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Pattern discrimination in a hawkmoth: innate preferences, learning performance and ecology

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Spatial patterns are important cues for flower detection and recognition by nectar-feeding insects. Pattern vision has been studied in much detail in bees and flies but rarely in butterflies and moths. In this paper, I present a first proof of pattern-learning abilities in a moth, and discuss reasons for the limitations to their pattern learning. The diurnal hawkmoth *Macroglossum stellatarum* spontaneously prefers patterned to uniformly coloured stimuli but can be trained to choose the uniform stimulus. By contrast, experience does not override the innate preferences for radial over tangential patterns, and for tangential over striped patterns. These results do not reflect bad visual discrimination but rather a lack of learning ability and motivation to abolish innate preferences. I propose that radial and tangential flower patterns are good predictors of nectar reward, a condition under which learning is unlikely to evolve. These patterns serve not only as cues for flower detection but also as guides to the reward. Hovering pollinators strongly depend on these guides and should therefore: (i) have rigid pattern preferences; and (ii) not be motivated to abolish these preferences as easily as their innate preferences for colours.

Keywords: vision; pattern discrimination; learning; motivation; insect; Lepidoptera

1. INTRODUCTION

The ability to discriminate between and to recognize spatial patterns and the shape of objects is important in many behavioural contexts. Predators might detect prey using pattern vision, prey recognize patterns consisting of two eyes as predators, mates recognize each other by means of colour patterns on the wings or plumage, and flower visitors recognize shapes and patterns of flowers. Among insects, bees and flies have been the focus of pattern-vision studies (Wehner 1981; Dafni *et al.* 1997; Ernst & Heisenberg 1999; Giurfa & Lehrer 2001). Pattern vision in lepidoptera has rarely been studied. It has been shown that butterfly males recognize wing patterns in order to recognize females, and that females in some species recognize the leaf shape of the larval food plant (for reviews see Wehner 1981; Rutowski 2002; Warrant *et al.* 2002).

In an early study, Ilse (1932) demonstrated that the butterflies *Argynnis paphia*, *Inachis io* and *Aglais urticae* (Nymphalidae) express spontaneous preferences for flower patterns and shapes. They prefer large patches of yellow or blue to small ones, and choose structured stimuli more frequently than uniformly coloured stimuli: for instance, a blue and black checkerboard (8 cm total size, with 2 cm squares) was chosen more frequently than a uniformly blue stimulus of equal size. A checkerboard with 0.5 cm squares, however, was chosen less frequently than the coarser pattern. Later experiments (Vaidya 1969) on the swallowtail butterfly *Papilio demoleus* yielded similar results: a preference for larger over smaller stimuli and a sector pattern with four sectors over one with eight or more sectors.

More recently, pattern preferences of the hummingbird hawkmoth *Macroglossum stellatarum* (Sphingidae) were analysed (Kelber 1997). In contrast to butterflies, these moths hover in front of a flower while extending the long proboscis to drink nectar. *Macroglossum stellatarum* spon-

taneously prefer a sector pattern over a ring pattern of equal size and contour length, and a circular blue stimulus (28 mm diameter) with a central yellow spot (8 mm diameter) over a uniformly blue stimulus (Kelber 1997). This nicely complements the observations of Knoll (1922) that these moths choose the yellow flowers of the common toadflax *Linaria vulgaris* only if they have the species-specific orange pattern.

In all studies of lepidopteran pattern vision described so far, spontaneous preferences were observed, mainly because butterflies cannot be trained as easily as can, for instance, honeybees. However, colour learning has recently been demonstrated in several butterfly species (for a review see Weiss 2001), and hummingbird hawkmoths learn the colour and size of artificial flowers fast and reliably (Kelber 1996; Kelber & Hénique 1999). Because of their excellent learning abilities, I used hummingbird hawkmoths as models for this study. I set out to study the relation between innate preferences and learning of flower patterns, to answer three questions. First, which patterns do flower-naive moths prefer? Second, can these preferences be changed by learning? Third, if not, what are the possible reasons?

2. MATERIAL AND METHODS

Macroglossum stellatarum were bred in the laboratory from animals obtained from Malta and southern France. For detailed breeding instructions see Farina *et al.* (1994). Experiments were performed in a flight cage (70 cm × 60 cm × 50 cm) illuminated from above by three fluorescent tubes (Osram Biolux), resulting in a light intensity of 100 Cd m^{-2}, a temperature of 25 °C and 50% humidity.

Stimuli were printed with an Epson Stylus Photo 700 inkjet printer on Epson quality inkjet paper using a light grey background (20% black in CMYK coordinates) and presented vertically on one cage wall. Blue-and-white patterns (circular in

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shape and 40 mm in diameter) were used because flower-naive hawkmoths avoid black-and-white patterns (Kelber 1997, unpublished observations). Patterned stimuli were dark blue (db; 100% cyan, 77% magenta) and white. This colour provides a high contrast for any insect green receptor (the receptor class most probably responsible for the achromatic task of pattern detection in hawkmoths; K. Bartsch, unpublished observations). Small versions of all patterns are given on the *x*-axes of the figures. Two lighter shades of blue were used for uniform stimuli, with lb2 (67.5% cyan, 47.5% magenta) reflecting less light (thus appearing darker to the human eye) than lb1 (45% cyan, 35% magenta). During training sessions, all patterns had a central hole, 3 mm in diameter, which opened into a reversed syringe needle that served as a feeder and could be refilled from a larger reservoir with a 20% sugar solution. During tests, the hole was substituted by a black spot 3 mm in diameter, and no sugar reward was present. In common with most hawkmoths, *M. stellatarum* feeds 'on the wing' without landing on flowers.

The training and testing procedure was almost identical to the procedure used in previous studies of colour learning (Kelber 1996; Kelber & Hénique 1999). Experiments started one day after eclosion. A single animal was released into the cage and given a choice between two or three stimuli. A naive animal, in a spontaneous preference test, would warm up the flight muscles, fly around in the cage for up to 2 min, approach the stimuli, hover in front of one stimulus while extending the proboscis and finally probe the pattern with the proboscis to find the entrance to the sugar reservoir. Each approach that ended in proboscis probing was counted as a choice. Experienced animals would approach the stimuli immediately after warming up. Five choices were registered during each test with a single animal. Occasionally, a naive moth would settle on the cage wall without making any choice. When this happened, the animal was tested again the following day. Experienced animals always made choices. Tests were immediately followed by a feeding session. In feeding sessions, animals found the hole in the rewarding pattern and received 10 μl of 20% sucrose solution during each visit. They were allowed to visit and feed until satiation. The positions of the stimuli were changed frequently in a pseudorandom way to avoid the moths learning the position of the rewarding stimulus. After feeding, animals were placed in numbered dark containers until the next test and training session on the following day, a procedure invented by Knoll (1922). Ten animals participated in each experiment, with the exception of the last experiment where one animal died early. Each animal participated in one experiment only. Figures give the mean choice frequency ± s.e.m. choice frequency of the animals. *G*-tests adjusted by William's correction were used to test whether choice distributions differed from chance and from choice distributions in other tests (Sokal & Rohlf 2000).

3. RESULTS

(a) *Pattern choices by flower-naive moths*

Given the choice between a ring and a radial pattern, the moths chose the latter with high frequency (figure 1*a*). Moths did not show a preference between a ring pattern where the outermost ring was blue and one where it was white (figure 1*b*). They preferred the ring pattern to a pattern of horizontal stripes (figure 1*c*), and horizontal and vertical stripes were chosen with almost the same frequencies (figure 1*d*). Both ring and radial patterns were more attractive than the uniformly blue (lb1 and lb2)
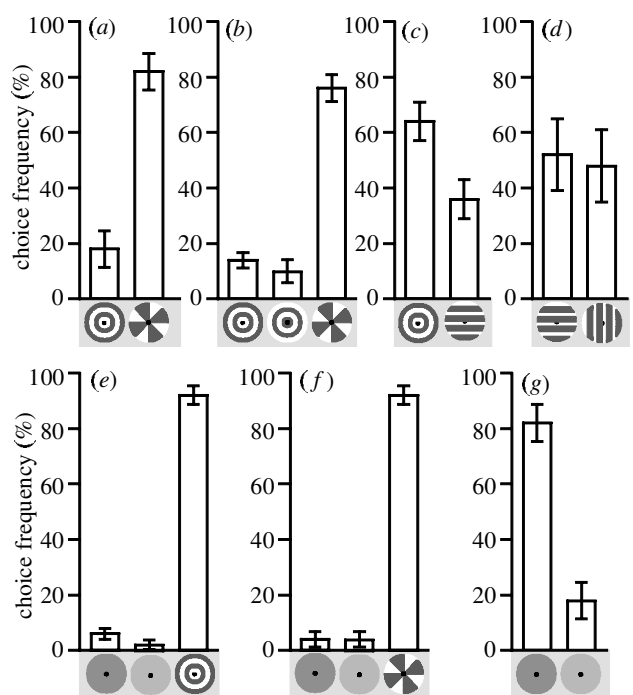

Figure 1. Spontaneous choices by naive moths, mean ± s.e.m., 50 choices by 10 animals in each experiment. All choice distributions differed significantly from chance, with the exception of the choices between horizontal and vertical stripes (*d*). (*a*) Ring pattern and radial pattern (*G*-test, 1 d.f.: $G_{adj.} = 21.95$, $p < 0.001$); (*b*) two ring patterns and radial pattern (*G*-test, 2 d.f.: $G_{adj.} = 38.07$, $p < 0.001$); (*c*) ring pattern and horizontal stripes (*G*-test, 1 d.f.: $G_{adj.} = 5.16$, $p < 0.05$); (*d*) horizontal and vertical stripes (*G*-test, 1 d.f.: $G_{adj.} = 0.15$, $p > 0.75$); (*e*) ring pattern and two uniform stimuli, lb1 and lb2, differing in the contrast to background (*G*-test, 2 d.f.: $G_{adj.} = 21.95$, $p < 0.001$); (*f*) radial pattern and two uniform stimuli; (*G*-test, 1 d.f.: $G_{adj.} = 21.95$, $p > 0.001$) and (*g*) two uniform stimuli, lb1 and lb2 (*G*-test, 1 d.f.: $G_{adj.} = 21.95$, $p < 0.001$).

stimuli (figure 1*e*,*f*). The darker blue shade (lb2) received more choices than the brighter lb1 (figure 1*g*).

(b) *Moths do not learn to prefer the ring pattern to the radial pattern*

In a first training experiment, a pattern with two blue and two white rings, with the outer ring being blue, was chosen as the rewarding stimulus. A ring pattern with reversed colours (outer white ring) and a radial pattern (four blue and four white sectors) were chosen as unrewarding stimuli (see *x*-axes in figure 2*a*,*b*). After 10 days of training, the choice distribution differed significantly from that of the naive animals but not from random choice (figure 2*b*). In separate tests with only two stimuli, moths chose between the two ring patterns randomly (figure 2*d*) but preferred the radial pattern to the rewarded ring pattern (figure 2*e*). The latter choice distribution did not differ significantly from that of naive animals (compare with figure 1*c*; *G*-test, 1 d.f.: $G_{adj.} = 2.62$, $p > 0.1$). By contrast, the moths chose the training pattern almost exclusively when it was presented together with a uniformly blue stimulus (lb1, figure 2*c*).

A possible explanation for the negative result is that the presence of the unrewarded ring pattern prevented moths
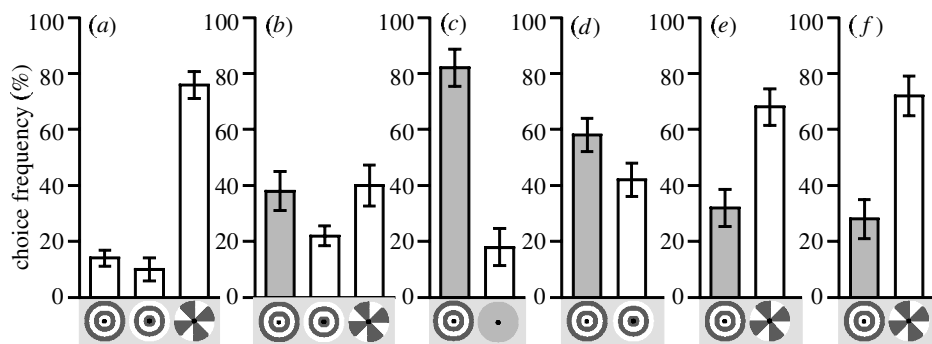
Figure 2. (*a–e*) Choices made by 10 animals trained with a ring pattern as the rewarded stimulus and a different ring pattern and a radial pattern as unrewarded stimuli; shaded bars indicate choices of the pattern that was rewarded during training. Five choices by each animal, mean ± s.e.m. (*a*) Choices by naive animals same data as in figure 1*b*. (*b*) Choices after 10 days of training differ from choices of naive animals (*G*-test, 2 d.f.: $G_{adj.} = 13.73$, $p < 0.005$) but not from random choice (*G*-test, 2 d.f.: $G_{adj.} = 3.09$, $p > 0.2$). (*c*) The rewarded pattern is preferred over a uniform stimulus (*G*-test, 1 d.f.: $G_{adj.} = 21.95$, $p < 0.001$). (*d,e*) In dual-choice tests with only one unrewarding stimulus, moths chose randomly between the two ring patterns (*G*-test, 1 d.f.: $G_{adj.} = 1.27$, $p > 0.2$) and preferred the radial pattern to the training pattern (*G*-test, 1 d.f.: $G_{adj.} = 6.56$, $p < 0.025$). (*f*) Fifty choices by 10 different animals trained to the ring pattern with only the radial pattern as an unrewarded stimulus. Results do not differ between (*e*) and (*f*) (*G*-test, 1 d.f.: $G_{adj.} = 0.19$, $p > 0.5$).
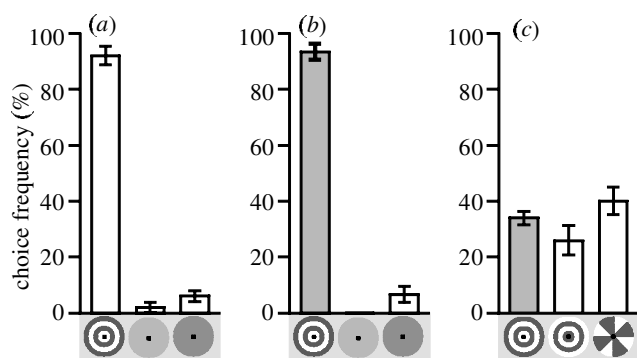

Figure 3. Choices by 10 animals trained with a ring pattern as the rewarded stimulus and two uniform unrewarded stimuli, lb1 and lb2. All conventions as in figure 2. (*a*) Choices by the naive animals (same data as figure 1*e*); (*b*) choices after 2 days of training do not differ significantly (*G*-test, 2 d.f.: $G_{adj.} = 2.96$, $p > 0.2$); (*c*) choices between the training stimulus and two patterns, not different from chance (*G*-test, 2 d.f.: $G_{adj.} = 1.49$, $p > 0.2$).

from learning the rewarded pattern. A new group of moths were therefore trained using the ring pattern, with the radial pattern as the only unrewarding stimulus. These moths did not choose the ring pattern either (figure 2*f*).

(c) *Moths do learn to choose uniform stimuli*

In a second attempt to test pattern learning in hummingbird hawkmoths, two uniformly blue stimuli (lb1 and lb2) and the ring pattern were used. Naive moths preferred the ring pattern, and this preference remained when the moths were rewarded on the ring pattern (figure 3*a,b*). Given a choice between the rewarding ring pattern, the reversed ring pattern and the radial pattern, the same moths showed almost the same choice behaviour as moths trained to discriminate between these three patterns (figures 3*c* and 2*b*; *G*-test, 2 d.f.: $G_{adj.} = 0.27$, $p > 0.5$).

A new group of moths were trained to associate the uniform stimulus (lb1) with food and the ring pattern with no food. These moths chose the rewarded lb1 stimulus significantly more frequently than the unrewarded pattern

(figure 4*a*). Training thus reversed their innate preference. The moths also preferred the training stimulus over patterns of vertical or horizontal stripes (figure 4*b,c*). However, given a choice between the training stimulus and the radial pattern, they chose the latter (figure 4*d*). In short, the moths learned a pattern but did not overcome their strong innate preference for the radial pattern.

(d) *Innate preferences can be stronger, even if learning takes place*

Is the resistance to overriding an innate preference specific to the radial pattern? To answer this question, I trained nine moths to horizontal stripes as the rewarded and rings as the unrewarded pattern. After 8 days of training, the rewarded pattern was not chosen more frequently than the unrewarded pattern (figure 5*b*), and the moths' choices did not differ significantly from their innate preference (figure 5*a,b*). The moths did, as in earlier experiments, prefer the striped pattern to the uniformly blue (lb1) stimulus (figure 5*c*). It came as a surprise, however, to find that they also preferred the horizontal stripes to vertical stripes (figure 5*d*). This is a strong indication that the moths are able to learn the horizontal-stripes pattern but did not choose it in the first test (figure 5*b*) because of their innate preference for the ring pattern.

4. DISCUSSION

My experiments demonstrate, for the first time, that lepidopterans learn spatial patterns of artificial flowers. Innate preferences of hummingbird hawkmoths for patterns can be reversed by learning in some cases but not in others. This is in contrast to fast colour learning in the same species (Kelber & Hénique 1999). Similar procedures were used in the colour-learning experiments and in the experiments described here. Differences in the results are, thus, unlikely to be caused by differences in handling and experimental procedure. They most probably reflect differences in visual discrimination, learning abilities or stimulus-related motivation. I will discuss these three possibilities separately.
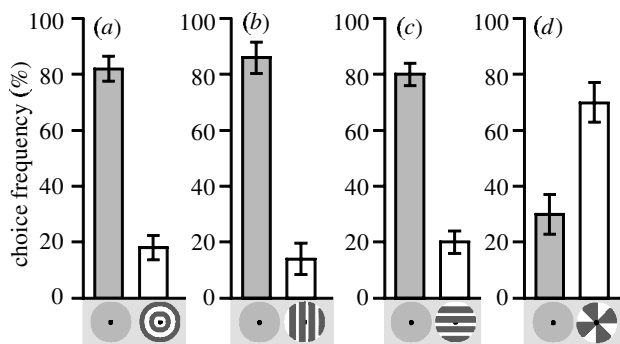
Figure 4. Choices by 10 moths trained with the uniform stimulus, lb2, as the rewarded stimulus and a ring pattern as the unrewarded stimulus. Conventions as in figure 2. Animals chose correctly in tests (*a*) with both training stimuli (*G*-test, 1 d.f.: $G_{adj.} = 21.95$, $p < 0.001$); (*b*) with vertical stripes (*G*-test, 1 d.f.: $G_{adj.} = 28.53$, $p < 0.001$); and (*c*) with horizontal stripes (*G*-test, 1 d.f.: $G_{adj.} = 19.08$, $p < 0.001$). (*d*) The radial pattern was chosen more frequently than the rewarded pattern (*G*-test, 1 d.f.: $G_{adj.} = 8.14$, $p < 0.001$).
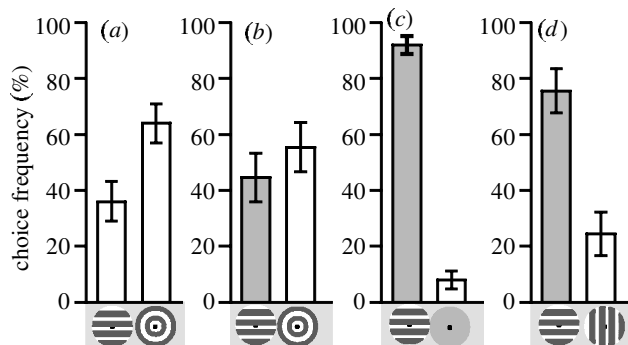

Figure 5. (*a*) Choices by 10 naive animals, same data as figure 1*c*. (*b–d*) Choices by nine moths after training with a rewarded pattern of horizontal stripes and an unrewarded ring pattern. (*b*) Choices with both training patterns do not differ from chance (*G*-test, 1 d.f.: $G_{adj.} = 0.55$, $p > 0.3$) and do not differ significantly from the innate preference (*G*-test, 1 d.f.: $G_{adj.} = 1.18$, $p > 0.2$). Moths prefer horizontal stripes to (*c*) a uniformly blue stimulus (*G*-test, 1 d.f.: $G_{adj.} = 34.99$, $p < 0.001$) and (*d*) vertical stripes (*G*-test, 1 d.f.: $G_{adj.} = 12.19$, $p < 0.001$).

(a) *Pattern discrimination*

Flower-naive moths were able to discriminate the ring pattern from the radial pattern, as well as stripes from rings, with high probability (figure 1*a–c*). The result of the last training experiment demonstrates that they can also discriminate between horizontal and vertical stripes (figure 5*d*). Random choices by animals trained to prefer the ring pattern over the radial pattern (figure 2*b,d–f*), and by those trained to prefer the striped pattern over the ring pattern (figure 5*b*) cannot be caused by a failure in visual discrimination. Obviously, moths did not use the discrimination ability of their visual system when making their choices in these tests. One possible explanation is that moths are unable to associate spatial patterns with a reward but instead retain innate preferences for specific flower patterns.

(b) *Learning ability*

Hummingbird hawkmoths express strong innate preferences for both colours and patterns (Kelber 1997). However, in training experiments, they learn to associate any spectral colour with a reward after only one rewarded trial (Kelber & Hénique 1999). This is true even if the unrewarded colour is highly attractive and the rewarded colour is not attractive to the naive animals at all. Innate preferences for colours can, thus, be reversed by experience. This seems not to apply to all spatial patterns used in my experiments.

Learning abilities should evolve under environmental conditions of intermediate predictability, too unpredictable for rigid behaviour to work but predictable enough to adjust individual behaviour to changes (Papaj & Lewis 1993). Flower colours do vary in this way, for an insect living several weeks or months (e.g. Weiss 2001). Radial and tangential flower patterns, in contrast, might predict a food reward reliably enough to prevent pattern-learning in hummingbird hawkmoths.

However, training changed the preferences at least to some extent: moths learned to prefer the uniformly blue stimulus to the ring pattern (figure 4) and moths rewarded on the ring pattern chose it more frequently than did naive moths (figures 2*b* and 3*c*). Finally, in contrast to naive animals, moths rewarded on the horizontal-stripes pattern preferred it to the vertical-stripes pattern (figure 5*d*). A lack of learning abilities cannot explain the results completely. The moths seem not to be motivated to abolish their innate preferences for patterns according to their experience, in contrast to their innate preferences for colours. This suggests that pattern preferences have a different function from colour preferences.

(c) *Innate preferences for structured stimuli, high contrast and 'flower-like' patterns*

An innate preference for patterned versus uniform stimuli has been found in lepidoptera and hymenoptera (Ilse 1932; Wehner 1981). Patterns are especially important to hawkmoths because visual contours allow them to control their hovering flight (Farina *et al.* 1994; Kelber 1997). The moths also preferred a darker blue (lb2) over a lighter blue (lb1), probably because it provided a higher contrast to the light grey background. Whether chromatic contrast, achromatic contrast or both are relevant cannot be determined. The preference for radial over ring patterns has been previously demonstrated in bees (Lehrer *et al.* 1995) and hawkmoths (Kelber 1997). Both bees and moths prefer radial and tangential patterns over other patterns (Lehrer *et al.* 1995), and this makes sense from the ecological point of view: flowers express exactly those patterns that insects prefer. However, in contrast to the moths, bees can be trained to reverse this preference, although learning is slow (e.g. Giurfa & Lehrer 2001).

(d) *Flower pattern and colour have different functions for pollinators*

The lack of learning ability and the missing motivation to override the preference for 'flower-like' patterns might be explained by the different functions that colour and patterns have for pollinators. Flower colours mainly act as signals. Innate colour preferences help pollinators to detect a first nectar source and to discriminate it from the

background (Giurfa *et al*. 1995; Kelber 1997; Goulson 2000), and colour learning allows them to adapt their behaviour to changing resources.

Patterns can be used for flower detection and discrimination in a similar way to colours (e.g. Giurfa & Lehrer 2001), but they also allow hovering pollinators to control their flight position, even on windy days, as mentioned in § 4c. In addition, flower patterns have long been known to serve as 'nectar guides' (e.g. Sprengel 1793), helping the pollinator to find the entrance to the nectar reservoir. This is particularly important for hovering pollinators, such as hummingbirds and hawkmoths. Their energetically costly flight forces them to forage fast and effectively. Hawkmoths probe and follow visual contours with the tip of their proboscis (Knoll 1924; A. Kelber, unpublished observations). Radial structures guide the proboscis into the central entrance to the nectar reservoir. Tangential contours (as in the ring pattern) mark the centre of the flower. For hovering pollinators, it might be highly relevant to retain a strong preference for patterns that guarantee fast and reliable access to the reward. It might be energetically too costly to abolish this preference in favour of a pattern that does not serve this purpose. Further experiments will have to determine exactly how visual patterns help hovering moths to find the reward.

(e) *Learning, motivation and negative results in discrimination tests*

The result of visual-discrimination experiments usually indicates whether an animal's visual system is capable of the discrimination or whether the animal's memory has the capacity to store the learned patterns. In my experiments, this is obviously not always the case. Hawkmoths are able to discriminate (figure 1*b,c*) and to learn patterns (figures 4 and 5). Negative results of training experiments—in animals known to learn other cues fast and reliably—thus do not always reveal an inability to discriminate, and need to be interpreted with more caution than previously thought.

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