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RESEARCH ARTICLE

Spectral sensitivity of the ctenid spider *Cupiennius salei*

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SUMMARY

The spectral sensitivity of adult male *Cupiennius salei* Keys, a nocturnal hunting spider, was studied in a behavioural test. As known from earlier behavioural tests, *C. salei* will walk towards a black target presented in front of a white background. In this study, a black target (size 42×70 cm) was presented in a white arena illuminated by monochromatic light in the range 365–695 nm using 19 monochromatic filters (half-width in the range 6–10 nm). In the first trial, the transmission of the optical filters was between 40% and 80%. In the second trial, the transmission was reduced to 5% using a neutral density filter. At the high intensity, the spiders showed a spectral sensitivity in the range 380–670 nm. In the second trial, the animals only showed directed walks if the illumination was in the range 449–599 nm, indicating a lower sensitivity at the margins of the spectral sensitivity. In previous intracellular recordings, the measured spectral sensitivity was between 320 and 620 nm. Interestingly, these results do not completely match the behaviourally tested spectral sensitivity of the photoreceptors, where the sensitivity range is shifted to longer wavelengths. In order to investigate the molecular background of spectral sensitivity, we searched for opsin genes in *C. salei*. We found three visual opsins that correspond to UV and middle to long wavelength sensitive opsins as described for jumping spiders.

Key words: behavioural test, gene expression, eyes, phylogeny, vision, opsins.

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INTRODUCTION

The hunting spider *Cupiennius salei* Keys is a nocturnal predator that has been the focus of interest for a long time because of its excellent mechanosensory systems. The function and use of the visual sense were unclear and were believed to play no great role in the behaviour of *C. salei*. For hunting and mating, the spider depends mainly on its mechanosensory systems (Barth and Schmitt, 1991; Eckweiler and Seyfarth, 1988; Hergenröder and Barth, 1983; Schüch and Barth, 1985; Schüch and Barth, 1990; Seyfarth et al., 1985). Recent studies, however, have shown that *C. salei* also has a well-developed visual system (Fenk and Schmid, 2010; Grusch et al., 1997; Kaps and Schmid, 1996; Land and Barth, 1992). Fenk and colleagues (Fenk et al., 2010) showed that a visual stimulus alone can elicit attack behaviour. Behavioural experiments showed that the animals are able to select adequate dwelling plants for daytime hiding (Schmid, 1998).

Like most spiders, *C. salei* has eight eyes; a pair of principal eyes (anterior–median, AM) and three pairs of secondary eyes (anterior–lateral, AL; posterior–median, PM; posterior–lateral, PL). The retinae of the AM eyes are moved by a pair of muscles (Kaps, 1998). The rhabdomeres of the receptor cells of the AM eyes are orientated towards the light. The secondary eyes possess a tapetum in the back of the eyes and have inverted photoreceptor cells (Land, 1985). The receptive fields of the eyes nearly cover the whole surrounding area of the spider, except a small section behind it. The visual fields of the AM and the PM eyes overlap almost completely; their overlapping visual fields and the different anatomy of the principal and secondary eyes suggests that these two pairs of eyes might have separate functions (Land, 1985). Only the AM eyes have muscles with spontaneous activity, which leads to the conclusion that they allow the discrimination of stationary targets, while the secondary eyes are tuned to detect movable objects (Land, 1985; Schmid, 1998; Neuhofer et al., 2009).

Behavioural studies with the nocturnal, desert-living jumping spider called the Dancing White Lady spider (*Leucorchestris arenicola*), which is known to cover some distance to find mating partners or food, have shown that its ability to find its way back home is diminished when its eyes are covered. Gravity, odour marks or vibrations of the ground seem to be of no importance (Nørgaard et al., 2008). In an investigation on the spectral sensitivity of the jumping spider *Maevia inclemens* it was shown that wavelengths between 330 and 700 nm could be detected (Peaslee and Wilson, 1989). The home of *C. salei* offers a lot more landmarks for orientation, so there is the possibility that the eyes do play a role in orientation behaviour, for example to find bromeliads, the preferred mating place of *C. salei*.

Electroretinogram (ERG) recordings revealed a possible spectral sensitivity from 300 to 700 nm and a sensitivity threshold for white light below 0.01 lx (Barth et al., 1993). Using intracellular electrophysiology recordings, Walla and colleagues (Walla et al., 1996) demonstrated the existence of three photoreceptors with sensitivity maxima at 340 nm (UV receptor), 480 nm (blue receptor) and 520 nm (green receptor). The blue and the green receptors both have a second peak in the range of the λ_{max} of the UV receptor. The UV receptors could only be found in the secondary eyes, with only one in each. The existence of UV cells, however, does not prove

that these animals use the information from this part of the spectrum in visually guided behaviour.

In previous behavioural experiments it was shown that *C. salei* runs towards a presented black target if there are no other visual stimuli. In a twofold choice experiment, different shapes of cardboard were tested. *Cupiennius salei* showed a preference for black oblongs that were presented upright (Schmid, 1998). Why the spiders are heading for a black target at all may be because it provides a good hiding place for the bay-coloured spider, which is nearly invisible on a dark background such as the bark of a tree. This makes it difficult for predators and also for potential prey to detect it. This crypsis through background matching is a strategy well investigated for the crab spiders *Misumena vatia* and *Thomismus spectabilis*. These spiders can even change the colour of their bodies from white to yellow depending on the colour of the flower they are sitting on, waiting for prey (Defrize et al., 2010; Heiling et al., 2005a; Insausti and Casas, 2008; Théry, 2007; Weigel, 1942).

In the present study, we use a behavioural test to assess whether *C. salei* uses the complete spectral sensitivity range that was detected in electrophysiological recordings. Specifically, we assayed the ability of *C. salei* to detect a black target on a background of monochromatic light at different wavelengths in the 365–695 nm range. In order for an eye to detect light of different wavelengths, it needs multiple opsins that respond to light of different wavelengths. In a study of two species of jumping spider that have colour vision, three opsins were found (Koyanagi et al., 2008). Phylogenetic analysis indicated that one of these opsins (Rh3) was UV sensitive, and the other two (Rh1 and Rh2) grouped with middle and long wavelength sensitive opsins of other arthropods.

To determine whether *C. salei* has the molecular equipment to detect light of different wavelengths, we searched for the presence of opsin RNA in the different eye types.

MATERIALS AND METHODS

Animals

Adult males of *C. salei* raised in our laboratory in Vienna were used for this experiment. The spiders were kept individually in glass jars (25 cm high, 14.5 cm diameter) and fed once per week on flies. The temperature was 22°C and the relative humidity above 60%.

Male spiders have much longer active phases than females and therefore were used in running experiments (Schmitt et al., 1990).

Experimental apparatus

The animals used in the experiments were kept under an artificial photoperiod (12 h:12 h light:dark). The experiments took place 1 h after the night phase started. Experiments were performed in a room without natural light. The size of the quadratic arena was 210×210 cm. The walls were painted white and the ground was covered with a white polythene sheet. A piece of black cardboard (42×70 cm) was used as the target. The arena was illuminated by a light projector (Xenotar, Götschmann, Munich, Germany), used in combination with monochromatic filters between 365 and 695 nm (Table 1) and a neutral density filter NG −9 (Schott, Mainz, Germany) (Table 2).

In the first experiment, only the 19 different monochromatic filters were used (transmission between 40% and 80% and a half-width in the range 6–10 nm). In the second experiment, a neutral density filter NG-9 (Schott) was used in combination with each monochromatic filter to reduce the transmission to 5%.

For statistical analysis, the arena was divided into 20 sectors, each sector corresponding to a specific orientation angle. Sector 0 deg corresponds to an angle from 351 to 8 deg (which is exactly the position of the black bar), sector 18 deg corresponds to an angle from 9 to 26 deg, and sector 36 deg corresponds to an angle from 27 to 44 deg, and so on (Fig. 1).

Table 1. Statistical evaluation of the data from the experiment with monochromatic filters

Filter (nm)	No. of positive runs	mvd (deg)	**r**	*s* (deg)	Rayleigh test
365	11	**353.6**	0.580	52.2	$P \leq 0.01$*
389.9	22	**357.8**	0.815	34.8	$P \leq 0.01$*
403.2	21	**2.3**	0.827	33.7	$P \leq 0.01$*
420.2	26	**359.0**	0.847	31.7	$P \leq 0.01$*
434.5	24	**357.0**	0.788	37.3	$P \leq 0.01$*
448.5	27	**4.6**	0.945	19.0	$P \leq 0.01$*
478	24	**0.7**	0.846	31.8	$P \leq 0.01$*
499.3	23	**5.5**	0.861	30.2	$P \leq 0.01$*
513.9	28	**0.0**	0.954	17.4	$P \leq 0.01$*
519.6	25	**357.5**	0.879	28.2	$P \leq 0.01$*
538.2	27	**2.0**	0.929	21.5	$P \leq 0.01$*
547.2	25	**359.3**	0.802	36.1	$P \leq 0.01$*
575.1	27	**356.2**	0.961	16.1	$P \leq 0.01$*
588.3	27	**358.7**	0.894	26.4	$P \leq 0.01$*
598.6	27	**5.7**	0.906	24.9	$P \leq 0.01$*
614.6	27	**358.0**	0.890	26.8	$P \leq 0.01$*
654	25	**353.4**	0.839	32.5	$P \leq 0.01$*
670.1	15	**2.3**	0.675	46.2	$P \leq 0.01$*
695	4	42.2	0.360	64.8	$P > 0.01$

mvd, mean vector direction; **r**, length of the mean vector; *s*, angular deviation.

r gives an indication of one-sidedness. **r** can have a minimum value of 0 and a maximum of 1. If **r** is sufficiently large, the hypothesis of randomness can be rejected in favour of one-sidedness.

Numbers in bold show the mean vectors that point within sector 0 deg, e.g. to the black bar (n=15, N=30). Asterisks mark significance.

The spiders were put into the arena at a distance of 2 m from the black target in a plastic box that was removed when the spiders were in the correct position, i.e. oriented towards the black target. If the spider walked erratically and touched the wall or showed a fright posture, the experiment was stopped and repeated the next day. If the spider did not move but was in a ready posture, we gently nudged its hind-legs using a cotton-coated stick to activate it. The walking path of the spider was observed by eye and plotted by hand.

In total, 15 animals (n) were tested in two runs each (N), and the number of runs within each sector was counted. A run to sector 0 deg, i.e. the black target, was rated as a positive run. The other runs were regarded as negative. All runs were measured and used for statistical analysis.

The mean vector and vector length were calculated with the program Rayleigh & Co. (Oxalis GmbH, Cologne, Germany), and the statistical support for directedness was tested using circular statistics (Batschelet, 1981). We used 95% confidence limits for the mean, and the level of significance was $P \leq 0.01$.

A control experiment with no target was performed to see whether the spiders showed any preference for one side of the arena even without a visual stimulus.

Screening for opsin genes

Total RNA was isolated with the Trizol method (Invitrogen/Life Technologies, Vienna, Austria) from mixed embryonic tissue, CNS from adults and adult retinas. The extracted RNA was sent to Genecore (EMBL, Heidelberg, Germany) for sequencing (Illumina hi-seq, paired-end 100 bp). Following *de novo* assembly, we searched the resulting transcript database for matches to a diverse

Table 2. Statistical evaluation of the data from the experiment with monochromatic filters in combination with a neutral density filter

Filter (nm)	No. of positive runs	mvd (deg)	**r**	*s* (deg)	Rayleigh test
389.9	4	308.2	0.218	71.6	*P*>0.01
403.2	4	70.0	0.200	72.5	*P*>0.01
420.2	6	13.9	0.345	65.6	*P*>0.01
434.5	12	15.3	0.627	49.5	*P*≤0.01*
448.5	21	**354.8**	0.877	28.4	*P*≤0.01*
478	25	**1.1**	0.912	24.1	*P*≤0.01*
499.3	23	**358.4**	0.977	12.3	*P*≤0.01*
513.9	22	349.8	0.765	39.3	*P*≤0.01*
519.6	19	**358.3**	0.703	44.2	*P*≤0.01*
538.2	21	345.7	0.775	38.4	*P*≤0.01*
547.2	21	**3.6**	0.766	39.2	*P*≤0.01*
575.1	22	**355.3**	0.841	32.3	*P*≤0.01*
588.3	24	**354.8**	0.887	27.3	*P*≤0.01*
598.6	17	**354.6**	0.665	46.9	*P*≤0.01*
614.6	10	342.4	0.407	62.4	*P*>0.01
654	2	20.7	0.168	73.9	*P*>0.01
670.1	2	20.5	0.160	74.3	*P*>0.01

mvd, mean vector direction; **r**, length of the mean vector; *s*, angular deviation.

Numbers in bold show the mean vectors that point within sector 0 deg, e.g. to the black bar (*n*=15, *N*=30). Asterisks mark significance.

set of opsin proteins downloaded from NCBI. BLAST searches and sequence analysis were done with the computer program Geneious version 5.6.6 created by Biomatters (http://www.geneious.com/). Opsin sequence orthology was established by aligning the identified *C. salei* sequences to arthropod visual opsin sequences, with an onychophoran rhodopsin sequence included as an outgroup, followed by calculation of a Bayesian tree using MrBayes with a Poisson distribution model of amino acid substitutions (Huelsenbeck and Ronquist, 2001). Opsin sequences were aligned with clustalW and regions outside of the seven transmembrane domains were excluded.

RT-PCR

Total RNA was isolated from dissected retinas from each of the four eye types; AM, PM, AL and PL. RNA was extracted with the Trizol method (Invitrogen/Life Technologies) and used for reverse transcription using Thermoscript (Invitrogen/Life Technologies). The resulting cDNA was used as template in subsequent PCR. Primers were constructed from opsin sequences found in the *C. salei* transcriptome database using the software primer3 (Rozen and Skaletsky, 2000). The following primers were used: Cs-Rh1 forward 5′ TTTTCGGACCCATACGAGAG 3′; Cs-Rh1 reverse 5′ GGTTTACCCAGGCATTTGAA 3′, Cs-Rh2 forward 5′ GTGGTCCTGTTGGCTAGCAT 3′; Cs-Rh2 reverse 5′ ATGACACTCGTTTCGGACCT 3′; Cs-Rh3 forward 5′ GGCATTCCTGGACGAGATAA 3′; Cs-Rh3 reverse 5′ ATTCATTTTGCGAGCCTGTT 3′. A PCR reaction was performed with primers from each of the three visual opsins on cDNA from each of the four eye types using GoTaq Flexi DNAPolymerase (Promega, Mannheim, Germany). The opsin sequences have been submitted to EMBL and have the following accession numbers: Cs-Rh1 HF549177, Cs-Rh2 HF549178, Cs-Rh3 HF549179.

RESULTS

Behaviour during the experiment

The animals were positioned at a release point in the arena, and after release they typically turned slightly to the left and to the right before they started walking. While running towards the bar, they showed a characteristic zigzag mode, which indicates a target-

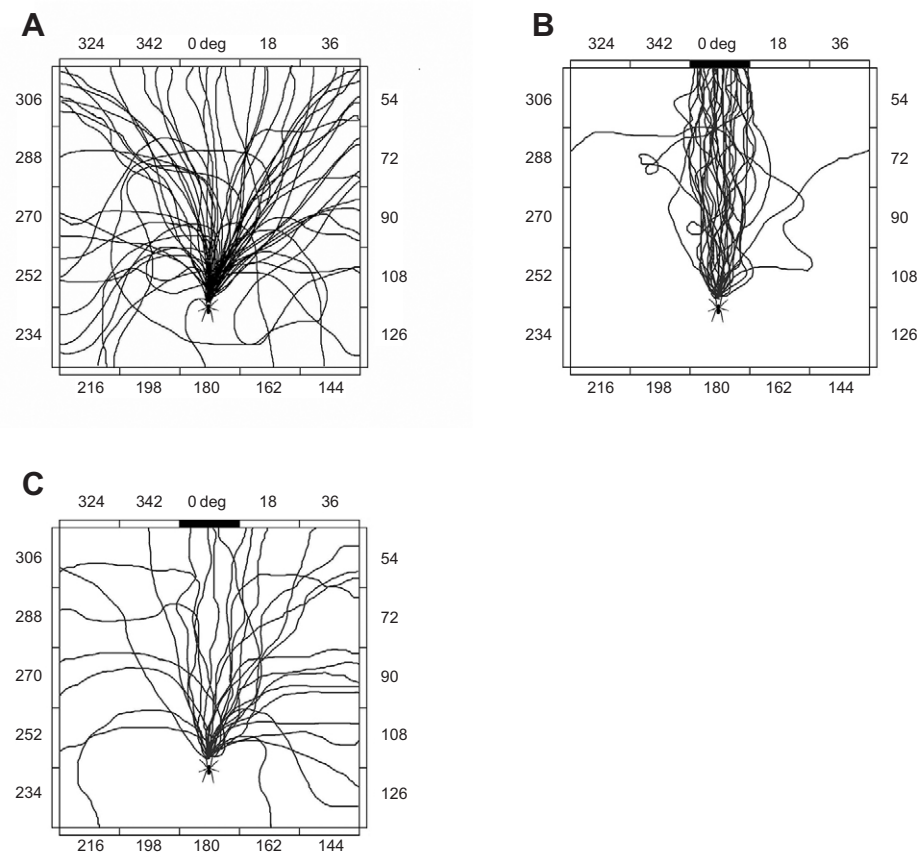

Fig. 1. (A) Pathways of 60 runs of 15 spiders in the control experiment, without a target and with white light illumination. (B) Pathways of 30 runs of 15 spiders illuminated by monochromatic light at 513.9 nm, displaying 28 positive runs, one spider touching the wall at sector 288 deg and another at 72 deg. (C) Pathways at 695 nm illumination. Only four runs ended at the black bar; the other runs were distributed over a wide range.

oriented behaviour. At a distance of about 50 cm to the target the spiders accelerated and ran straight to the bar. In most cases, they did not head for the middle of the bar, but for an edge. If the spiders did not run towards the bar, their paths showed various curves terminating at the wall.

Control experiment

In the control experiment, performed under white light illumination but without a target, the spiders showed no preference for any side of the arena. The mean vector points towards 12.7 deg. The runs were distributed randomly, as shown by the length of the mean vector of 0.299, and the angular deviation was considerably high at 67.8 deg (Fig. 1).

Experiment with monochromatic filters

The spiders showed very good spectral sensitivity to wavelengths between 389.9 and 654 nm. On average, 82% of the spiders showed positive runs (directed walk to the black bar) and the mean vector was within sector 0 deg (between 351 and 9 deg). The vector length minimum was 0.6 and the angular deviation was below 40 deg. The best result, with 28 out of 30 positive runs, was observed at 513.9 nm. The pathways of the spiders at this wavelength are shown in Fig. 1B.

The mean vector at a wavelength of 365 nm points within sector 0 deg, but the short length of the vector (0.58) and the big angular deviation (52.2 deg) indicate a less distinctive result, despite the statistical significance of $P \leq 0.01$. The results for the 365 and 670.1 nm filters were significant, with angular deviations of 52.2 and 46.2 deg, and mean vector lengths of 0.580 and 0.675, respectively; however, these results were lower than the results for the intervening wavelengths, suggesting that the wavelengths at 365 and 670.1 nm are close to the limit of the spiders' spectral sensitivity. The results clearly show that *C. salei* is not able to detect the black bar at 695 nm illumination, as the mean vector points to 42.2 deg, the vector length is very short at 0.36 and the angular deviation very big at 64.8 deg. The pathways of the spiders at 695 nm are shown in Fig. 1C.

Monochromatic filters in combination with a neutral density filter

From 389.9 to 420.2 nm, the runs were distributed randomly. At 434.5 nm the mean vector only approximated to sector 0 deg but pointed to the neighbouring sector. Not until 448.5 nm was the mean vector within sector 0 deg and the results significant. Between 448.5 and 598.6 nm on average 72% of the spiders showed positive runs. The mean vectors at wavelengths of 513.9 and 538.2 nm were slightly shifted to the left. Here, most of the negative runs were directed to the left wall. From 614.6 to 670.1 nm, the runs were again distributed randomly. Therefore, the spectral sensitivity was limited to a range between 448.5 and 589.6 nm.

Opsin genes in *C. salei*

We found six opsin genes in our screening of the transcriptomes. Two were only detected in the transcriptome based on CNS-specific RNA that excluded eye tissue (Eriksson et al., 2013), and were therefore not considered further in this paper. Phylogenetic analysis (Fig. 2) showed that three of the remaining four opsin sequences clearly grouped with arthropod visual opsins. Cs-Rh1 and Cs-Rh2 grouped together with jumping spider opsin Rh1 and Rh2, with the long to middle wavelength sensitive opsins, and Cs-Rh3 grouped together with jumping spider Rh3, with UV and short wavelength sensitive opsins. The Cs-Rh3 sequence also contains the lysine residue in transmembrane region 2 that has been shown to be

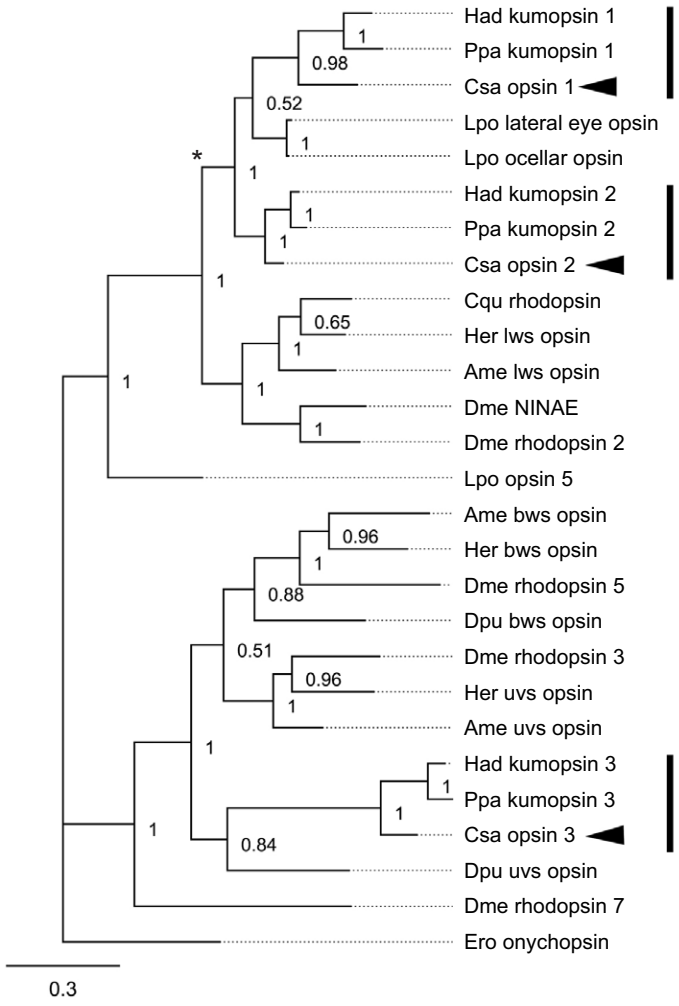

Fig. 2. Phylogenetic reconstruction of arthropod and onychophoran visual opsins. The tree is from Bayesian likelihood analysis using MrBayes on protein sequences: half-compatibility consensus from 451,000 replicates, burn-in of 100,000 replicates. One onychophoran rhodopsin was used as out-group (Ero onychopsin). Numbers at nodes represent posterior probabilities of Bayesian likelihood analysis. Asterisk marks chelicerate opsins except for UV opsins. Arrowheads mark opsins of *Cupiennius salei*. Vertical bars mark spider opsins. Scale bar shows 0.3 substitutions per site. Csa opsin 1–3=CS Rh1–Rh3. Species included in the analysis are: Ame, *Apis mellifera*; Cqu, *Culex quinquefasciatus*; Csa, *Cupiennius salei*; Dme, *Drosophila melanogaster*; Dpu, *Daphnia pulex*; Her, *Heliconius erato*; Ero, *Euperipatoides rowelli*; Had, *Hasarius adansoni*; Lpo, *Limulus polyphemus*; and Ppa, *Plexippus paykulli*.

responsible for UV sensitivity (Salcedo et al., 2003). The fourth opsin sequence detected in the retina showed greatest similarity to peropsin of the jumping spider *Hasarius adansoni* and is not further discussed here. The three opsins were expressed in all of the eyes (Fig. 3). The quantity of the transcripts of the three different visual opsins was very different, with Cs-Rh2 representing 31% of all transcripts [reads per kilobase per million reads (RPKM) of 243,860], Cs-Rh1 representing 0.6% of transcripts (6400 RPKM) and Cs-Rh3 with 41 p.p.m. (45 RPKM).

DISCUSSION

The results of the control experiment showed that when no target is present, *C. salei* is more likely to turn left, right or wander aimlessly, than to walk straight ahead. At wavelengths outside their

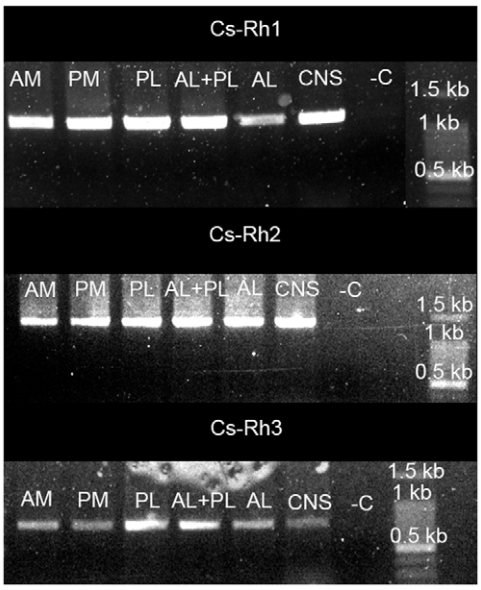

Fig. 3. Images of gel electrophoresis of RT-PCR products from different tissues. The image shows products of: Cs-Rh1 (1164 base pairs, bp), Cs-Rh2 (1285 bp) and Cs-Rh3 (748 bp). AM, anterior median eye (retina); PM, posterior median eye (retina); AL, anterior lateral eye (retina); PL, posterior lateral eye (retina); CNS, central nervous system; –C, negative control.

spectral sensitivity range, the spiders walked very slowly and used the first pair of legs as guide sticks, which indicates that they cannot see (Schmid, 1997). During the behavioural experiments with monochromatic light, *C. salei* showed an overall sensitivity to light from 389.9 to 654 nm at the higher intensity. This range is narrow compared with the results of ERG recordings (300–700 nm) (Barth et al., 1993), and differs from the spectral sensitivity range of the intracellular recordings of single photoreceptors (Walla et al., 1996). The spectral sensitivity shown by the intracellular recordings ceased at 620 nm, while in our experiment at least half of the tested spiders could detect the black target up to 670 nm at the bright illumination. Although the ERG recordings indicate that the spectral sensitivity begins at 300 nm and the intracellular recordings demonstrate the existence of a UV receptor with λ_{max} at 340 nm, the spiders were clearly able to see the target down to wavelengths of 389.9 nm, and in a less pronounced way to a wavelength of 365 nm; this may be due to a very low number of UV receptors or possibly that they have other functions, e.g. navigation. However, the perception in the red colour range of the spectrum was better than expected and might be due to the large spectral sensitivity range of the green receptor.

In the second experiment at the lower intensity, the range of spectral sensitivity was reduced to 448.5–598.6 nm (blue to green). This fits with our expectation, as the light reflected by the leaves of the dwelling plants dominates at these wavelengths (Menzel, 1979; Chittka et al., 1994). The spectral reflectance of *Aechmea bractea*, one of the preferred mating places of *C. salei*, ranges from 300 to 500 nm, with a greater peak from 400 to 500 nm (measured in Vienna, October 2010 at midday). de Omena and Romero suggested that the colour of bromeliads could play a role in microhabitat selection for jumping spiders (de Omena and Romero, 2010).

The green and blue receptors show a second peak in the UV-range in the electrophysiological recordings (Walla et al., 1996), which is likely to be the result of β-band peaks of visual pigments (Dyer, 1998; Dyer, 1999). The UV receptor in the PL eyes has a second peak at the λ_{max} of the blue receptor too. This could be an indication of the existence of a sensitizing pigment, like in fly photoreceptors (Minke and Kirschfeld, 1979; Stavenga, 2004). In this case, the UV receptor transfers the energy to the blue receptors to enlarge its sensitivity. Blue receptors are usually of great importance for nocturnal animals. Barth showed a tenfold increase of the sensitivity of the blue receptors in the PM eyes at night (Barth, 2001).

The reason why the spiders could not see the target at very short wavelenghts could be the different function of the principal and secondary eyes. If the AM eyes really do lack UV receptors, as indicated by Walla and colleagues (Walla et al., 1996), the perception of UV light could be used only for detecting movable objects using the PM eyes. Alternatively, the number of UV receptors may simply be too small to be sufficient. The number of UV receptors in the electrophysiology recordings was very small. From 57 intracellular recordings, only three UV receptors could be found. No recordings of UV receptors could be gained from the AM eyes. One reason for this may be that the AM eyes possesss eye muscles to move the retina, a circumstance that makes the work of an electrophysiologist considerably harder. But they could still be useful to discriminate between different shades of grey.

The RT-PCR experiments showed that all three visual opsins were present in all eyes, therefore fulfilling the molecular prerequisite for the detection of light in the UV part of the spectrum up to longer wavelengths. However, the fact that, according to quantity of expression, the Rh2 gene is by far the most abundant and that it groups with the middle to long wavelength sensitive opsin might indicate that the UV spectrum is of less importance to the spider.

The UV perception of *C. salei* has been discussed earlier (Barth, 2001). We know that jumping spiders use UV-reflecting marks on their body for intraspecific communication (Lim and Li, 2006; Lim et al., 2008), but in *C. salei* both sexes lack such UV cues. It is possible that the UV receptors are positioned at the bottom of the retina and point upwards as described for several species of lycosid spiders (Kovoor et al., 1993; Dacke et al., 2001). In this case, they could be used for orientation at night, as moonlight reaches the UV range. The black bar presented in our experiments would be outside of the sensitivity range of the UV receptors. But this explanation seems to be unlikely, as not even the desert-living wandering spider *Leucorchestris arenicola* uses the moon or polarized light for orientation (Nørgaard et al., 2008).

In summary, we found that the behaviour of *C. salei* is guided by visual input from only a fraction of the spectrum indicated by ERG experiments. Particularly surprising was its inability to utilize short wavelengths. Although *C. salei* possess UV receptors, their function remains unclear.

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AUTHOR CONTRIBUTIONS

L.M.Z. contributed to writing of the manuscript and carried out behavioural experiments and analysis of data. A.S. planned the behavioural experiments and contributed to the planning of the molecular experiments and writing of the manuscript. D.F. assembled the transcriptomes and participated in writing the manuscript. B.J.E. contributed to the planning of molecular experiments and writing of the manuscript, and carried out molecular experiments and phylogenetic analysis.

COMPETING INTERESTS

No competing interests declared.

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