# Depth Perception from Image Defocus in a Jumping Spider

**Article** *in* Science · January 2012

DOI: 10.1126/science.1211667 · Source: PubMed



**10 authors**, including:

Takashi Nagata
The University of Tokyo
**51** PUBLICATIONS **582** CITATIONS
SEE PROFILE

Mitsumasa Koyanagi
Osaka City University
**111** PUBLICATIONS **2,139** CITATIONS
SEE PROFILE

Hisao Tsukamoto
Kobe University
**60** PUBLICATIONS **1,287** CITATIONS
SEE PROFILE

Shinjiro Saeki
Kobe University
**11** PUBLICATIONS **225** CITATIONS
SEE PROFILE

# Depth Perception from Image Defocus in a Jumping Spider

Takashi Nagata, *et al.*

*Science* **335**, 469 (2012);
DOI: 10.1126/science.1211667

**Table 1.** Nitrogen enrichment of field plots decreased the palatability of *S. grandis* (the preferred host plant), and heavy grazing increased palatability in paired-choice tests using either dried/ground (8-hour assay) or fresh leaves (single-meal assay, average percentage of leaf area consumed).

| Treatment (*S. grandis*) | Number of wins | Amount consumed | Chi- squared *P* |
|---|---|---|---|
| | | *Ground leaf* | |
| Unfertilized | 18 | 13.8 ± 2* | <0.01 |
| Fertilized | 7 | 8.6 ± 2* | |
| Heavily grazed | 9 | 4.1 ± 1* | 0.01 |
| Ungrazed | 3 | 2.9 ± 1* | |
| | | *Fresh leaf* | |
| Heavily grazed | 8 | 28 ± 7† | 0.03 |
| Ungrazed | 3 | 15 ± 5† | |

**Table 2.** Nitrogen enrichment of field plots increased the N content (percentage of dry mass) and protein content (percentage of dry mass) of *S. grandis* and *L. chinensis*. All comparisons were analyzed using Student's *t* tests after arcsine transformation of proportional data.

| Nutrient | Unfertilized | N-fertilized | *P* | N | Heavily grazed | Ungrazed | *P* | N |
|---|---|---|---|---|---|---|---|---|
| | | | *S. grandis* | | | | | |
| % C | 46 ± 0.8 | 46 ± 0.8 | 0.77 | 24 | 47 ± 0.2 | 44 ± 2 | 0.12 | 9 |
| % N | 1.4 ± 0.05 | 2.4 ± 0.06 | <0.001 | 24 | 1.7 ± 0.05 | 2.1 ± 0.04 | <0.001 | 9 |
| % protein | 4.3 ± 0.5 | 11.1 ± 1.8 | <0.01 | 24 | | | | |
| Protein/N ratio | 3.1 ± 0.4 | 4.6 ± 0.7 | 0.10 | 24 | | | | |
| | | | *L. chinensis* | | | | | |
| % C | 46 ± 1 | 46 ± 0.8 | 0.99 | 24 | 46 ± 0.3 | 46 ± 0.3 | 0.18 | 8 |
| % N | 1.8 ± 0.08 | 2.9 ± 0.1 | <0.001 | 24 | 2.4 ± 0.09 | 2.7 ± 0.03 | 0.12 | 8 |
| % protein | 8.7 ± 1 | 11.9 ± 1 | 0.03 | 23 | | | | |
| Protein/N ratio | 4.9 ± 0.5 | 4.2 ± 0.4 | 0.37 | 23 | | | | |

excess is playing a role. Furthermore, these findings reinforce the realization that differential responses of herbivore species to plant nutrient content can structure herbivore communities (*27*), providing new insights that may improve livestock and fertilization management strategies to limit the occurrence of economically damaging locust outbreaks.

### References and Notes


1. W. J. Mattson Jr., *Annu. Rev. Ecol. Syst.* **11**, 119 (1980).
2. T. White, *The Inadequate Environment: Nitrogen and the Abundance of Animals* (Springer-Verlag Berlin, 1993).
3. J. J. Elser *et al.*, *Ecol. Lett.* **10**, 1135 (2007).
4. D. Raubenheimer, S. J. Simpson, *Anim. Behav.* **45**, 953 (1993).
5. K. P. Lee *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 2498 (2008).
6. S. J. Simpson, D. Raubenheimer, *Aging* **1**, 875 (2009).
7. E. A. Bernays, in *Nitrogen as an Ecological Factor*, J. A. Lee, S. McNeill, I. H. Ronson, Eds. (Blackwell, Oxford, 1983), pp. 321–344.
8. F. J. Clissold, G. D. Sanson, J. Read, *J. Anim. Ecol.* **75**, 1000 (2006).
9. J. Galloway *et al.*, *Biogeochemistry* **70**, 153 (2004).
10. L. Wu, N. He, Y. Wang, X. Han, *J. Environ. Qual.* **37**, 663 (2008).
11. H. Song, *Psyche* **2011**, 1 (2011).
12. A. J. Cease, S. Hao, L. Kang, J. J. Elser, J. F. Harrison, *J. Insect Physiol.* **56**, 926 (2010).
13. L. Kang, X. G. Han, Z. B. Zhang, O. J. Sun, *Philos. Trans. R. Soc. London Ser. B* **362**, 997 (2007).
14. Materials and methods are available as supporting material on *Science* Online.
15. IFA/IFDC/FAO, *Fertilizer Use by Crop*. (Food and Agriculture Organization of the United Nations, Rome, ed. 5, 2006).
16. D. Raubenheimer, S. Simpson, *Entomol. Exp. Appl.* **91**, 67 (1999).
17. D. Raubenheimer, S. Jones, *Anim. Behav.* **71**, 1253 (2006).
18. D. F. B. Flynn, thesis, Columbia University, New York, (2011).
19. F. J. Clissold, G. D. Sanson, J. Read, S. J. Simpson, *Ecology* **90**, 3393 (2009).
20. D. Raubenheimer, S. J. Simpson, *J. Exp. Biol.* **206**, 1669 (2003).
21. S. T. Behmer, *Annu. Rev. Entomol.* **54**, 165 (2009).
22. Z. Chen, S. Wang, *Typical Steppe Ecosystems of China* (Science Press, Beijing, 2000).
23. D. H. Branson, A. Joern, G. A. Sword, *Bioscience* **56**, 743 (2006).
24. L. Kang, Y. L. Chen, *Insect Sci.* **2**, 265 (1995).
25. A. Joern, S. T. Behmer, *Oecologia* **112**, 201 (1997).
26. D. Berner, W. U. Blanckenhorn, C. Korner, *Oikos* **111**, 525 (2005).
27. S. T. Behmer, A. Joern, *Proc. Natl. Acad. Sci. U.S.A.* **105**, 1977 (2008).
28. S. Simpson, D. Raubenheimer, *Philos. Trans. R. Soc. London Ser. B* **342**, 381 (1993).
29. C. Tong, J. Wu, S. Yong, J. Yang, W. Yong, *J. Arid Environ.* **59**, 133 (2004).
30. J. Wu, C. Overton, *Bull. Ecol. Soc. Am.* **83**, 189 (2002).
31. J. Han *et al.*, *Rangeland J.* **30**, 233 (2008).



**Acknowledgments:** The authors thank F. Jin, D. Niren, D. Flynn, Y. Kong, Z. Fan, J. Esman, Q. Chen, and G. Zhang for field and laboratory assistance; M. Quinlan, D. Denardo, J. VandenBrooks, C. Klok, S. Behmer, and J. Sabo for helpful discussion of experimental design; J. Wu for funding and scientific support; and M. McCrackin, F. Clissold, and three anonymous reviewers for valuable comments on the manuscript. This work was supported by the National Science Foundation (EAPSI, DDEP to A.J.C., DEB-0925017 to J.J.E., and EAR-0746352 to J.F.H.), Sigma Xi, Achievement Rewards for College Scientists (Marley-Webb and Johnston Foundations), P.E.O. Scholar Award to A.J.C., the Chinese Research Grants of Public Welfare Fund for Agriculture (Project 200903021), and the Foundation of Chinese Academy of Sciences (Project Kscx2-yw-z-1021). A.J.C. designed and performed experiments, analyzed data, and wrote the paper. J.J.E. and J.F.H. designed experiments and wrote the paper. C.F.F. and S.H. designed and performed experiments. L.K. gave scientific support and guidance. Data used in the analyses are available in the Supporting Online Material.


**Supporting Online Material**

www.sciencemag.org/cgi/content/full/335/6067/467/DC1
Materials and Methods
Fig. S1
Table S1
References (*32*–*36*)

26 September 2011; accepted 15 November 2011
10.1126/science.1214433

# Depth Perception from Image Defocus in a Jumping Spider

**Takashi Nagata,[1]* Mitsumasa Koyanagi,[1]† Hisao Tsukamoto,[1] Shinjiro Saeki,[2] Kunio Isono,[2] Yoshinori Shichida,[3] Fumio Tokunaga,[4] Michiyo Kinoshita,[5] Kentaro Arikawa,[5] Akihisa Terakita[1]†**

The principal eyes of jumping spiders have a unique retina with four tiered photoreceptor layers, on each of which light of different wavelengths is focused by a lens with appreciable chromatic aberration. We found that all photoreceptors in both the deepest and second-deepest layers contain a green-sensitive visual pigment, although green light is only focused on the deepest layer. This mismatch indicates that the second-deepest layer always receives defocused images, which contain depth information of the scene in optical theory. Behavioral experiments revealed that depth perception in the spider was affected by the wavelength of the illuminating light, which affects the amount of defocus in the images resulting from chromatic aberration. Therefore, we propose a depth perception mechanism based on how much the retinal image is defocused.

Visual systems that accurately and reliably judge distance or depth are valuable. A wide variety of animals, including humans, perform this task with binocular stereoscopic depth perception (*1*). Two types of monocular depth cues also provide absolute depth perception in some animals: accommodation (i.e., focal adjustment) in chameleons and other vertebrates (*2*, *3*)

and motion parallax (i.e., image motion on the retina, the amount of which depends on the distance to an object) in some insects (*4*). The insects obtain motion parallax information by typical side-to-side translational movements of the head. Theoretically, however, the amount of image defocus (i.e., how much an image defocused) can be used as an absolute depth cue by comparing a defocused image with one or more additional images in which the same object is sharply focused or differently defocused (*5*). Humans use image defocus for a rough estimation of the relative depth positions of objects (*6*), but until now no animals have been known to use image defocus as an absolute depth cue. We show here that jumping spiders (*Hasarius adansoni*) perceive absolute depth by using image defocus.

Jumping spiders approach their prey and jump accurately by using two pairs of forward-facing eyes, the principal eyes (PEs) and the anterior lateral eyes (ALEs) (*7*, *8*) (Fig. 1A). If both ALEs are occluded, spiders can make accurate jumps, demonstrating that PEs provide absolute depth perception (*7*). Interestingly, however, PEs have neither overlapping fields of view nor a focal adjustment mechanism (*9*). Furthermore, no kind of motion that could generate motion parallax during the hunting behavior has been reported. To check whether jumping spiders use motion parallax cues, we investigated hunting behavior by using the apparatus shown in fig. S1 and compared the distance of jumps to the actual distance from the spider to a target fly. Spiders whose bilateral ALEs and a PE were occluded, with a single PE left untouched, made accurate jumps and caught the fly without any motion that could generate motion parallax (movie S1 and Fig. 1B). This indicates that the spiders accurately measured the distance without the use of any of the three kinds of cues known in animals.

A clue to the depth perception mechanism is found in the unique structure of the PE retina, which has four layers consisting of rhabdomeres, the photoreceptive portions of photoreceptor cells (*10*, *11*) (Fig. 1C). In the retina, the position of an image focused by the lens is determined by the distance to the object and the wavelength of light because of the chromatic aberration of the lens. Blest *et al*. electrophysiologically found some green-sensitive photoreceptor cells in the second-deepest layer, L2, but green light is not focused on L2 but rather on the deepest layer, L1, in jumping spiders of genus *Plexippus* (*12*). Therefore, these authors suggested that the green-sensitive photoreceptor cells in L2 receive defocused images. This appears to be true for the species used in this study, *H. adansoni*, because the chromatic aberration of PE lens of *H. adansoni* is similar to that of *Plexippus* (*12*) (fig. S2). We hypothesized that jumping spiders perceive depth on the basis of the amount of defocus in images received by L2 because, in principle, the distance to objects can be uniquely determined from the amount of defocus in L2 (Fig. 1D).

We then investigated the visual pigments in the PE retina. A basic premise of our hypothesis is that green-sensitive photoreceptors are widely and densely distributed in L2, but the spectral sensitivity of most of the photoreceptors in L2 remains unknown. We found two visual pigments, Rh1 and Rh3, in the PE (Fig. 2A) among four visual pigments, Rh1 to 4 (fig. S3). Rh1 is a green-sensitive pigment (Fig. 2B) and localized in all rhabdomeres of L2 and L1, whereas Rh3 is an ultraviolet (UV)-sensitive pigment (fig. S4) and localized only in L3 and L4 (Fig. 2C and fig. S5), demonstrating that the photoreceptors in L2 and L1 are all green-sensitive whereas those in L3 and L4 are all UV-sensitive. This is consistent with the electroretinographically determined sensitivity spectrum of PEs (fig. S6) as well as the reported intracellular recordings (*12*–*14*) and supports our hypothesis.

Rh2, a blue-sensitive pigment (fig. S7), was never detected in PEs (fig. S8). This strongly suggests that the green-sensitive Rh1 is more suitable for the function of L2, although Rh2 seems more appropriate to receive focused images because blue light should be focused in L2 (*12*). This supports the idea that the defocus of images received by L2 is physiologically important.

To test our hypothesis, we investigated jumps under monochromatic green (≈520 nm) and red (≈630 nm) light (fig. S9), to which only L2 and

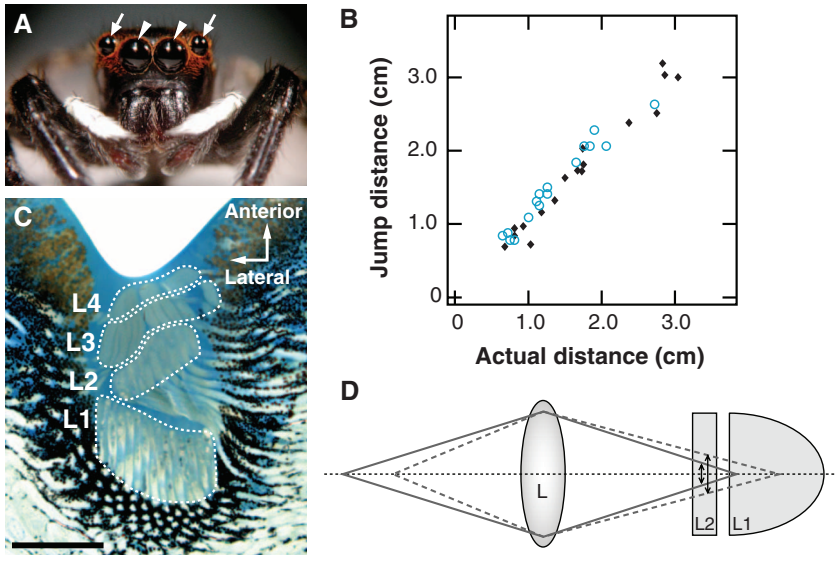


**Fig. 1.** Depth perception of jumping spiders with the principal eyes and its hypothetical mechanism. (**A**) Anterior view of the jumping spider, *H. adansoni*. PEs (arrowheads) and ALEs (arrows) are indicated. (**B**) Jump distance versus the actual distance of intact jumping spiders (black diamonds; $n = 4$) and spiders with one PE and both ALEs occluded (blue open circles; $n = 3$). (**C**) Horizontal section of PE retina stained with toluidine blue. The photoreceptor layers are traced. Incoming light comes from above. Scale bar, 50 μm. (**D**) Schematic drawing of the paths of green light passing through the lens (L) and received by L1 and L2 (solid and broken lines). The amount of defocus on L2 (arrows) depends on the distance between the lens and the object.

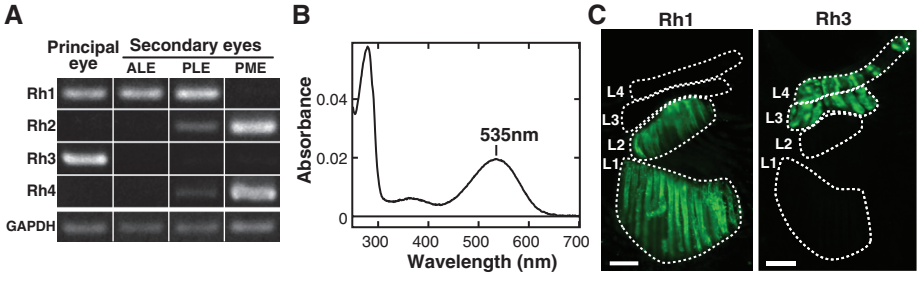


**Fig. 2.** Distribution and absorption spectrum of visual pigments expressed in the principal eye. (**A**) Reverse-transcription polymerase chain reaction analyses of visual pigment gene expression in PE, ALE, posterior lateral eye (PLE), and posterior median eye (PME). GAPDH (glyceraldehyde-3-phosphate dehydrogenase) serves as an internal standard. (**B**) Absorption spectrum of purified Rh1 with 11-*cis*-retinal (fig. S12). (**C**) Immunofluorescence labeling of Rh1 and Rh3 in PE retina. Scale bars, 10 μm.

[1]Department of Biology and Geosciences, Graduate School of Science, Osaka City University, Osaka 558-8585, Japan. [2]Graduate School of Information Sciences, Tohoku University, Sendai 980-8579, Japan. [3]Department of Biophysics, Graduate School of Science, Kyoto University, Kyoto 606-8502, Japan. [4]Department of Earth and Space Science, Graduate School of Science, Osaka University, Toyonaka 560-0043, Japan. [5]Laboratory of Neuroethology, The Graduate University for Advanced Studies (Sokendai), Hayama 240-0193, Japan.

*Present address: Laboratory of Neuroethology, The Graduate University for Advanced Studies (Sokendai), Hayama 240-0193, Japan.

†To whom correspondence should be addressed. E-mail: koyanagi@sci.osaka-cu.ac.jp (Mitsumasa K.); terakita@sci.osaka-cu.ac.jp (A.T.)

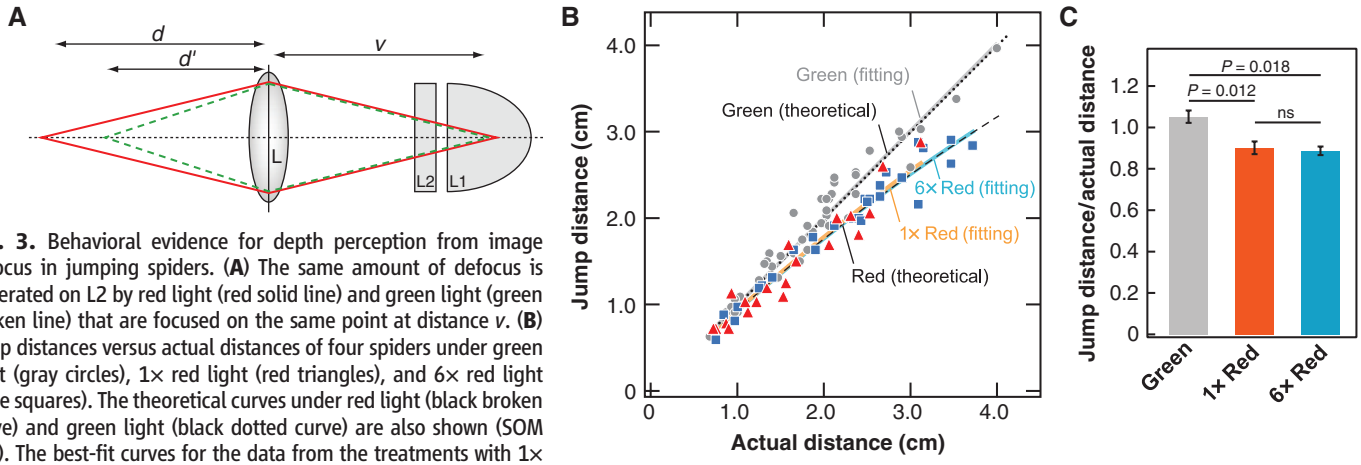


**Fig. 3.** Behavioral evidence for depth perception from image defocus in jumping spiders. (**A**) The same amount of defocus is generated on L2 by red light (red solid line) and green light (green broken line) that are focused on the same point at distance *v*. (**B**) Jump distances versus actual distances of four spiders under green light (gray circles), 1× red light (red triangles), and 6× red light (blue squares). The theoretical curves under red light (black broken curve) and green light (black dotted curve) are also shown (SOM text). The best-fit curves for the data from the treatments with 1× red light (orange curve), 6× red light (blue curve), and green light (gray curve) were obtained by using Eq. 1. (**C**) Ratios of the jump distance to the actual distance. Data are presented as the mean ± SEM ($n$ = 4). ns, not significant. Statistical analysis was performed by ANOVA.

L1 are sensitive. The focal length of red light is greater than that of green light (fig. S2), and the defocus amount under red light is equal to that generated by a closer object under green light (Fig. 3A). Accordingly, if jumping spiders estimate distance by using the amount of defocus, they are expected to underestimate the distance and make shorter jumps under red light because they would basically judge the distance by basing distance-defocus relationship in green light, which Rh1 absorbs most effectively under natural light conditions (fig. S10). We occluded bilateral ALEs of spiders and measured the jump distances under green light and under two intensities (1× and 6×) of red light and compared them with the actual distances. The spiders jumped accurately onto the targets under green light, whereas they exhibited shorter jumps under red light ($n$ = 4) (Fig. 3B). In fact, the spiders sometimes failed to capture targets in a single jump under red light because their jumps were too short (movie S2). The mean ratio of the jump distance to the actual distance under 1× red light (≈0.90, $n$ = 4) was significantly lower than the ratio under green light (≈1.0, $n$ = 4) [$P$ = 0.012, analysis of variance (ANOVA) with Bonferroni correction] (Fig. 3C), showing that jump distances were shorter than actual distances under red light.

In the above experiment, the intensities of the green and 1× red lights were adjusted by using purified Rh1 pigment so that the two types of light activated Rh1 with the same efficiency (fig. S11); that is, the subjective brightness of the two lights for the spider appeared to be identical. Additionally, the ratio of the jump distance to the actual distance under a sixfold brighter red light (6× red light) was ≈0.89 ($n$ = 4), which was similar to the ratio under the 1× red light and also significantly lower than the ratio under the green light ($P$ = 0.018, ANOVA with Bonferroni correction) (Fig. 3C). Therefore, the shorter jump distances observed under red light can be attributed to the wavelength rather than the intensity.

To evaluate these results, we compared jump distances with theoretically predicted distances based on our hypothesis. Figure 3A shows paths of red light from a point at distance $d$ and green light from another point at distance $d'$, both causing the same amount of defocus. If the hypothesis is correct, $d'$ corresponds to the distance estimated by the spiders and therefore would correspond to the jump distance. From the lens equation,

$$d' = \frac{1}{f}\left(1 - \frac{1}{1 + fd}\right), \quad f = \frac{1}{F_g} - \frac{1}{F_r}, \quad (1)$$

where $F_r$ and $F_g$ are focal lengths of the lens under red and green light, respectively [supporting online material (SOM) text]. We determined the focal lengths of the lens (table S1) and obtained the theoretical curves of $d'$ (black broken and dotted curves in Fig. 3B). These theoretical curves correspond well with the experimental data on jump distances, and this result is supported by the agreement of these curves with fitting curves of the experimental data (solid curves in Fig. 3B, see SOM text). These results show that the model based on the amount of defocus (Figs. 1D and 3A) could account for the shorter jump distances under the red light, which strongly supports the hypothesis that depth perception in jumping spiders has its basis in the amount of defocus in images received by L2.

Blest *et al.* (*12*) reported that the staircase-like organization of the distal ends of L1 (Fig. 1C) enables a wide focus range because different parts of L1 receive focused images from objects at different distances. Because jumping spiders jumped accurately under green light to which only L1 and L2 are sensitive, depth perception might be achieved by comparison of defocused images received by L2 with focused images received by L1, although at present there is no evidence for an underlying neuronal mechanism. In addition, the staircase-like organization of L1 suggests that during lateral scanning (*9*) the location on L1 of the best-focused image could provide distance information, although Blest *et al.* (*12*) considered this unlikely. Similarly, the changing separation of L1 and L2 across the retina might provide a changing defocus signal that could be used in a similar way. Whether and how such mechanisms are used in depth perception remains an open question.

PEs of jumping spiders may be a real-life example of "depth from defocus," a notable depth measurement technique that is being developed for computer vision. Further investigation of the optics, retinal structure, and neural basis of depth perception in jumping spiders may provide biological inspiration for computer vision as well.

### References and Notes


1. J. M. Harris, *Philos. Trans. R. Soc. London Ser. A* **362**, 2721 (2004).
2. L. Harkness, *Nature* **267**, 346 (1977).
3. H. Wagner, F. Schaeffel, *J. Comp. Physiol. A* **169**, 515 (1991).
4. K. Kral, *Behav. Processes* **64**, 1 (2003).
5. S. Chaudhuri, A. N. Rajagopalan, *Depth from Defocus: A Real Aperture Imaging Approach* (Springer-Verlag, New York, 1999).
6. A. P. Pentland, *IEEE Trans. Pattern Anal. Mach. Intell.* **9**, 523 (1987).
7. L. M. Forster, *N. Z. J. Zool.* **6**, 79 (1979).
8. D. B. Zurek, A. J. Taylor, C. S. Evans, X. J. Nelson, *J. Exp. Biol.* **213**, 2372 (2010).
9. M. F. Land, *J. Exp. Biol.* **51**, 471 (1969).
10. M. F. Land, *J. Exp. Biol.* **51**, 443 (1969).
11. R. M. Eakin, J. L. Brandenburger, *J. Ultrastruct. Res.* **37**, 618 (1971).
12. A. D. Blest, R. C. Hardie, P. McIntyre, D. S. Williams, *J. Comp. Physiol. A* **145**, 227 (1981).
13. R. D. DeVoe, *J. Gen. Physiol.* **66**, 193 (1975).
14. S. Yamashita, H. Tateda, *J. Comp. Physiol. A* **105**, 29 (1976).



**Acknowledgments:** We thank R. S. Molday for supplying the rho 1D4–producing hybridoma, T. Suzuki for supplying the antibody against $G\alpha_q$, R. J. Lucas for his comments on the manuscript and T. Matsuyama for building the light-emitting diode (LED) lighting equipment. This work was supported by Grants-in-Aid for Scientific Research (K.A., Mitsumasa K., Y.S., and A.T.) and Grant-in-Aid for Japan Society for the Promotion of Science Fellows (T.N.). Sequences are available from the DNA Data Bank of Japan (AB506462 and AB506463).


### Supporting Online Material

www.sciencemag.org/cgi/content/full/335/6067/469/DC1
Materials and Methods
SOM Text
Figs. S1 to S12
Table S1
References (*15–23*)
Movies S1 and S2


25 July 2011; accepted 7 December 2011
10.1126/science.1211667