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Limitations of the Innate Proboscis Reflex in *Eristalis tenax* L. (Diptera: Syrphidae) by the Spatial Resolution of the Compound Eye

Limitierungen des angeborenen Rüsselreflexes bei *Eristalis tenax* L. (Diptera: Syrphidae) durch das räumliche Auflösungsvermögen des Facettenauges

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Summary: Naive hoverflies of *Eristalis tenax* show an innate proboscis reflex towards yellow UV-absorbing dots. In natural flowers yellow pollen and pollen mimicking floral guides display the colour hue to which *Eristalis tenax* flies extend their proboscis. In this study the floral signals were simulated by yellow dots presented against the background colour of an artificial flower. We asked which factors trigger the proboscis reflex. We tested the minimal size of the yellow, UV-absorbing stimuli needed to elicit the proboscis reflex; in addition the impact of the background colour and of the ambient light intensity on the proboscis reflex was investigated. Some flies showed a proboscis reaction towards yellow dot stimuli of 0.10 mm to 0.15 mm dot diameter. The significant detection level of yellow dots is between 0.20 mm dot diameter for blue, 0.35 mm for pale yellow, and 0.25 mm for white background colour. The influence of light intensity on the triggering of the proboscis reaction remained unclear.

Keywords: Innate proboscis reflex, *Eristalis tenax*, spatial resolution

Zusammenfassung: Naive Schwebfliegen von *Eristalis tenax* zeigen einen angeborenen Rüsselreflex auf gelbe, UV-absorbierende Punktmale. Der gelbe Farbton des Pollens und die Pollen imitierenden Blütenmale von Blüten führen dazu, dass Fliegen der Art *Eristalis tenax* ihren Rüssel ausstrecken. In dieser Studie wurden die Blütensignale durch gelbe Punkte, die vor dem farbigen Hintergrund der eingesetzten Blütenattrappen präsentiert wurden, simuliert. Wir fragten, welche Faktoren den Rüsselreflex auslösen. Wir testeten die kleinste Größe der gelben, UV-absorbierenden Stimuli, die zum Auslösen des Rüsselreflexes notwendig ist. Darüber hinaus wurde der Einfluss der Hintergrundfarbe und der Umgebungshelligkeit auf den Rüsselreflex untersucht. Die Tiere zeigten vereinzelt Rüsselreaktionen ab einem Durchmesser der gelben Male von 0,10 mm bis 0,15 mm. Die signifikante Erkennungsschwelle der gelben Male liegt zwischen 0,20 mm Punktdurchmesser vor blauem, 0,35 mm vor hellgelbem und 0,25 mm vor weißem Hintergrund. Es konnte kein signifikanter Einfluss der Umgebungshelligkeit auf das Auslösen des Rüsselreflexes gefunden werden.

Schlüsselwörter: *Eristalis tenax,* angeborener Rüsselreflex, räumliches Auflösungsvermögen

1. Introduction

The hoverfly *Eristalis tenax* (Syrphidae: Diptera) lives in rural areas. While imagoes can generally be observed from March to October visiting flowers, adult females overwinter and can be found at manure heaps and eutrophic water when laying eggs. The hoverfly is about 14 to 18 millimeter in size and has a honeybee-like shape, colour and behaviour (Smith & Smith 2009). *Eristalis tenax* hoverflies can often easily be identified

by their characteristic orange-yellow dots on the second abdominal segment, however, a colour variation with completely dark brown abdomen exists. From similar other species of the genus *Eristalis*, *E. tenax* can be distinguished by two vertical hair-bands on the eye. Males can be distinguished fairly easy from females due to more orange-yellow abdominal markings, smaller size and holoptic compound eyes. The compound eyes of males merge at the front, while the females' eyes are distinctly separated from each other. The compound eyes of flies are made of thousands of individual eyes, the ommatidia. An ommatidium has 8 photoreceptor cells. In each ommatidium the retinula cells R1 to R6 are arranged in a trapezoid pattern around the tandem of the retinula cells R7 and R8 (HARDIE 1985). In the tandem R8 is proximal to R7. The individual photoreceptor cells have a different spectral sensitivity and are assigned to two visual systems (LUNAU & WACHT 1994, 1997a; LUNAU 2014). The colourblind neural superposition system with the retinula cells R1 to R6 is used for motion detection and the tetrachromatic apposition system including the retinula cells R7 and R8 is used for colour vision. The apposition system consists of the four retinula cells R7/8y (yellow) and R7/8p (pale), which both occur as receptor tandems in different ommatidia (KIRSCHFELD et al. 1978).

In contrast to humans flies are supposed to use these two visual systems in parallel (LUNAU 2014). As only one of the two retinula cell tandems is present in an ommatidium, at least two different ommatidia have to be stimulated to perceive colour. According to TROJE (1993) flies possess a categorial colour vision system and discriminate between only four colour hues. The innate proboscis reflex of naive hoverflies is triggered by the stronger stimulation of the R8y retinula cell (LUNAU & WACHT 1997b) as compared to the R7y retinula cell and the stronger stimulation of the R8p retinula cell as compared to the R7p retinula cell (LUNAU 2014). The innate proboscis reflex in *Eristalis tenax* is thus released only by yellow light in the range of wavelengths from 510 nm to 600 nm and inhibited by admixed small amounts of ultraviolet and/or blue light, while red light has no significant effect on the response of flies (LUNAU & WACHT 1997a). Upon release of the proboscis reaction by optical stimuli, the hoverfly extends the proboscis and touches the stimulus with the opened labella. Yellow pollen, which selectively reflects light of wavelengths longer than 520 nm (LUNAU 1996), is thought to represent the natural stimulus to which the proboscis reflex is fine-tuned. Little is known about the spatial properties of target stimuli that trigger the releasing of the proboscis extension. Here we ask how small the minimal diameter of yellow UV-absorbing color stimuli is that release the proboscis reflex. In addition the effect of ambient light intensity and background colour on the releasing of the proboscis extension towards yellow UV-absorbing stimuli is investigated.

2. Material and Methods

2.1. Collection and Keeping of *Eristalis tenax*

The hoverflies *Eristalis tenax* to be tested were collected in a nearby farm in Düsseldorf, Himmelgeist. There, the larvae of the third larval stage (the walking stage) and already pupated animals were collected. Pupated animals were separated and placed in an acrylic glass box (width x depth x height = 15 x 15 x 9 cm). The box was stored in a room that was illuminated with fluorescent tubes (58 W Cool White) at day from 10:30 a.m. to 7:00 p.m. with an intensity of 2580 lx. The larvae were placed in metal boxes and held until pupation. The metal boxes (width x depth x height = 62 x 42 x 30 cm) had a top window made of acrylic glass. The metal boxes were placed in a greenhouse at

the university. The hatched flies were put in boxes of a slightly different size (width x depth x height = 31 x 30 x 20 cm). To supply the animals, the boxes contained two Petri dishes with plugs of high-density foam, one with pure water and one with a honey-water mixture (ratio 1:2) and pollen (2 g in 160 ml of mixture).

As the collected larvae were all in the same larval stage, most animals pupated at the same time and imagoes hatched after about two weeks (Gladis 1994). To prolong the time for hatching most of the pupated animals were placed in a refrigerator for some days or weeks. By this method it was possible to delay the hatching for about one month.

2.2. Experimental design

The freshly emerged flower-naive flies after full hardening of the body and wings were tested as naive flies at artificial flowers providing pollen dummies. The tested flies were taken to the test arena half an hour before the test started and put in transparent tubes without food. All experiments were carried out after 10:30 a.m. In order to test the minimal size of yellow dots, towards which naive flies will respond with an innate proboscis reflex, the flies were placed on artificial flowers with yellow, UV-absorbing dots. The artificial flowers consisted of a photographic paper (5 cm x 2 cm) of either white, pale yellow, or blue background and of 4 yellow dots. The yellow dots were positioned centrally and arranged at a distance of about 1.0 cm between each other. The dots had different diameters ranging from 0.1 mm to 0.8 mm; each artificial flower had four yellow dots of identical diameter with about 1.0 cm distance between neighboring dots. The artificial flowers were placed in a small box made of acrylic glass in order to avoid escaping of the tested flies. The box was 8.0 cm long, 2.5 cm wide and 2.5 cm high and was covered with a white mosquito net that was fixed to the sides with hook-and-loop tape. Artificial flowers without dots were used as a control. In order to test the proboscis reaction towards yellow dots presented on artificial flowers with different backgrounds, the yellow dots were printed on artificial flowers with blue, pale yellow or white background. In order to investigate the possible effect of the intensity of ambient light on the proboscis reaction, a test series including artificial flowers with dots of all sizes and background colours was run under artificial light by fluorescent tubes at constant light intensity of 2580 lx, and another test series in natural outdoor light. In all cases light intensity was measured by means of a luxmeter. During the tests each fly was placed three times on the same artificial flower resulting in twelve opportunities for a proboscis reflex. The proboscis reactions of individual flies placed on the artificial flowers were registered; a single proboscis reaction towards a yellow dot of an artificial flower during the three tests was sufficient to be registered as a proboscis reflex at this stimulus combination. In order to be documented as proboscis reflex, the fly had to extend the proboscis towards the yellow dot in such a manner that the spread-out labella touched the yellow dot. It was ensured that each fly was tested only once with a specific background colour in order to exclude effects of learning or habituation.

2.3. Statistical analysis

The number of measured proboscis reactions towards yellow dots of various diameters was used to determine the limit of perception and the detection level of the hoverflies. The limit of perception denotes the smallest dot diameter that could be documented for reacting animals, as this allows conclusions about the spatial resolution of the hoverflies. The limits of perception are described without any statistical analysis.

The detection level refers to the dot diameter and is defined as a significantly higher

number of responding animals as compared to the control. The number of responding animals points to the number of the animals, which have shown a proboscis reaction in the three tests at all. A total of 20 animals has been tested in all experiments. To determine the significant detection level one-sided Chi-square tests were conducted comparing the number of responding flies to the test dummies and to the corresponding control dummies without yellow dots.

In order to examine the effect of background colour on the releasing of the proboscis reaction, a linear model (LM) was used and computed in the statistical program "R". The first full model accounts for all possible variables: The number of reacting animals, the proboscis reaction frequency and the background colour against the number of reacting animals as a fixed factor were tested. In the second and third test series, therefore, the effect of the background colour on the proboscis reaction frequency and the correlation between proboscis reaction frequency and number of reacting animals were examined.

In order to study the effect of background colours also with regard to the number of reacting animals and the dot diameter triggering the proboscis reaction at different stimulus sizes a binomial distribution of errors in a "general linear model" (GLM) was used in the program "R". For this purpose, the first full test series contained all relevant experimental variables: The number of reacting animals, the dot diameter (PG) and the background colours (HG). This approach allowed investigation of the variables. Also a correlation analysis was carried out with the frequency of flies exhibiting the proboscis reaction in dependence of the dot diameter.

To investigate whether the sex of the tested flies has in influence on the reaction frequency, the values, including sex, were tested in a general linear model (GLM) using the program "R".

3. Results

Few naive hoverflies reacted with proboscis extension towards yellow dots in experiments with white background in laboratory conditions even at the smallest tested size of 0.10 mm dot diameter, i.e. four of the total of 20 tested flies showed the proboscis reflex towards yellow stimuli of this dot diameter. With blue background only one fly exhibited proboscis extension towards 0.10 mm sized dots, with pale yellow background, no fly extended the proboscis towards the smallest dot size tested. At larger dot size, i.e. 0.15 mm dot diameter, one or few flies responded to the yellow dots irrespective of the background color. No fly exhibited proboscis extension towards the control irrespective of the background color (Fig. 1).

A significantly larger number of flies exhibited a proboscis reflex towards yellow dots as compared to the control (without yellow dots) for dots of 0.20 mm dot diameter presented against blue background, for dots of 0.35 dot diameter presented against pale yellow background, and for dots of 0.25 mm dot diameter presented against white background (Fig. 1). With increasing dot diameter the portion of flies responding with a proboscis reaction increased. More male than female flies were reacting to the yellow dots; however, the GLM test shows that the sex is no significant factor (Fig. 2, Table 1) determining proboscis reflex.

There is a linear correlation between the number of reacting animals, i.e. the number of tested flies exhibiting at least one proboscis reaction and the mean frequency of proboscis reactions with a maximum of 12 proboscis reactions in three tests with artificial flowers of a distinct stimulus combination. This relationship is independent of the background colour. The correlation coefficients R^2 surpass the value of 0.68 (Fig. 3, Table 2).

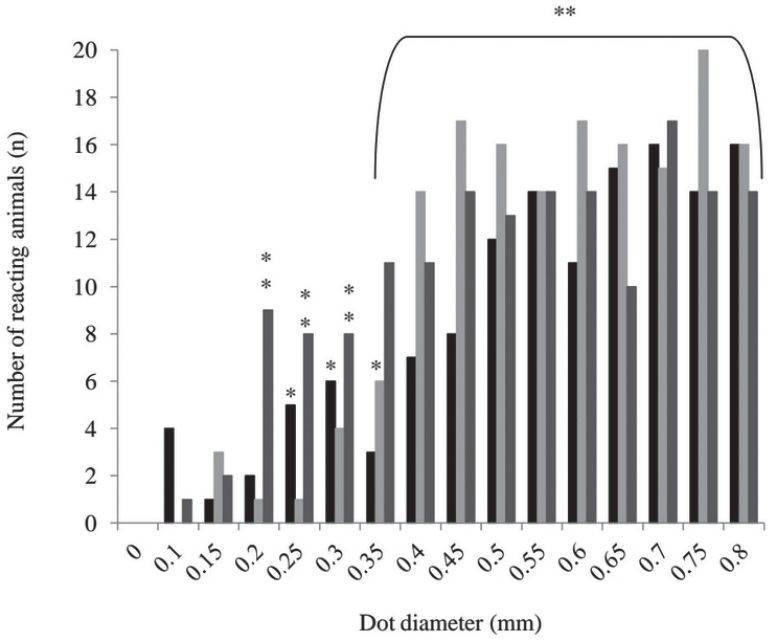

Fig. 1: Innate proboscis reflex of naive *Eristalis tenax* hoverflies towards yellow dots presented against white background (black), pale yellow background (light gray), blue background (dark gray) in dependence of dot diameter. For each background colour 20 naive flies, ten males and ten females, have been tested. The results of the one-sided Chi-square test are indicated as follows: * $P < 0.05$, ** $P < 0.01$.

Abb. 1: Angeborener Rüsselreflex von naiven *Eristalis tenax*-Schwebfliegen auf gelben Punkten vor weißem (schwarz), hellgelbem (hellgrau), blauem (dunkelgrau) Hintergrund, abhängig vom Fleckdurchmesser. Für jede Hintergrundfarbe wurden jeweils 20 naive Tiere, zehn weibliche und zehn männliche, getestet. Die Ergebnisse des einseitigen Chi-Quadrat-Test wurden wie folgt angegeben: * $P < 0{,}05$, ** $P < 0{,}01$.

Tab. 1: GLM general linear model. Total scattering 1328.02, residual scattering 909.28. The first full test series contained all relevant experimental variables. By reducing the variables important factors for release the proboscis reflex can be identify (df_1 = freedom degree, df_2 = second freedom degree).

Tab. 1: GLM allgemeine lineare Modell. Gesamtstreuung 1328,02, residuelle Streuung 909,28. Die erste volle Testserie enthält alle experimentell relevanten Variablen. Durch Reduktion der Variablen können entscheidende Faktoren für das Auslösen des Rüsselreflexes identifiziert werden (df_1 = Freiheitsgrad, df_2 = zweiter Freiheitsgrad).

	df_1	**df_2**	**explained scattering**	**p-value**	**significance**
model1<-glm(Value~PG*HG+sex, binomial)	911	959	418.74	2.2e-16	***
model2<-glm(Value~PG*HG, binomial)	911	912	6.7083	0.009596	**
model3<-glm(Value~PG, binomial)	912	944	74.708	2.868e-05	***
model4<-glm(Value~1, binomial)	944	959	337.33	2.2e-16	***

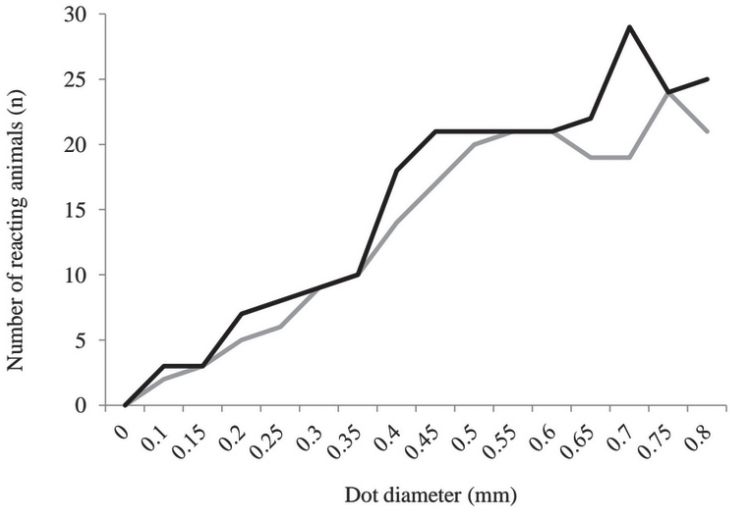

Fig. 2: Number of reacting male and female *Eristalis tenax* flies dependent of dot diameter. The data for the three backgrounds have been pooled. A total number of 30 flies of each sex has been tested for proboscis reactions to the yellow dots (males = black, females = light gray).
Abb. 2: Anzahl der reagierenden männlichen und weiblichen *Eristalis tenax* Schwebfliegen in Abhängigkeit vom Fleckdurchmesser. Die Daten der drei Hintergründe wurden gepoolt. In Summe wurden 30 Tiere jedes Geschlechts auf Rüsselreaktionen auf gelbe Punkte getestet (männlich = schwarz, weiblich = hellgrau).

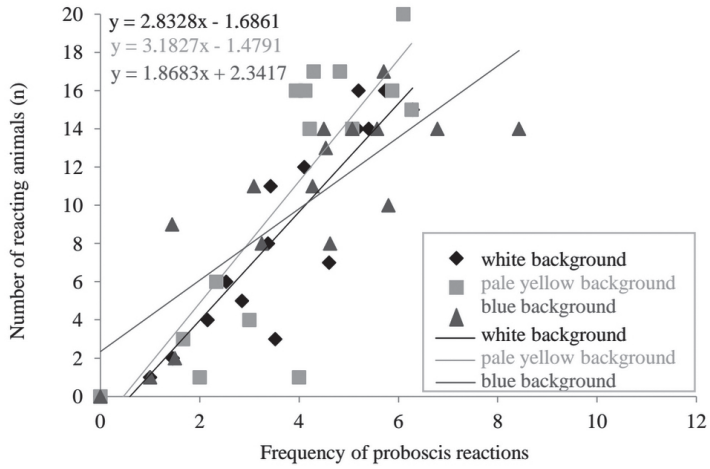

Fig. 3: Number of reacting animals in dependence of the mean proboscis reaction frequency for yellow dots presented on white (black), pale yellow (light gray) and blue (dark gray) background. Linear regression analysis: 20 animals per dot diameter and background colour were tested. The maximal number of proboscis reactions amounted to twelve reactions.
Abb. 3: Anzahl der reagierenden Tiere in Abhängigkeit von der mittleren Rüsselreaktionshäufigkeit auf gelbe Farbflecken bei weißem (schwarz), hellgelbem (hellgrau) und blauem (dunkelgrau) Hintergrund. Lineare Regressionsanalyse: 20 Tiere pro Punktdurchmesser und Hintergrundfarbe wurden getestet. Die maximale Rüsselreaktionshäufigkeit eines Tieres lag bei zwölf Rüsselreaktionen.

Tab. 2: Correlation analysis for the mean number of responding animals and the mean frequency of proboscis reactions.
Tab. 2: Korrelationsanalyse für die Anzahl der reagierenden Tiere und den Mittelwert der Rüsselreaktionshäufigkeit.

Background color	p-value	df	R^2
White	$4.344e^{-05}$	14	0.7084
Pale yellow	$7.809e^{-07}$	14	0.8341
Blue	$7.887e^{-05}$	14	0.6832
White + pale yellow + blue	$2.098e^{-13}$	46	0.6937

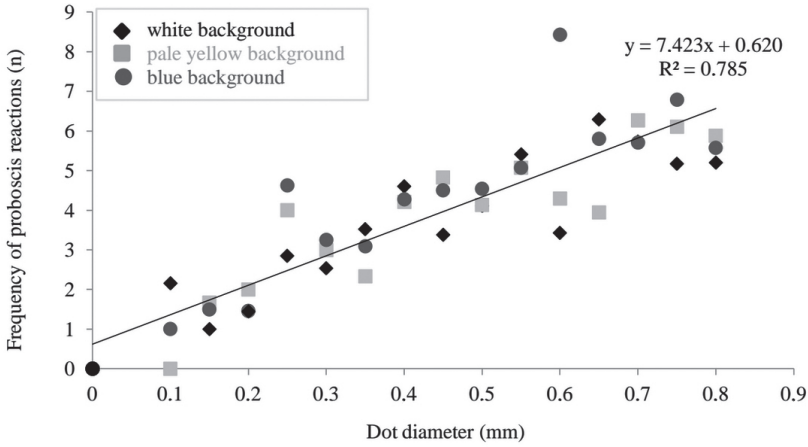

Fig. 4: Mean of frequency proboscis reactions of *Eristalis tenax* in dependence of dot diameter. Linear regression analysis: Correlation-test according to Pearson, t = 12.9607, df = 46, *p-value* < 2.2e-16, R^2 = 0.79, linear trend line: y = 7.423x + 0.620. The animals were placed on the artificial flowers with four yellow dots each for three times; the maximum frequency of proboscis responses per animal and test thus amounts to twelve. Data for three different backgrounds were pooled.
Abb. 4: Mittelwerte der Rüsselreaktionshäufigkeit von *Eristalis tenax* in Abhängigkeit vom Punktdurchmesser. Korrelationstest nach Pearson, t = 12,9607, df = 46, *p-Wert* < 2,2e-16, R^2 = 0,79, lineare Trendlinie = y = 7,423x + 0,620. Die Tiere wurden auf künstlichen Blüten mit vier gelben Punkten insgesamt drei Mal getestet, die maximale Rüsselreaktionshäufigkeit pro Tier und Test betrug zwölf. Die Daten für drei verschiedene Hintergründe wurden gepoolt.

The mean frequency of proboscis reactions shows a positive linear correlation with the dot diameter within the tested range between 0.1 and 0.8 mm dot diameter (Fig. 4).

In order to test the effect of the background colour, the test results were analysed by means of a linear model (LM). For this purpose the background colour, the proboscis reaction frequency and the number of responding animals were tested as possible explanatory variables. The background colour had no significant influence on the frequency of proboscis reactions. The frequency of proboscis reactions and the number of reacting animals, however, correlated well with each other, regardless of the background colour (Table 3).

The proboscis reaction was also tested in natural light conditions ranging from about 4,000 lx to 25,000 lx. Within this range of

Analysed variables	df_1	df_2	explained scattering	p-value
Model 1: number ~ frequency + color **Model 2:** number ~ 1	3	47	-1216.4	<0.001***
Model 1: number ~ frequency + **color** **Model 3:** number ~ frequency	2	46	-20.371	0.4207
Model 3: number ~ **frequency** **Model 4:** number ~ 1	1	46	1196	<0.001***

Tab. 3 Linear model, comparison of number of responding animals, the average frequency proboscis reactions and background colour. Total scattering 1724, residual scattering 507.5.
Tab. 3 Lineares Modell, Vergleich von Anzahl der reagierenden Tiere, der durchschnittlichen Rüsselreaktionshäufigkeit und der Hintergrundfarbe. Gesamtstreuung 1724, Residuelle Streuung 507,5.

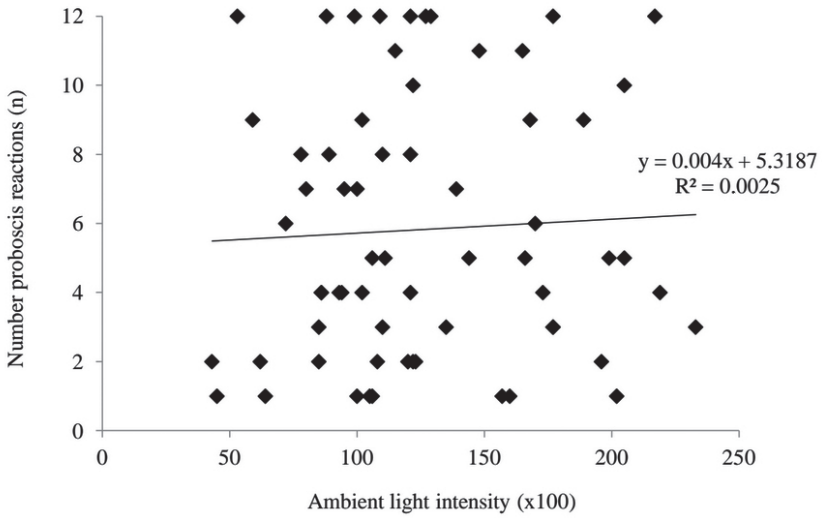

Fig. 5: Number of proboscis reactions in dependence of ambient light conditions. The ambient light intensity was measured after the tests.
Abb. 5: Anzahl der Rüsselreaktionen in Abhängigkeit von dem Umgebungslicht. Die Umgebungshelligkeit wurde nach den Tests gemessen.

area brightness the proboscis reaction was largely independent of the ambient light intensity (Fig. 5).

4. Discussion

Naive hoverflies *Eristalis tenax* (Syrphidae) show innate proboscis reactions in response to stimulation of the visual system by yellow and UV-absorbing colours (LUNAU 1993). This innate proboscis reflex is interpreted as a fine-tuned response to the most common yellow and UV-absorbing colour of pollen (LUNAU 2014). It is questionable, however, whether the spatial resolution is sufficient to allow flies to react with a proboscis reflex to single pollen grains or small amounts of pollen grains. The experiments aimed at identifying the perception limit, i.e. the minimal stimulus size to which the flies occasionally respond, and the detection level, i.e. the minimal stimulus size to which the

flies respond significantly more often as compared to a control stimulus. Few flies extended their proboscis towards yellow dots of the smallest tested diameter, which amounted to 0.10 mm. This dot diameter corresponds to the size of individual large pollen grains, which amounts up to 0.25 mm (Muller 1979). However, in tests in which individual yellow pollen grains of about 100 µm in diameter were offered instead of yellow dots, the flies did not react with a proboscis reflex (Riedel unpublished). Nonetheless, the flies should be able to visually recognize and respond to assemblages of few pollen grains.

The detection level for the proboscis reflex in *Eristalis tenax* is different for the different background colours studied. Since naive hoverflies responded to a smaller diameter of yellow dots if presented against a blue or a white background as compared to yellow dots presented against a pale yellow background colour contrast seems to play a role. Using LM and GLM the results indicate that yellow dot size and background colour are decisive factors and that both sexes of the hoverflies responded similarly. In nature, *Eristalis* hoverflies prefer white and yellow flowers (Kugler 1950; de Buck 1990) but also visit flowers of other colours (Haslett 1989). Many of those flowers offer visible yellow anthers and yellow pollen (Lunau 1995). It is known that the *Eristalis* hoverflies do not necessarily rely on visual cues when visiting flowers but are able to detect pollen and open nectar by means of chemical cues detected by gustatory receptors on the tarsi or on the labellum (Wacht et al. 1996; Woodcock et al. 2014)

In order to assess the effect of ambient light conditions as a limiting factor of spatial resolution for the triggering of the proboscis reaction, the light conditions, i.e. light intensities, were documented for the indoor and for all outdoor experiments. Within the range of light intensity from 4,000 lx to 25,000 lx no influence on the proboscis reflex was found. At light intensities surpassing 25,000 lx the flies suffered from the heat.

To determine the spatial resolution of the hoverflies precisely, the structure of the compound eye has to be taken into consideration. It can be assumed that a minimum of two ommatidia of the hoverfly eye have to be stimulated by yellow dots at the perception limit to trigger a proboscis reaction. Tsukahara & Horrige (1977) measured for ommatidia in *Eristalis* flies an opening angel of 1° which corresponds to opening angles of ommatidia in bees (Land & Nilsson 2002). Assuming further that the hoverflies in the tests had an average distance of 2.8 mm between the compound eye and surface of the dummy, it follows that at least 4-9 ommatidia have to be stimulated to trigger a proboscis reaction. The different systems of receptor tandems R7/8y (yellow) and R7/8p (pale) are irregularly distributed over the compound eye (Kirschfeld 1978) and are both required for colour perception after the colour model of Troje (1993). Therefore both systems have to occur in the stimulated ventral area of the compound eye to trigger a proboscis reaction by the decisive colour impression.

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