). (c) Visualization of test colours on the bee colour hexagon. The experiment was carried out indoors under white fluorescent light (daylight spectrum lamps).
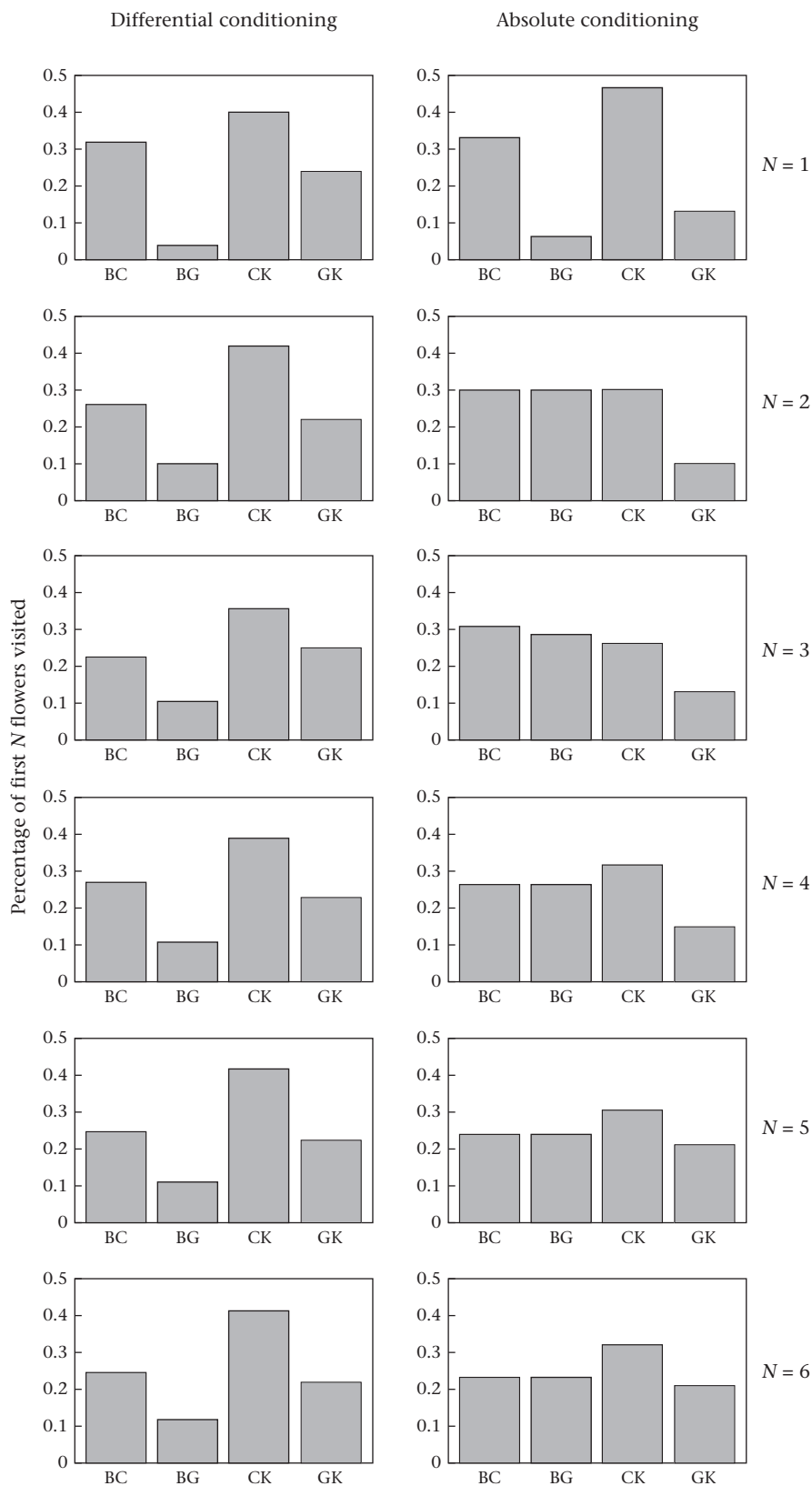
**Figure A2.** Relative visiting rates to the first *N* flowers visited by bees in the test trial after differential (experiment 1) and absolute (experiment 2) conditioning. The pattern of visits was consistent following differential conditioning but changed dramatically with each new flower visited following absolute conditioning. B = blue; C = cyan; G = green; K = grey. This suggests that any apparent trend towards visiting CK flowers in experiment 2 is an artefact.