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What is This?

How Do Hawkmoths Learn Multimodal Stimuli?
A Comparison of Three Models

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The moth *Macroglossum stellatarum* can learn the color and sometimes the odor of a rewarding food source. We present data from 20 different experiments with different combinations of blue and yellow artificial flowers and the two odors, honeysuckle and lavender. The experiments show that learning about the odors depends on the color used. By training on different color–odor combinations and testing on others, it becomes possible to investigate the exact relation between the two modalities during learning. Three computational models were tested in the same experimental situations as the real moths and their predictions were compared with the experimental data. The average error over all experiments as well as the largest deviation from the experimental data were calculated. Neither the Rescorla–Wagner model nor a learning model with independent learning for each stimulus component were able to explain the experimental data. We present the new hawkmoth learning model, which assumes that the moth learns a template for the sensory attributes of the rewarding stimulus. This model produces behavior that closely matches that of the real moth in all 20 experiments.

1 Introduction

Flowers attract pollinators mainly by color and odor stimuli. For newly eclosed moths and butterflies, it is important to quickly recognize a rewarding flower. Innate color and odor preferences contribute to this ability (Cunningham, Moore, Zalucki, & West, 2004; Weiss, 1997). By their innate preference for blue, naïve honeybees are guided to flowers with a large amount of nectar (Giurfa, Núñez, Chittka, & Menzel, 1995). A preference for blue is shared by other insects but innate color preferences can differ between species (Weiss, 2001). Rapid and flexible learning to associate color or odor with a reward has been demonstrated in honeybees,

butterflies, and moths (Andersson, 2003; Kelber, Vorobyev, & Osorio, 2003; Menzel, 1967; Srinivasan, Zhang, & Zhu, 1998; von Frisch, 1914, 1919; Weiss, 1997).

The diurnal hummingbird hawkmoth, *Macroglossum stellatarum*, uses color vision in searching for food, and spontaneously forages from colored artificial flowers without any odor (Kelber, 1997; Kelber & Hénique, 1999). *M. stellatarum* has a strong innate preference for blue flowers as a food source and a weaker preference for yellow (Kelber, 1997), but it can easily and equally fast learn other colors including green, which is not a color of a typical flower (Balkenius & Kelber, 2004; Kelber, 1997).

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349

M. stellatarum has most probably evolved from a nocturnal ancestor, and in nocturnal hawkmoths odor is very important in searching for food (Brantjes, 1978; Raguso & Willis, 2002). It has recently been shown that the ability of *M. stellatarum* to learn an odor that accompanies a color depends on the choice of color (Balkenius & Kelber, 2006). When an innately preferred blue color is learned together with an odor, the moth will not learn the odor. However, if the less preferred color yellow is used instead, the moths can readily learn the odor.

Stimuli of one sensory modality can influence learning of stimuli of another modality in different ways. In most cases, two stimuli are more effective than one, and the advantages of multisensory integration are of great importance in many animals (Luo & Kay, 1992). In honeybees, colors attract attention before odor, while odor attracts attention when the bees are very close to the food source (Giurfa, Núñez, & Backhaus, 1994; von Frisch, 1919). There is also evidence for increased learning when two stimulus types are combined (Rowe, 1999). In bumblebees, it has been shown that the presence of odor enhances color discrimination, and increases attention and memory formation (Kunze & Gumbert, 2001). In honeybees, the similarity between colors modulates odor learning (Giurfa et al., 1994; von Frisch, 1919). The similarity between colors has also been shown to modulate place learning in a hawkmoth (Balkenius, Kelber, & Balkenius, 2004).

A special case of multimodal learning is configural learning where an animal learns to respond to a configuration of stimuli, but not to the single stimulus modalities themselves (Mackintosh, 1974). The hawkmoth *Manduca sexta* needs both an odor and a visual stimulus to unroll the proboscis for feeding (Raguso & Willis, 2002), which also might be a preference for a configuration of both cues.

In contrast, two different situations have been found where learning of one stimulus prevents the learning of another stimulus. First, animals trained to a stimulus compound consisting of, for instance, a color and an odor, sometimes only learn one of the components. For example, they learn the color but not the odor. This effect is called overshadowing (Pavlov, 1927). Second, when animals are first trained to one stimulus component and later to the compound, they will not learn the stimulus component that was initially absent. The first component already predicts the reward and blocks learning of the second component (Kamin, 1969).

Blocking and overshadowing were originally defined for classical conditioning but have also been found in instrumental conditioning (Couvillon, Campos, Bass, & Bitterman, 2001; Couvillon, Mateo, & Bitterman, 1996; Mackintosh, 1974). A possible reason for the lack of learning of the second stimulus may be that the animal directs its attention only to the first stimulus (Zentall & Riley, 2000). The existence of blocking and overshadowing in insects is controversial and experiments have given mixed results (Couvillon et al., 1996, 2001; Couvillon, Arakaki, & Bitterman, 1997; Funayama, Couvillon, & Bitterman, 1995; Gerber & Ullrich, 1999). In particular, it has been disputed whether the learning of one stimulus modality depends on the other.

To test this, we collected data from 20 different learning experiments with *M. stellatarum* where multimodal stimuli were used. Most of the animal data have been previously published (Balkenius & Kelber, 2006), but experiments 8–12 are reported here for the first time. We also tested a number of learning models on these experiments using computer simulations. Although a number of models of insect learning exist (e.g., Borisyuk & Smith, 2004; Linster & Smith, 1997; Wessnitzer, Webb, & Smith, 2007), most of these are not applicable to our data. Because we were specifically interested in the role of interaction between stimulus components during learning, the primary models tested were the following:

1. The Rescorla–Wagner model, which assumes that learning depends on all stimulus components present and the prediction error of the reward magnitude.
2. The independence model, which assumes that learning of each stimulus component is independent of the other.
3. The new hawkmoth learning model, which assumes that the moth learns a template for the rewarded stimulus.

The first two models were selected as they have previously been suggested to explain learning in moths (Couvillon et al., 1997; Funayama et al., 1995). The new model was developed to overcome some of the limitations of the first two models.
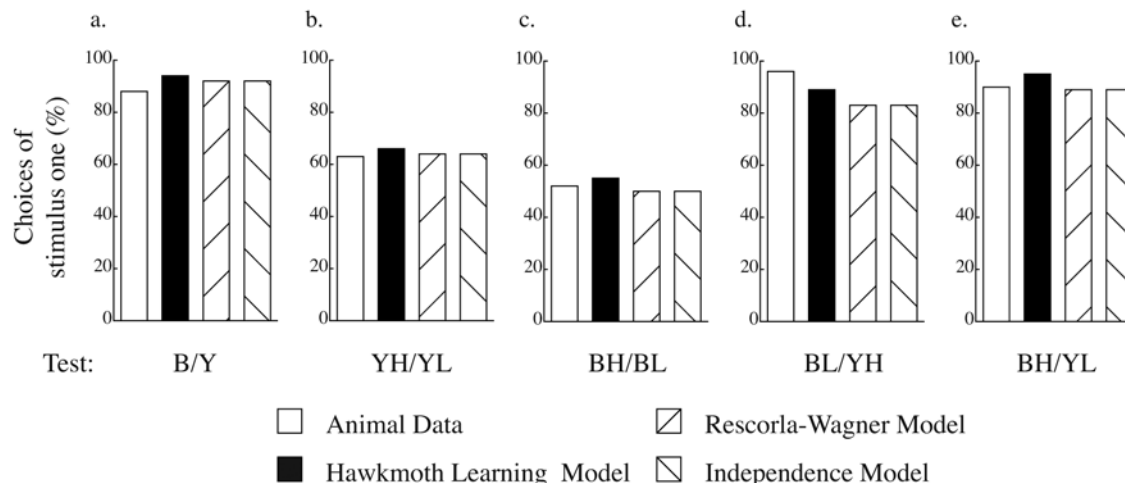
Figure 1 The results of the preference tests (experiments 1–5). All models reproduce the results of the preference tests very well (animal data from Balkenius & Kelber, 2006). B, blue; Y, yellow; H, honeysuckle; L, lavender.

2 Materials and Methods

M. stellatarum were bred in the laboratory throughout the year. The larvae were fed their natural food plant, and the pupae were kept at 20 °C. On the day after eclosion, the naïve moths were released in the cage with two feeders (Pfaff & Kelber, 2003). The experimental cage measured $50 \times 60 \times 70$ cm^3 and was illuminated from above with four fluorescent tubes (Osram, Biolux). Two feeders were placed 35 cm above the cage floor and 30 cm apart from each other. To prevent place learning (Balkenius et al., 2004), the feeders were randomly shifted between four locations during learning. During training, the rewarded feeder was filled with sucrose solution and the unrewarded feeder contained water. Groups of up to 25 moths were flying and feeding in the same cage. The tests occurred after 4 days of training. During tests, both feeders were filled with water and each moth was tested on its own. In all experiments, only the first artificial flower the moth touched with its proboscis was recorded.

Two colors—blue (B) and yellow (Y)—and two odors—artificial honeysuckle (H) and extract of lavender oil (L)—were used in the experiments. We distributed 25 µl of the odor extract in 10 ml of water or sucrose solution in the feeders and refilled every second day to make sure odor as well as reward was always available to the moths. Both honeysuckle and lavender flowers are visited by *M. stellatarum* in the wild (Herrera, 1992). In electroantennograms, *M. stel-*

latarum responded strongly to both odors (Balkenius, Rosén, & Kelber, 2006).

We ran 20 different experiments with different combinations of colors and odors. Experiments 1–5 were different preference tests (Figure 1). Untrained moths were presented with two stimuli and their first choice was recorded. The stimulus combinations used were B/Y, YH/YL, BH/BL, BL/YH, and BH/YL. Note that it is not possible to present an odor without a visual stimulus or to compare the preference for a color with the preference for an odor. The results of the preference tests were used to set the initial weights of the different computational models. The numbers of animals tested in the first five experiments were 25, 38, 21, 25, and 10, respectively.

In experiments 6 and 7, we tested the ability of the moths to learn which color was rewarded. The training used B+/Y and Y+/B, respectively, where + indicates that this stimulus was rewarded. The tests used the same stimuli, but without any reward. There were 20 animals in each experiment.

In experiments 8–12, the moths were trained on one combination of color and odor, and tested on another. These combinations are shown in Figure 2. The numbers of animals tested in these experiments were 50, 18, 21, 10, and 18, respectively.

We also used additional data from eight experiments previously reported by Balkenius and Kelber (2006), summarized in Figures 3 and 4. The experiments shown in Figure 4 started with a pretraining phase where the
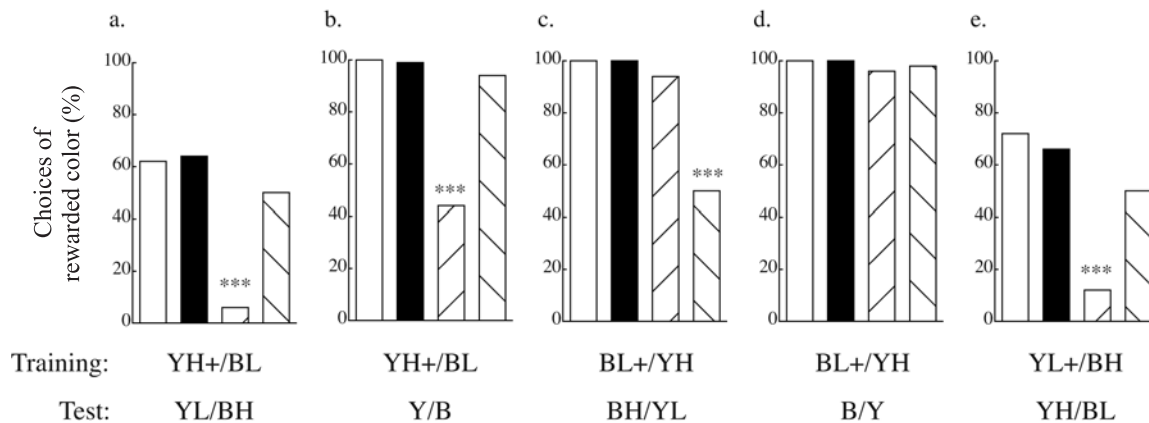
Figure 2 Results of experiment 12–16. Choices of the stimulus with the rewarded color after discrimination training in five experiments for the real moth and the three models. In the experiments, the moths (and models) were first trained on one combination of color and odor and later tested on another combination, to see how much of the learning involved color and odor, respectively. The three stars indicate that the behavior of the model was significantly different from the moth with $p < .001$ for Fisher's exact test. See Figure 3 for further explanation.
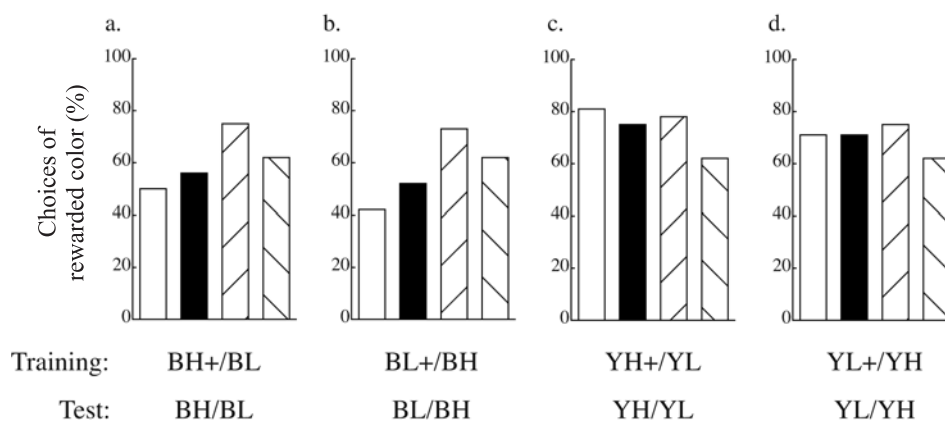
Figure 3 Choices of the stimulus with the rewarded odor after discrimination training in experiments 8–11 for the real moth (data from Balkenius & Kelber, 2006) and the three models. With the yellow color, the moths learn the odors, but with the blue color, they do not. This is predicted by the hawkmoth learning model, but not by the Rescorla–Wagner or independence models.

preference for a color was changed. In two of the experiments, the weak preference for yellow was strengthened by a pretraining procedure. In the two other experiments, the strong preference for blue was weakened to see how this would influence subsequent learning (for details, see Balkenius & Kelber, 2006).

3 Computational Models

The experiments run with the real moths were also tested with three computational models to see if these models were able to explain the behavior of the animals. These models were the Rescorla–Wagner model, an independence model, and the new hawkmoth learning model, which is described here for the first time.

For all models, each flower stimulus was coded as a vector $s = \langle s_0, s_1, s_2, s_3 \rangle$ with four components coding for blue color (s_0), yellow color (s_1), honeysuckle odor (s_2), and lavender odor (s_3). Each of these components was set to 1 when the corresponding stimulus component was available, and 0 otherwise. For example, the stimulus BL was coded as $s = \langle 1, 0, 0, 1 \rangle$.
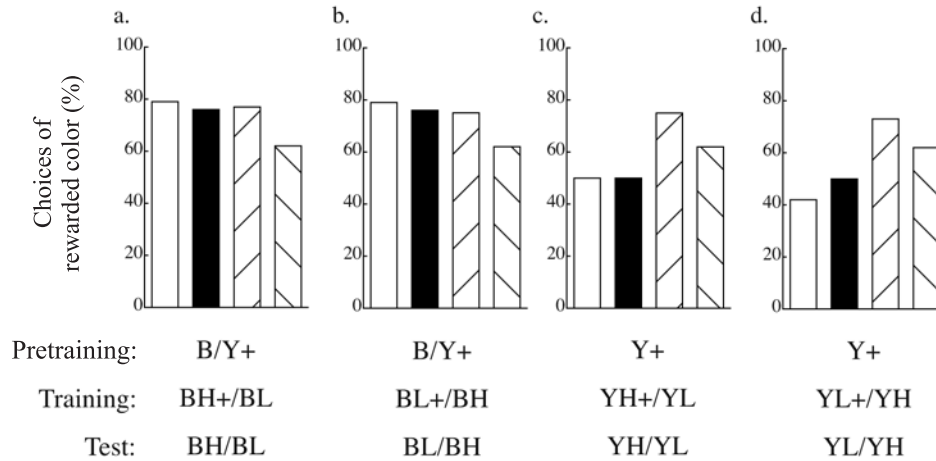
Figure 4 Choices of the rewarded color in the training phase in experiments 17–20 for the real moth (data from Balkenius & Kelber, 2006) and the three models. By pretraining the moths, their learning could be changed. (a), (b) When the innate preference for blue was extinguished through discrimination learning, the moths could learn to discriminate between the two odors. This behavior was predicted by all models. (c), (d) When the moths were pretrained to prefer yellow, they lost their ability to learn a discrimination between the two odors. The hawkmoth learning and independence models predict this behavior, while the Rescorla–Wagner model fails. See Figure 3 for further explanation.

3.1 Rescorla–Wagner Model

As it appears that learning of one stimulus component can block learning of another in the moth experiments, it seems reasonable to test how well the Rescorla–Wagner model is able to reproduce the results of the experiments (Rescorla & Wagner, 1972). Let $w(t)$ be the current weight vector, $s(t)$ the stimulus vector, and $R(t)$ the reward at time t. When the moth attempts to forage, the weights are updated according to the equation

$$w_i(t + 1) = w_i(t) + \gamma\delta(t)s_i(t), \qquad (1)$$

for both rewarded and unrewarded trials. Here, γ is the learning rate and $\delta(t)$ is the difference between the actual and expected reward

$$\delta(t) = R(t) - \sum_{i=0}^{n} w_i(t)s_i(t), \qquad (2)$$

where $n = 3$, as there were four different stimulus components. This formulation of the Rescorla–Wagner model is equivalent to the delta-rule commonly used in neural network models (Widrow & Hoff,

1960). When the model moth senses a stimulus $s(t)$, it is selected according to the probability

$$p[s(t)] = \sum_{i=0}^{n} w_i(t)s_i(t). \qquad (3)$$

This probability thus determines whether the model moth will try to forage from a single flower at a single point in time. Note that this is not the probability of selecting one stimulus type in relation to another.

3.2 Independence Model

There is not a single established mathematical formulation of the idea that each stimulus component acquires associations independently of other stimulus components. We collectively call these models the independence model. Here, we use a mathematical formulation that is similar to the Rescorla–Wagner model, except that the stimulus components do not interact during learning. In this model, one stimulus component is not able to block learning of another and Equations 1 and 2 are replaced by

$$w_i(t + 1) = w_i(t) + \gamma\delta_i(t)s_i(t) \qquad (4)$$

and

$$\delta_i(t) = R(t) - w_i(t)s_i(t). \tag{5}$$

For the binary stimuli used here, this learning rule is equivalent to the Bush–Mostellar model (Bush & Mostellar, 1955). The probability with which a stimulus is selected is calculated in the same manner as for the Rescorla–Wagner model (Equation 3).

3.3 Hawkmoth Learning Model

The hawkmoth learning model assumes that the animal learns a single template for the sensory attributes of the flowers that are rewarded during foraging. The template is updated when the moth is rewarded such that it more closely matches the vector associated with the current flower. If the moth is unrewarded, the template is left unaltered. Let $w(t)$ be the current weight vector coding for the flower template, and $R(t)$ the current reward. When the moth is rewarded, the weights are updated according to the following equation

$$w_i(t+1) = \frac{u_i(t+1)}{\sum\limits_{i=0}^{n} u_i(t+1)} \tag{6}$$

where

$$u_i(t+1) = \begin{cases} w_i(t) + \gamma\delta(t) & \text{when } s_i = 1 \\ w_i(t) - \epsilon & \text{otherwise} \end{cases} \tag{7}$$

and $\delta(t)$ is calculated as for the Rescorla–Wagner model (Equation 2). Weights are not allowed to become negative. To function as a template, it is necessary that the weight vector w is normalized as described by Equation 6. This makes the model sensitive to the stimulus pattern and not to its magnitude. The match between the template and the current external stimulus is thus used to predict the reward. Unlike the Rescorla–Wagner model, however, the learning attempts to move the learned template towards the rewarded stimulus pattern instead of directly decreasing the prediction error. As a consequence, the prediction error will reach zero as the template approaches the rewarded stimulus (see the Appendix).

Because of δ in Equation 7, excitatory learning only occurs when there is a prediction error, which makes blocking possible when the reward is already predicted by the stimulus. As the template is normalized, but the stimulus input is not, it is possible for a stimulus component to completely block learning even if the stimulus and the template are not identical. In this case, learning will converge before the template reaches the stimulus pattern.

The probability of selecting a stimulus is set to

$$p[s(t)] = \left[\sum_{i=0}^{n} w_i s_i(t) \right]^q. \tag{8}$$

The sum describes the matching process and the exponent q is a parameter that is used to derive selection probabilities from the matching. This parameter was set to $q = 2.00$ to quantitatively fit the experimental data.

3.4 Simulations

The three models were tested on the 20 experiments described above. During each simulation, the simulated moth was randomly presented with one of two stimuli and was allowed to select it with the probability given by the selection functions described above. Data from 100,000 simulated animals were recorded for each experiment and each model. The simulated moths were rewarded 50 times during each learning phase to approximate the number of visits to flowers by the real moths. The exact number of rewards are not critical to our results as learning parameters for each model were optimized to compensate for the number of trials used.

To allow a fair comparison of the performance of the different models, the initial weights for each model were set to parallel the stimulus preferences of the moth as closely as possible (Figure 1). The weights of each model were optimized to two decimal places to make the model perform as well as possible on the preference data. There were no significant differences between the results of the real moth and any of the models on the preference tests (Fisher's exact test: hawkmoth learning model $p = .37$, Rescorla–Wagner model $p = .35$, independence model $p = .35$).

The constants for each model were subsequently numerically optimized to minimize the average error over all experiments for each model. These constants and initial weight values are given in Table 1.

Table 1 Optimal parameter for each of the models. Note that the sum of the weights for the hawkmoth learning model equals 1.

Model	γ	ϵ	w_0	w_1	w_2	w_3
Rescorla–Wagner	0.04	–	0.09	1.00	0.12	0.03
Independence	0.27	–	0.09	1.00	0.12	0.03
Hawkmoth learning	0.09	0.12	0.19	0.74	0.07	0.00

Each experiment with each model was tested against the data from the real moth using Fisher's exact test. The simulation results were used to calculate the expected number of choices based on the actual number of choices in the experiments with real moths, and these were compared with the moth data. Finally, we combined the results of each individual test into a combined measure for the whole model.

4 Results

The results of experiments 1–5 showed that the moth had a marked preference for blue, but no clear preference for any of the odors (Figure 1). Because the parameters of each model were optimized to reflect these preferences, all models behaved as the real moth in these preference tests. Experiments 6 and 7 verified that the moth could be trained to select either a blue or yellow flower. The real moth selected yellow in 80% of the trials after being trained on yellow, and blue in 95% of the trials after being trained on blue. All models, except the random selection, were able to learn these discriminations.

Figure 3 shows the result of experiments 8–11 with the same color but different odors (Balkenius & Kelber, 2006). In the real moth, the blue color prevents odor learning from occurring, but with the yellow color, the moth is able to learn which odor is rewarded. The hawkmoth learning model gives almost the same result as the real moth on all experiments. In contrast to the real moth, the Rescorla–Wagner model learns the odor in all experiments. The same is true about the independence model, although the learning is less pronounced for this model, regardless of which color was used.

The behavior of the real moth and the different models differ even more in experiments 12–16, shown in Figure 2. Here, it is again evident that the real moth

learns odor when it is presented together with yellow (Figure 2a and e). The fact that the test with color and odor (Figure 2a) and the test with only color (Figure 2b) differ, also shows that the animals must have learned the odor. With the blue color, the animals did not learn the odor and the result is the same with and without odor (Figure 2c and d).

Again, the predictions of the hawkmoth learning model were very close to the actual data, but the other two models differed in different ways. In experiments 12 and 16 (Figure 2a and e), the Rescorla–Wagner model did not make the correct discrimination, and appears to select the correct odor and ignore the color. The independence model does not take the color into account when learning odor and learns the color in experiment 10 (Figure 2c), when the other models and the real moth does not.

For the real moth, the preference for the color could be changed by pretraining (Balkenius & Kelber, 2006). In the experiments shown in Figure 4a and b, the innate preference for blue is decreased during pretraining. As a result, the moth can later learn odors together with a blue artificial flower. The opposite situation is shown in Figure 4c and d where the less preferred yellow is made more attractive during pretraining. As a consequence, the real moth no longer learns the odor together with yellow.

Like the real moth, the hawkmoth learning model behaves differently depending on which color is used and whether it was pretrained or not. This is also true of the independence model, although the difference in the two cases is not as large. For the Rescorla–Wagner model, however, the learning is almost the same regardless of the color or pretraining.

Figure 5 shows the overall results of the simulations for the different models. The average error of the new hawkmoth learning model is clearly much lower than that of the other models. Both the Rescorla–Wagner and the independence models are much better than
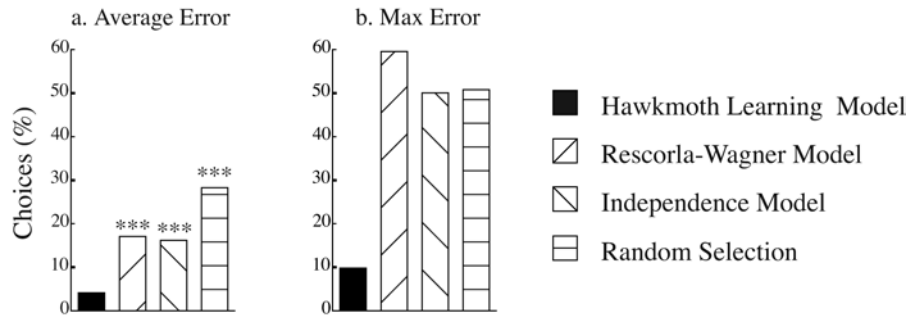
Figure 5 Overall results of the three models and a random selection strategy (horizontal stripes). (a) Average error on all 20 experiments. The new model clearly outperforms the other models with an average error of 4.14%. (b) The maximum error for each of the models and the random selection strategy. Again, the new model is much better than the two alternatives. The behaviors of the Rescorla–Wagner and independence models and the random strategy differ significantly from that of the real moth.

random selection, where the two stimuli are both selected with equal probability. Looking at the maximal error, the hawkmoth learning model reproduces the data much more closely than the other models. Surprisingly, both the Rescorla–Wagner and the independence models perform at close to the random model in the worst case. The Rescorla–Wagner model is even worse than the random model on some experiments.

The difference between the real moth and the different choices in the simulations for each model and each experiment were statistically analyzed using Fisher's exact test. The average simulation results from 100,000 trials were used as the expected values and were adapted to the number of choices recorded with the real moths.

The results of all experiments for each model were combined to test whether the behavior of each model differed significantly from the moth data. There were no significant differences between the behavior of the hawkmoth learning model and the real moth ($p = .12$). The behavior of the Rescorla–Wagner model differed significantly from the moth data ($p < .0001$). This was also the case for the independence model ($p < .0001$).

5   Alternative Models

The two critical assumptions of the hawkmoth learning model are that the moth learns a template for the rewarded stimulus and that learning only occurs on

rewarded trials. To test if the other models would do better if they incorporated these assumptions, we ran a number of simulations with modified versions of the independence and Rescorla–Wagner models.

We first tested the behavior of the two models when they did not learn on unrewarded trials. For the modified independence model, the average error increased to 16% and the maximum error became 50%. The behavior of the modified model is significantly different from the animal data (Fisher's exact test, $p < .001$). The average error of the Rescorla–Wagner model decreased slightly to 15% but the maximum error increased to 68%. The behavior of the modified model is still significantly different from the animal data (Fisher's exact test, $p < .001$).

As a second step, we tested the assumption that a template is used. The Rescorla–Wagner model can be modified to operate on stimulus configurations rather than stimulus components as the hawkmoth learning model. According to the configural theory of Pearce (1994), new configurations are learned as new stimuli are encountered, and associations are formed from these configurational codes rather than from the individual stimulus components. As this model does not specify how innate preferences should be handled, we tested two versions of this model.

In the first case, we used the original version of the model without any preferences. For this model, the average error was 18% and the maximum error 50%. In the second case, we added direct innate associations from the stimulus vector to produce the same preferences as for the Rescorla–Wagner model. The

learned associations were added (or subtracted) from these preferences. For this model, the average and maximum errors were 16% and 61%, respectively. The behavior of the two versions of the model differs significantly from the animal data (Fisher's exact test, $p < .001$ in both cases).

None of the modified models came close to the performance of the hawkmoth learning model. It is thus not sufficient to add the assumption of learning to only rewarded trials or the assumption of template learning to the other models to account for the learning of the moth.

6   Discussion

We have reported the results of 20 experiments with moths in different discrimination tasks involving multimodal stimuli with color and odor. Three computational models were tested on the data to try to determine the mechanisms behind this type of learning in hawkmoths. This is the first time multimodal learning in sphingids has been modeled and the results show that the learning mechanisms in insects can be far from trivial.

We observed behaviors that are reminiscent of overshadowing (Figure 3a and b) and blocking (Figure 4c and d). In naïve moths, the degree of odor learning depended on the color used during training (Figure 3). Although the Rescorla–Wagner model is often proposed as an explanation for these phenomena (Rescorla & Wagner, 1972), it was not able to reproduce our experimental results without changing the parameters for each individual experiment. Because the parameters were set to minimize the overall error on all experiments, the model failed in some instances. In fact, in one case, this model performed worse than random selection (Figure 5). This parameter sensitivity is a well-known problem with this model (Gallistel, 1990). Although the model is able to handle a wide range of conditioning experiments, it cannot do so with identical parameters. For example, in the experiments shown in Figure 3a and b, the blue color is not able to block odor learning as the association from the blue color undergoes extinction on the non-rewarded trials, and thus loses its ability to block odor learning. For the same reason, the Rescorla–Wagner model fails to reproduce the blocking-like situation in Figure 4c and d. The influence of the non-rewarded trials on the result is highly dependent on the precise learning rate and the number of trials. In contrast, in the real moth, the behavior does not critically depend on the number of trials.

This was the motivation for the learning rule in the hawkmoth learning model, where learning only occurs during rewarded trials. This model is thus immune to extinction during non-rewarded trials and can accurately predict the behavior of the moth in all the experiments in Figures 3 and 4. In particular, the model will never learn the odor with a blue color as this color is never extinguished as long as it is the only rewarded color. Thus, blocking remains intact throughout the experiment (Figure 3a and b). However, extinction of blue can occur if another color is rewarded as in experiments 17 and 18 (Figure 4a and b).

Although the hawkmoth learning model cannot handle extinction through presentation of a single non-rewarded stimulus in its current form, it can easily be extended with a non-specific extinction mechanism that decreases the overall response probability after a non-rewarded trial. In order not to interfere with the blocking mechanism in the model, such extinction would have to influence all stimuli and not only the non-rewarded one. However, no experimental data are currently available on the properties of extinction in moths in the free-flying paradigm.

To only learn on rewarded trials cannot by itself explain the results of the hawkmoth learning model. A modified Rescorla–Wagner model or independence model that only learns at rewarded trials is not able to predict the experimental results as well as the original models. While extinction at unrewarded trials is necessary for the Rescorla–Wagner and independence models to avoid constantly increasing weights, the hawkmoth learning model uses normalization to keep the weights within bounds. This also results in the formation of a template for the rewarded stimulus combination. This template acts as an adaptive search image that can be used to lead the animal to rewarding flowers (Goulson, 2000; Tinbergen, 1960).

Surprisingly, the independence model was slightly better than the Rescorla–Wagner model, both on average and in the worst case (Figure 5). In particular, this was the case in the blocking-like experiments in Figure 4. The reason for this is the interaction between the initial preferences and the particular number of trials, despite a fundamental disability to handle these learning situations. However, from the animal data, it is

clear that the learning of one modality depends on the other.

These experiments are in line with color preference tests that have shown that *M. stellatarum* prefers blue to yellow (Kelber, 1997). Blocking has been demonstrated with free-flying honeybees. Experiments have shown that the blocking effect depended on the salience of the different stimuli, that is, how easy it was for the animal to detect the stimulus (Couvillon et al., 1997). In honeybees, the salience of a stimulus (e.g., the concentration of an odor) also influenced its ability to overshadow other stimuli (Pelz, Gerber, & Menzel, 1997).

The results of our simulations differ from the results that would be obtained in the standard case when the different models start out without any preferences and all weights are zero. With initial weights at zero, the Rescorla–Wagner model would be better at handling the blocking-like experiment. However, its overall score would decrease, as its ability to handle many of the other experiments would be reduced. This is a consequence of our methodology where the parameters for each model were optimized in relation to all experiments taken together. Given that the models claim to describe the learning of an animal in many different situations, it is important that the parameters are not tweaked to fit each experiment.

The different modalities could be handled in the same way by the hawkmoth learning model. It was sufficient to set the initial weights in accordance with the observed preferences of the moths. This shows that it is not necessary to assume that different modalities are handled in different ways in hawkmoth learning.

As the initial weights are not zero, the behaviors of the different models are not always what would be expected. The hawkmoth is innately prepared for the stimuli used in these experiments, which contrasts with the stimuli often used in conditioning studies (Seligman, 1970).

In the future, we would also like to further study two of the assumptions of the model in experiments with real moths. One is that extinction never occurs or is non-specific. The other is that the moth can only learn a single template.

In summary, we have presented experimental results from 20 different experiments with the hawkmoth *M. stellatarum*, which show that the particular color of an artificial flower determines whether the moth will learn its odor or not. Also, when the moth has learned a combination of color and odor, color is most important. By manipulating the preference for the colors, its effect on odor learning could be changed. Furthermore, we have shown that neither the Rescorla–Wagner model nor the independence model are able to explain the experimental results. Instead, we have proposed a new model, the hawkmoth learning model, which is based on the idea that the moth learns a template for the rewarded multimodal stimulus when it is rewarded. This new model faithfully reproduces all the experimental data.

Appendix

In this appendix, we show that learning in the hawkmoth learning model converges when trained in a discrimination task with two binary stimulus vectors *a* and *b*, where *a* is rewarded, but *b* is not. As no learning occurs for stimulus *b*, we only need to consider the rewarded trials where $s_i = a_i$. Let $X = \{i | s_i = 1\}$ and $Y = \{i | s_i = 0\}$. According to Equation 7, the weights w_i for $i \in Y$ trivially converge to zero. It remains to show that the weights w_i, for which $i \in X$, converge. It is sufficient to show that the learning converges once w_i (for which $i \in Y$) have reached zero. At this stage, Equation 7 can be simplified to $\delta(t) = 1 - \sum_{i \in X} w_i(t)$. However, as the vector w is normalized, $\sum_{i \in X} w_i(t) = 1$, which implies that $\delta(t) = 0$. This proves that the learning converges.

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