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RESEARCH ARTICLE

Colour blindness of the movement-detecting system of the spider *Cupiennius salei*

Eva Orlando and Axel Schmid*

Department of Neurobiology, Faculty of Life Sciences, University of Vienna, Althanstr. 14, 1090 Wien, Austria

*Author for correspondence (axel.schmid@univie.ac.at)

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SUMMARY

The nocturnal wandering spider *Cupiennius salei* has one pair of principal eyes and three pairs of secondary eyes located on the prosoma, which differ in both morphology and function. Their spectral sensitivity, measured with intracellular recordings, is due to three different types of photoreceptors with absorbance maxima in the mid-range of the spectrum, at 480 nm and 520 nm and in the UV at 360 nm. Based on these physiological data colour vision might be possible. In the present study, the ability to discriminate coloured moving stimuli from grey backgrounds was tested. The perception of moving coloured stripes in front of backgrounds with 29 different grey levels was measured by using extracellular recordings from the anterior median eye muscles as a monitoring system. Each of these eyes has two muscles, which increase their activity when moving stimuli are presented in front of a secondary eye. This variation in eye muscle activity can be recorded extracellulary in a living spider using a single channel telemetry device. If colour perception exists, the animal should be able to detect a moving coloured stripe in front of any grey level. Blue, green and red stripes were used as moving stimuli, in front of all 29 grey backgrounds. The results indicate that *C. salei* is not able to discriminate the coloured stimuli from distinct shades of grey. It is therefore evident that the movement-detecting system in this spider appears to be colour blind.

Key words: colour vision, *Cupiennius salei*, eye muscle, movement detection, photoreceptor, telemetry, wandering spider.

INTRODUCTION

The visual system of the Central American wandering spider *Cupiennius salei* (Keyserling 1877) consists of one pair of principal eyes [anterior median (AM) eyes] and three pairs of secondary eyes [posterior median (PM), posterior lateral (PL) and anterior lateral (AL) eyes], which differ in various functions. The visual fields of the AM and PM eyes overlap to a large extent, suggesting division of different tasks (Land and Barth, 1992).

Behavioural experiments indicate that the AM eyes are responsible for the detection and discrimination of stationary objects (Schmid, 1998), whereas the PM, AL and PL eyes detect moving targets and enable the detection of objects without the ability to discriminate between them (Neuhofer et al., 2009). This difference in function is also observed in salticids. The secondary eyes are able to detect movement, whilst the principal eyes analyse stationary objects (Land, 1970; Land, 1972; Duelli, 1978; Forster, 1985). As shown in behavioural tests Lycosid spiders also use their PM eyes to detect moving targets (Rovner, 1993). Very recently it could be shown that visual stimuli, i.e. a black spot moving on a green background, could elicit attack behaviour in *C. salei* (Fenk et al., 2010).

Up to four different types of photoreceptors were found in salticids (Land, 1969; De Voe, 1975; Yamashita and Tateda, 1976; Blest et al., 1981), leading to a broad spectral sensitivity from 330 nm up to 700 nm (Peaslee and Wilson, 1989). Colour vision abilities were investigated in simple behavioural experiments where coloured stripes could be discriminated (Kästner, 1950), and in a more elaborate heat-avoidance learning test the animals could discriminate the colours blue, green, yellow and red (Nakamura and Yamashita, 2000). Lycosids seem to have only two types of photoreceptors that are sensitive in the UV and green and no colour vision is shown up to now (De Voe et al., 1969; De Voe, 1972).

The absolute and spectral sensitivities of the photoreceptors in *C. salei* have been studied in great detail (Barth et al., 1993; Walla et al., 1996). All eyes exhibit nearly the same sensitivity and can be adapted to different brightness conditions (Grusch et al., 1997). The threshold for absolute sensitivity measured in electroretinogram (ERG) recordings is below 0.01 lx (Barth et al., 1993). Spectral sensitivity is characterized by the existence of three different types of photoreceptors with distinct absorbance maxima at 360 nm, 480 nm and 520 nm found in all three eyes, with the only exception that the UV receptor could not be found in the AM eyes (Walla et al., 1996). These facts indicate that colour vision might be possible.

Each of the AM eyes of *C. salei* has a dorsal and a ventral eye muscle controlling the retina (Kaps and Schmid, 1996). There are spontaneous microsaccades, with a deflection of the visual field of about 2 deg. These are produced only by the dorsal eye muscles with a frequency of about 12 Hz, and might prevent the adaptation of photoreceptors. The second kind of movement is an induced one and is caused by both the ventral and dorsal muscles, and can move the retina to a much greater extent of up to 50 deg (Kaps and Schmid, 1996). This occurs whenever the spider moves, but also if moving targets are presented in the visual fields of the secondary eyes.

The perception of moving objects in the visual fields of the secondary eyes therefore correlates with changes in eye muscle activity of the principal eyes, which themselves are not sensitive to motion (Kaps and Schmid, 1996; Neuhofer et al., 2009). These eye muscle activities can only be recorded in an animal that is free to move, and they do not occur in tethered animals as used in standard electrophysiological experiments. A telemetric device must therefore be used.

In the present study, the spider's reaction to moving coloured stripes in front of 29 different grey levels was tested by recording

the eye muscle activity. If the spider is capable of colour vision, it should be able to detect the moving coloured stimulus in front of any grey background regardless of its brightness. The animals should be able to discriminate at least blue and green from any grey level.

As their photoreceptors are not sensitive to wavelength beyond 620 nm, the red stimulus might not be perceived as colour, but should instead be confused with a dark shade of grey. However, if the animal is not able to detect the coloured stimuli and only can discriminate various shades of grey, then no reaction should be observed if the stripe and its background have the same subjective brightness.

MATERIALS AND METHODS

Animals

The experiments were carried out on adult females of the Central American hunting spider *Cupiennius salei* from the breeding stock in our laboratory. The animals were kept in glass jars, under natural daylight conditions, at temperatures between 23°C and 27°C, with a relative humidity of 70–80%. They were fed once a week with flies or crickets.

Telemetry

For the extracellular recordings from the dorsal eye muscles, a single-channel telemetric transmitter device was used, consisting of an amplifier, oscillator and transmitter, with a small battery as a power source (Kutsch et al., 1993; Neuhofer et al., 2009). The recording electrode (30 µm, coated manganin wire; Isabellenhütte, Dillenburg, Germany) and the reference electrode (silver wire) were attached to the transmitter device. The muscle potentials recorded from the eye muscles were amplified, transmitted to a wide band receiver, digitised using an A/D converter (CED, Cambridge, England, UK) and stored on a PC for further analysis. The electromyograms are the same as shown by Neuhofer et al. (Neuhofer et al., 2009).

To reduce the mobility of the animal it was chilled for approximately one hour at 8°C. It was then held down on a holder using parafilm. A small lateral part of the prosoma and the area between the eyes were carefully shaved. The transmitter device was fixed on the prosoma with beeswax and the battery was applied. The complete transmitter device excluding the battery weighed 670 mg, which is a load *C. salei* should be able to bear without any problems.

The reference electrode was inserted laterally into the prosoma. The hole for the recording electrode was prepared with a tapered tungsten electrode, and subsequently the manganin wire was implanted. To enable reliable data analysis, it was ensured that the signal-to-noise ratio of the recorded signal exceeded at least 5:1.

Experimental setup

The animals were positioned in the middle of the bottom of a partially open cylinder (0.5 m diameter, 0.33 m high), with an area through which the stripes were visible of 32%. The inner surface was covered with medium grey cardboard (relative reflectance 40%). The cylinder was fixed to the upper side of a Faraday cage to prevent vibrations from below, where the motor driving the stripe was fixed to a different holder isolated from the rest of the setup (Fig. 1). The setup was illuminated from above. The intensity in the cylinder varied from 250 lx up to 600 lx, depending on the current background. A coloured stripe moved around the outside of the cylinder at a velocity of 0.13 m s^{-1}, so it only became visible as it passed the open part. The distance from the animals to the wall, and therefore also the coloured stripe, was 0.25 m, so the subtended angle of the stripe (0.05 m) was 12.6 deg. This is much greater than the spatial resolution of the eyes (Land and Barth, 1992). All tests were performed during the animals' subjective day, to ensure that the photoreceptors are in the day-adapted state with reduced sensitivity, i.e. the microvillar surface was almost completely degraded, and the photoreceptors therefore should not be saturated (Grusch et al., 1997).

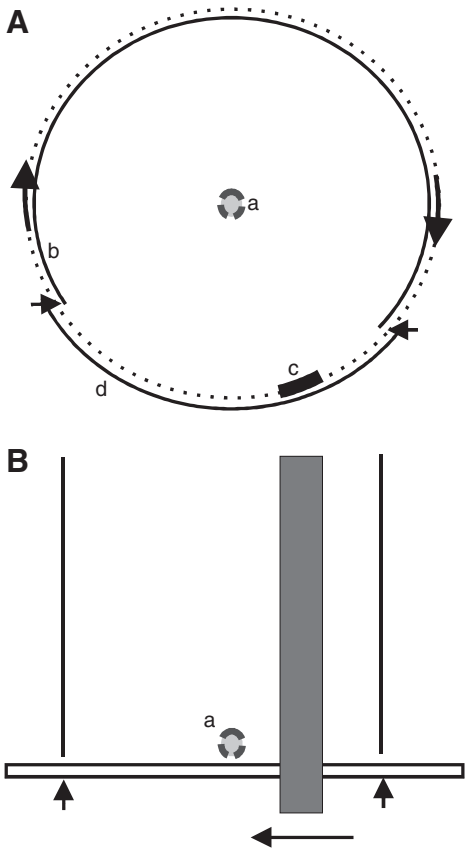

Fig. 1. Schematic drawing of the experimental setup, showing the top view (A) and the frontal view (B), where a is the position of the spider, b is the open cylinder, c is the coloured stripe, and d is the holder for the background. Small arrows indicate the position of the light barriers; larger arrows indicate the moving direction of the stripe.

The appearance and the disappearance of the stripe were measured by the means of two light barriers. These signals were also recorded, A/D converted and stored on the PC. The stripe was visible for 4 s; the interstimulus interval lasted 8 s, so that one entire rotation took 12 s. The 29 different grey papers used as variable backgrounds were put onto a holder, which could be moved close to the open part of the cylinder. The coloured stripes therefore moved through the spider's visual field directly in front of these grey backgrounds. Spontaneous microsaccades could be observed during the whole experiment, but induced eye muscle activities were only produced if the animal saw the moving stripe.

Visual stimulation

For the experiments 29 grey photo papers ranging from white to black were used as backgrounds. Using a spectroradiometer (International Light IL 1700, Research Radiometer–Photometer, Newburyport, England, UK), their relative reflectance compared with a white standard (SentroHeadWhite, Sentronic, Dresden, Germany) was measured for wavelengths from 420 nm to 700 nm (Table 1). Blue, green and red stripes were used as test stimuli, and their relative reflectance was measured in the same way. They showed reflectance maxima at 475 nm (blue), 515 nm (green) and 645 nm (red).

The height of the stripe was 40 cm and its width was 5 cm, which corresponds to 14 deg; this is far beyond the spatial cut-off frequency of 2 deg for vertical stripes as shown previously (Fenk and Schmid, 2010).

Experiments with blue, green and red stripes

Although the coloured stripe moved very closely in front of the background, the possibility of producing shadows had to be considered. After adjusting the illumination exactly from above, a grey stripe was moved in front of an identical grey background. This setup was tested with five animals, and none of them showed any reaction; therefore, it could be assumed that the setup had been arranged and illuminated appropriately.

Testing one coloured stripe in front of 29 grey backgrounds required several hours. None of the animals were active for such a long time. After about 30 min at the most they stopped responding, and in some cases even the spontaneous microsaccades ceased. Therefore, up to 10 animals were necessary to complete one full cycle, i.e. one coloured stripe in front of all 29 grey backgrounds. The blue stripe was tested seven times in front of the white background, i.e. it moved seven times around the cylinder.

The background was then replaced by all of the subsequent grey levels, until all 29 backgrounds had also been tested seven times. This complete procedure was repeated three times. Experiments with the green and red stripes were carried out in the same way. Ten animals were used to test the blue stripe, nine animals for the green stripe and 12 animals for the red stripe.

Additional experiments with the green stripe

In additional experiments, with 15 more animals the range of confusion for the colour green was tested in more detail. Here, a more narrow range of the grey levels 2–9 was tested, and due to the reduced number of backgrounds all animals could be measured for the complete range.

Data analysis

In all experiments the change in eye muscle activity during the presentation of stimuli was analysed. The mean frequency of seven stimulus and seven interstimulus activities was measured for a specific colour in front of each background. The differences between the mean stimulus and interstimulus frequencies were calculated and averaged. This difference was measured for all spiders with three colours in combination with all 29 backgrounds. The data sets of the experiments with the green stripe were tested with a Wilcoxon matched-pairs test.

RESULTS

In the 609 experiments, the animals were not able to discriminate the blue, green and red stripes from all of the tested 29 different grey backgrounds. For each colour there was always at least one grey background level from which it could not be distinguished.

Experiments with blue, green and red stripes

The blue stripe seemed to be as bright as grey levels 2–5 (Fig. 2A), because the eye muscle activity did not show any increase when these were presented as backgrounds.

The green stripe was perceived to be as bright as grey levels 4–7 (Fig. 2B), and the red stripe seemed to be as dark as the grey levels 19–22 (Fig. 2C).

These experiments, however, only indicate a wide range of equal brightness and could not show a more specific individual range, because an average of 10 animals was used to test the blue, 9 animals to test the green stripe and 12 animals to test the red stripe. It might be possible that a narrower confusion range with distinct variations between individual animals might cause such a broad range. Additional animals were therefore tested with only the green stripe to pinpoint individual variations.

Table 1. Relative reflectance of the grey papers that were used as background in all experiments

Number	R (%)	Grey level
0	100.0	
1	84.5	
2	66.7	
3	59.0	
4	56.7	
5	51.7	
6	44.0	
7	41.7	
8	36.8	
9	33.0	
10	30.2	
11	28.8	
12	27.3	
13	26.5	
14	25.7	
15	21.5	
16	20.5	
17	19.0	
18	17.7	
19	16.8	
20	15.2	
21	13.3	
22	12.7	
23	11.7	
24	10.7	
25	9.8	
26	9.2	
27	7.7	
28	3.3	

29 photo papers in gradation from white to black were used. The wavelengths were measured from 450 nm to 700 nm. R (%), relative reflectance.

Additional experiments with the green stripe

Looking at the results of the experiments with the green stripe, it can be concluded that the animals cannot discriminate the colour green from the grey levels 4–7 (Fig. 2B). Therefore, in these additional experiments, the individual differences concerning the extent of the confusion range, as well as the number of grey levels that seemed to have the same brightness as the colour, were determined in more detail with 15 animals, with all of them tested in the range of grey levels 2–9 (Fig. 3). The Wilcoxon matched-pairs test shows significant differences between levels 3 and 4 (Z-score >2.58; α=1%) and between levels 7 and 8 (Z-score >2.58; α=1%).

In Fig. 4, the crucial ranges are shown for six different individuals. Two animals (Fig. 4A) show a wide confusion range from grey levels 4–6, whereas four other animals show a much narrower confusion range of only one single grey level, which is either level 4 (Fig. 4B) or level 7 (Fig. 4C). The confusion range of the remaining nine animals was in between.

To summarise, animals were tested that could not distinguish the colour from three backgrounds and other animals could not distinguish the colour from only one background.

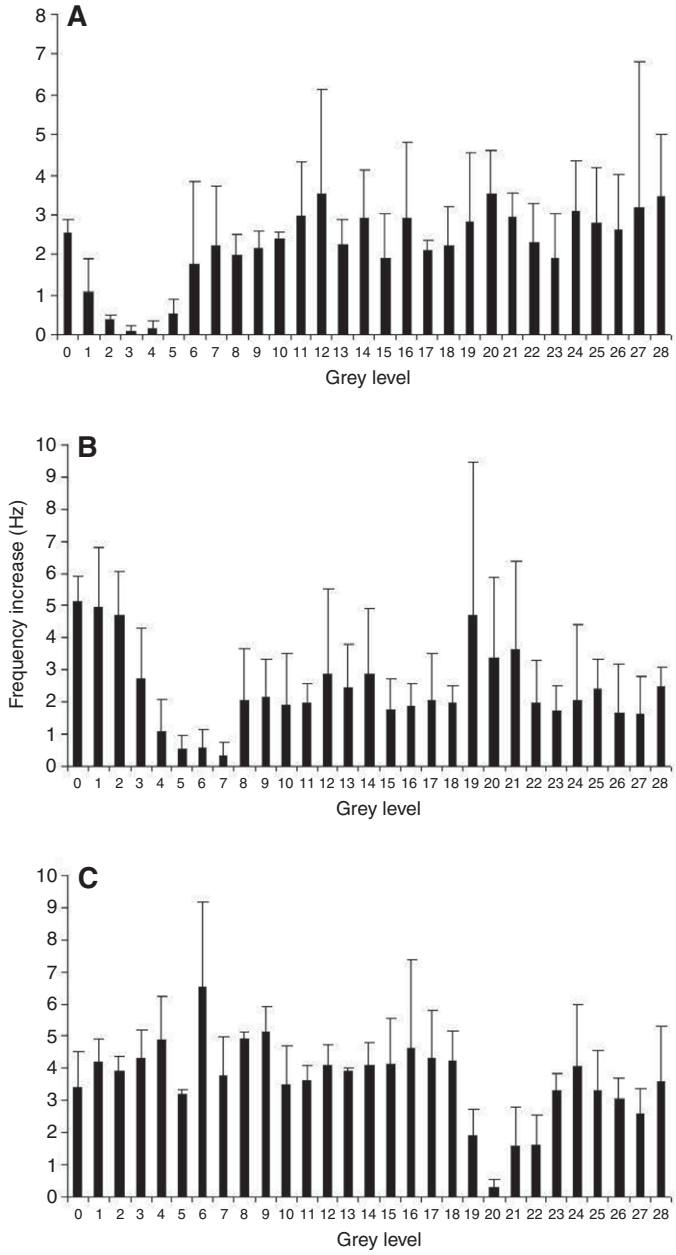

Fig. 2. Average mean frequency (given with s.e.) increase of the eye muscle activity. In (A) a moving blue stripe was presented in front of 29 different grey backgrounds (10 animals). The stimulus seemed to be as bright as the grey levels 2–5. (B) Average mean frequency increase of the eye muscle activity of 9 animals when the green stripe was presented. The green colour was as bright as grey levels 4–7. (C) Average mean frequency increase of the eye muscle activity of 12 animals when the red stripe was presented. The colour red is as dark as the grey levels 19–22.

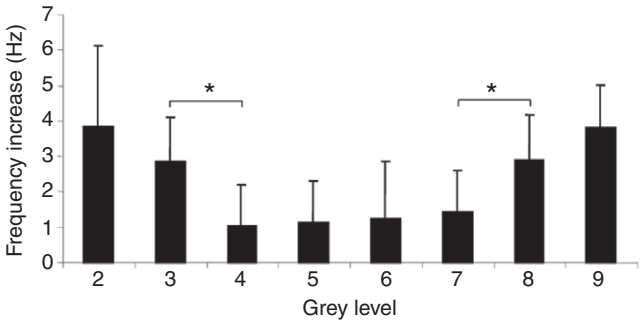

Fig. 3. Average increase of frequency (with s.e.) of the eye muscle activity at the grey levels 2–9 of 15 additional animals when the green stimulus was presented. The Wilcoxon matched-pairs test showed a significant difference for the grey levels from 3 to 4 and also from 7 to 8 both with a *Z*-score >2.58 (α=1%).

DISCUSSION

In the present study, colour vision ability in association with moving stimuli was investigated for the Central American wandering spider *C. salei*. The results show that there was always a small range of grey backgrounds from which the coloured moving stripes could not be discriminated.

Furthermore, individual differences concerning the ranges of confusion were found to vary from only one up to three grey levels. Each tested colour was confused with at least one grey level, showing that the gradation of the grey backgrounds was indeed fine enough.

The experiments showed that *C. salei* is not able to discriminate blue, green and red moving objects from various grey backgrounds. Depending on the subjective brightness of the colour, different ranges could be determined where the animals could not discriminate a coloured stripe from a grey background. As their photoreceptors are highly sensitive between 480 nm and 640 nm (Walla et al., 1996), and as the reflectance of the blue and green papers were chosen according to these findings, the stimuli are expected to seem very bright to the spiders. This was indeed the case, because they confused the blue stripe with the very bright grey levels in the range of 1–5 and the green stripe with the grey levels 4–7. Conversely they are much less sensitive to wavelengths over 620 nm, so it was not surprising that the confusion range for the red stimulus was at the dark grey levels 19–22. However, this also indicates that the spectrum of the red stripe (peak wavelength 645 nm) was not completely beyond the visible range, because otherwise the stripe would then have been confused only with the very darkest backgrounds 26–28.

Two possible reasons for this lack of colour perception can be considered. Firstly, the input for processing motion detection in distinct neuronal pathways could be derived from only one type of photoreceptor. This mechanism would preclude colour perception abilities in combination with movement detection. This has been demonstrated in bees, where the optomotor behaviour of stationary flying bees is colour blind (Kaiser and Liske, 1974). Moreover, scanning behaviour, object discrimination and the orientation discrimination of gratings are provided only by the green receptors (Lehrer et al., 1985; Srinivasan and Lehrer, 1988, Lehrer et al., 1988; Lehrer, 1994). In the bumblebee *Bombus impatiens*, however, a subset of mushroom body neurons was shown to be colour and motion sensitive (Paulk and Gronenberg, 2008). In *Drosophila*, motion detection, monitored by the optomotor response, is shown to be colour blind (Yamaguchi et al., 2008). Moreover, the neuronal circuitry, underlying colour and motion detection in the optic lobes, might be unravelled by means of single-cell clones (Morante and Desplan, 2008). Also in the human visual system, colour and motion are processed along different visual pathways in the periphery and a subsequent conjunction enables these two features to be merged (Seymour et al., 2009).

For the spider, however, it may be that the pathways of the secondary eyes, which are sensitive to movement, are not capable of processing colour information at all. We cannot exclude the possibility

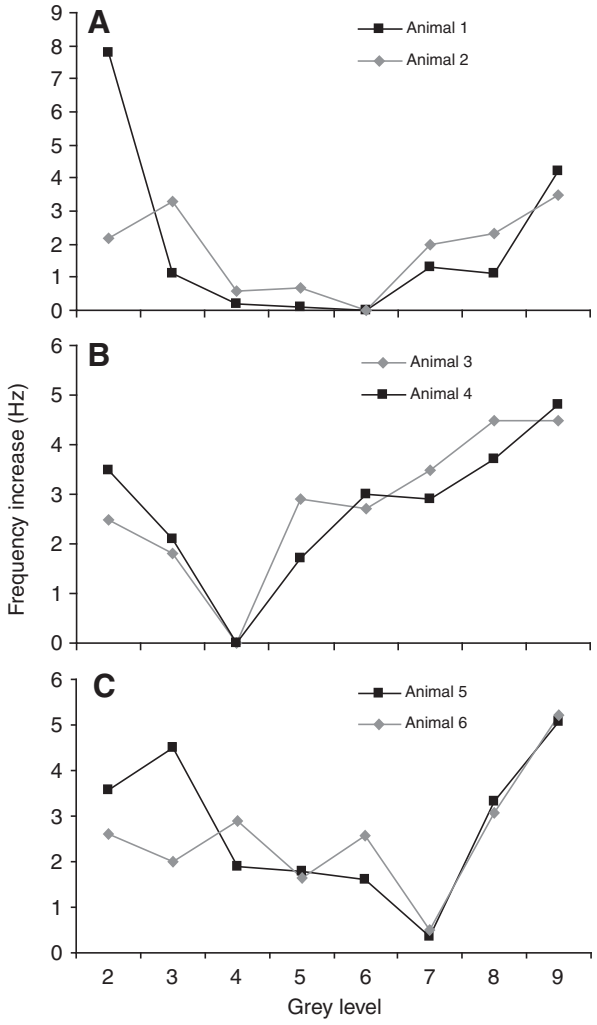

Fig. 4. Increase in frequency of the eye muscle activity of individual animals at grey levels 2–9. (A) Two animals did not show any activity at the grey levels 4–6. (B) Two examples for animals that had a very narrow confusion range of only grey level 4. (C) Two animals with a similar confusion range but at grey level 7.

that the principal eyes have the ability to process colour, because they do not respond to moving stimuli of the kind presented here.

To test for differences in the behaviour of single animals, and to find out if the crucial range can be narrowed by concentrating on individual animals, additional experiments were performed. An additional 15 animals were tested with the green stripe, presented with grey levels 2–9, and the individual differences were evident. Seven animals mixed the colour with only one grey level; four of them are shown in Fig. 4B,C. Eight animals perceived two or three grey levels being as bright as the green stripe; two of which are shown in Fig. 4A. These results indicate that *C. salei* is able to discriminate brightness with great accuracy. The fact that this distinct grey level differs among the animals shows that the sensitivity to brightness varies within the species.

The present study indicates that colour vision combined with movement detection is not possible for *C. salei*. The fact that it possesses three different types of photoreceptors does not necessarily contradict this result. We presume that these animals might have a broad spectral range to enhance their overall sensitivity. Furthermore, they might use this physiological capability to discriminate grey levels to a hitherto unexpected amount, which might be of importance for such an active predator hunting in dim habitats to identify prey.

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