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# Optics and information processes of horsefly polarization vision that underlie visual searching

**Doekele Stavenga**
**RIJKSUNIVERSITEIT GRONINGEN**
**BROERSTRAAT 5**
**GRONINGEN, 9712 CP**
**NL**

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The collaborative efforts have greatly expanded our knowledge and understanding of polarization vision, specifically concerning the architecture of the compound eye of horseflies. The photoreceptor anatomy and spectral characteristics of the Ljubljana work-horse fly Tabanus bromius are now unravelled into exquisite detail. The study of the higher order processing in the neural network will be the challenge of the coming years. And how this results in the polarization-dependent behavior will be the next level. Present hypotheses concerning the involvement of the central photoreceptors in specific eye areas can now be well tested. Two further themes of high interest are understanding when polarization provides an information benefit for task specific behaviours and whether or not polarization vision in different arthropods follows the same rules. This last topic will be intensely pursued in the new grant, provided to the same team joined by the Wernet-group in Berlin.

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Final Performance report of AFOSR/EOARD grant

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**Final Performance Report**

**15 December 2014 - 14 December 2018)**

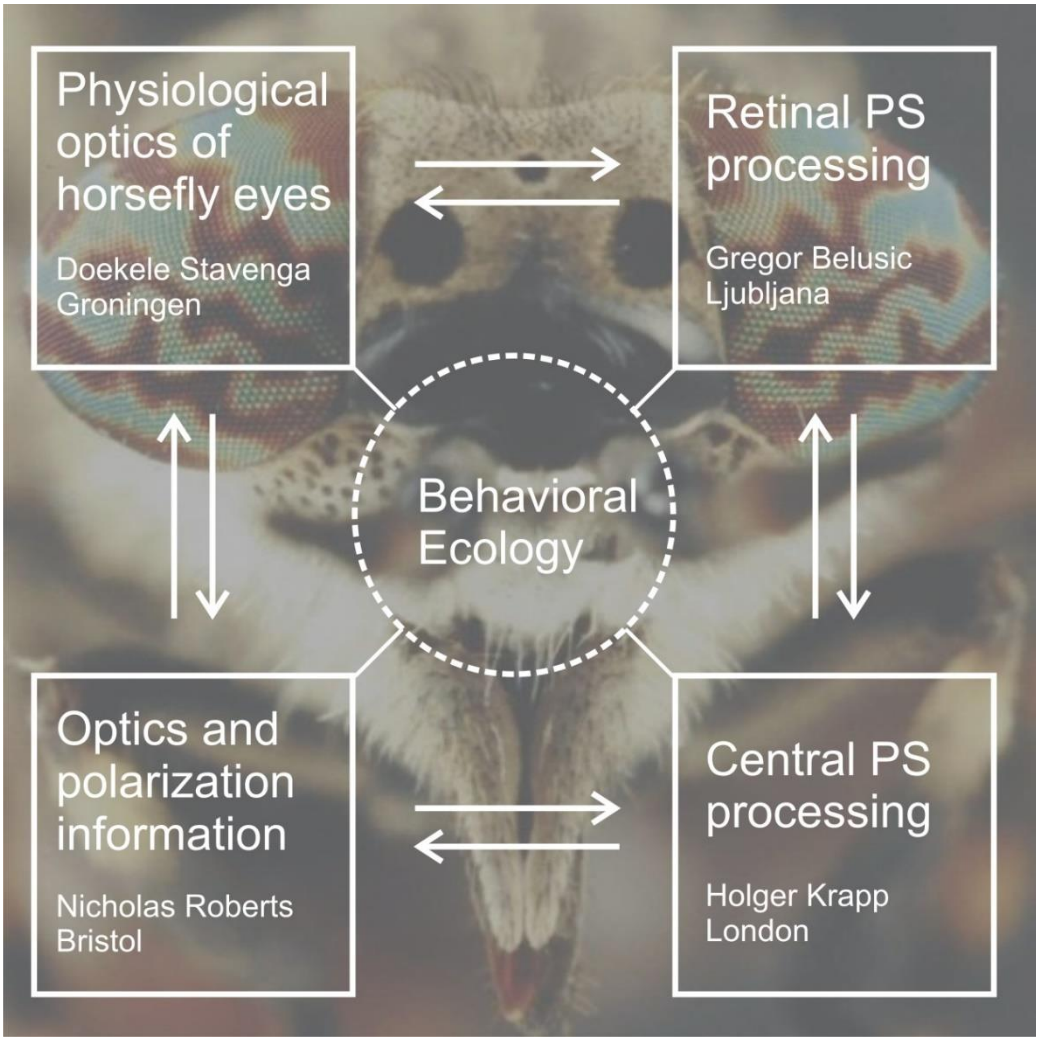
*Participants*:

Dr Gregor Belušič, Biotechnical Faculty, University of Ljubljana, Slovenia

Dr Holger G. Krapp, Dept Bioengineering, Imperial College, London, UK

Dr Nicholas W. Roberts, School of Biological Sciences, University of Bristol, UK

Dr Doekele G. Stavenga, Computational Physics, Groningen University, the Netherlands (coordinator)



*Historical background and scientific questions*

The central theme of the grant project has been polarization vision. Generally, vision is a crucial sensory modality of most animals. Research of the last century has yielded a profound insight into motion vision, colour vision and pattern recognition. However, polarization vision, possessed by many arthropods, has been studied much less extensively, presumably due to human bias, as polarization vision is absent, or at least poor, in vertebrates.

Behavioral and electrophysiological work in ants, crickets, butterflies and locusts suggested that these animals use celestial cues for navigation. Polarization detection capabilities located in the so-called dorsal rim area of the compound eyes of insects have been documented in several insect species, and butterflies have been shown to possess well-developed polarization vision in non-dorsal eye areas, presumably for egg deposition on leaves and interspecific recognition. Polarization vision is also well-developed in marine arthropods, including stomatopods and decapods. These animals use the polarization of light for numerous tasks such as intraspecific signalling and visual contrast enhancement.

Amongst flying insects, horseflies present a special case. Female horseflies are severe pests, because they prey on horses and cattle by biting and sucking blood, thus obtaining the essential food supply for producing eggs. As sunlight is reflected from the coats of the animals at oblique directions it becomes polarized and this has been proposed to act as a visual cue for the flies. In the grant project, we have chosen to investigate horsefly polarization vision on multiple levels of the visual system, from the first level of compound eye optics, to its anatomy, the spectral and polarization properties of the photoreceptors, polarization sensitive neurons, and the behavior towards various polarized light stimuli. Our efforts concern the following aims, themes, and collaborative initiatives.

**General aims of the program**

1. What are the stimulus parameters related to polarized light that horseflies exploit for target (cattle, water) detection and approach?
2. What are the structural adaptations in the compound eyes enabling behavior based on polarization vision?
3. What are the neuronal adaptations supporting the integration of signals induced by polarized light?
4. At which neural stage are signals mediated by the polarization vision and motion vision pathways integrated to enable coherent guidance and control signals?

*Specific themes within the main objectives were:*

- Ecology of vision: exploitation of polarization vision for target detection.
- The enigmatic interference reflectors of the corneal facet lenses.
- The spectral and polarization sensitivities of the retinal photoreceptors.
- Structural adaptations in the compound-eye visual system mediating polarization vision.
- The coding of visual information by the higher neural ganglia, specifically concerning motion and polarization detection.
- Behavioral integration of outer-loop (navigation/guidance) polarized light information with inner-loop (control) motion vision information.
- Neuronal integration of outer-loop (navigation and guidance) polarized light signals with inner loop-(control) motion vision signals.

*Overview of activities*

Each of the participating teams performed experiments in its laboratories as well as in the field when appropriate. In addition to frequent contact via email, phone and skype, we had yearly review meetings, where we visited the labs to get intimate knowledge of the ongoing research, and we discussed our scientific progress, with each of the participating groups presenting their work in detailed lectures. Our key person, Ric Wehling (Eglin AFB), always added his guiding views in a presentation. Next to the scientific sessions, we had a field day where we continued discussions and exchanged emerging ideas.

We convened in London (December 2015), Ljubljana (June 2016), Groningen (May 2017), Bristol (May 2018). The meetings were also well attended by the program officers of the EOARD (i.e. Greg Abate, Lee Poepelmann, Jason Foley, Nandini Iyer). Several members of the AFOSR Eglin AFB also intensely participated (e.g. Nick Rummelt, Jennifer Talley, John Douglass).

In June 2017, Ric Wehling and John Douglass, stayed in the Ljubljana lab, collaborating in experiments, followed in August 2017 by four researchers from the Bristol and London labs. The Bristol group performed behavioral experiments, and together with the London duo, lobula plate tangential cells were recorded.

The scientific achievements have been reported in quarterly reports (QRs; 14 in total) and in yearly reports. The highlights are summarized below (for details, see the QRs).

### ***Technical developments enabling novel research***

During the past research period, we developed a number of new, mainly optical systems and methods.

- Imaging polarimetry systems, for visualizing and analyzing polarization signals, were developed in Ljubljana and Bristol (QR9, QR10).
- The LED 'organ', a spectral device enabling extremely rapid measurements of the spectral sensitivity as well as polarization sensitivity of photoreceptors was conceived, built and perfected in Ljubljana. This device, consisting of an array of leds focused via a grating at an optical fiber, thus delivers a set of narrow-band stimuli. It is becoming a 'must-have' for many labs working on visual sensory systems (QR6).
- A simple automated and portable method for calibrating polarization monitors was developed in Bristol (QR8).
- High speed DLP-systems suitable for polarization pattern stimuli were developed and applied in the London, Bristol and Ljubljana labs, where the London system enables the electrophysiological characterization of neurons for both intensity- and polarization-contrast sensitivities across the entire compound eye (QR4, QR6, QR8, QR11, QR14).
- A versatile goniometric apparatus combined with a so-called telemicroscopic imaging system in the Groningen lab has recently reached the state of perfection for rapid mapping of the spatial distribution of the ommatidial axes of insect eyes (QR14).

### ***Scientific results and achievements***

<u>The colorful cornea of horsefly eyes</u>

The long-standing enigma of the colored facetlenses of horseflies has, to our annoyment, not yet been fully resolved. The optical basis of the phenomenon is the same as in dolichopodids, which have eyes with brightly reflecting, colorful facets. In the latter case, we could demonstrate (and report in a scientific paper) that the facets act as optical filters, although with moderate effect. Studies on horsefly eye facets showed that the facet coloration also is due to optical multilayer effects, but the spectral filtering function is so minor that the importance for polarization vision seems unlikely. The prominent facet coloration, which is very characteristic for the different horsefly species, clearly needs further study.

<u>The horsefly retina</u>

The study of the anatomy of the compound eyes of the horsefly *Tabanus bromius* offered many surprises. Compared to other dipteran species, the compound eyes are full of air. Presumably the function is twofold, namely supplying ample oxygen serving the high energy demand of the photoreceptors and creating a large, lightweight eye that has high spatial resolution.

The organization of the microvilli in the rhabdomeres appeared to crucially differ between the various types of photoreceptor cells. This important finding allowed the interpretation of the measured polarization characteristics of the photoreceptors. The processing of spectral and polarization signals by the central photoreceptors R7 and R8 is now understood. The anatomy of the male and female horseflies is highly sex-specific (QR5, QR7, QR8, QR9, QR10, QR12, QR13; Ljubljana lab). The eye anatomy was also investigated by synchrotron X-ray microtomography (Bristol lab).

The role of the screening pigments for the photochemistry of the visual pigments of fly eyes was elucidated in a comparative analysis of dipteran rhodopsins (QR6, QR10, QR14; collaboration Groningen, Ljubljana.)

Recordings of neurons in the horsefly visual system

Lobula plate neurons in eyes subjected to polarized light stimuli, supplied by gratings and moving patterns, were recorded and characterized in a number of different fly species. The highly tasking studies, including electrophysiological recordings from neurons in tethered animals and behavioral experiments on gaze stabilization in animals with or without halteres, demonstrated the distinctly species-dependent properties of visuomotor control systems. Successful recordings of horsefly neurons can now be routinely made, which is an essential achievement for advancing our understanding of polarization signal processing (QR7, QR10, QR11, QR12; London and Ljubljana labs).

Behavioral experiments

Horseflies are attracted by polarized visual signals. This has been extensively investigated in field studies. Horseflies appear to become very excited by polarized blues (QR7, QR10; Ljubljana lab). Studies of flying flies performing a landing response to polarization or only looming stimuli demonstrated pronounced dependencies on intensity contrast. The role of polarization in gaze stabilization was tested in the horsefly *Haematopota fluvialis*, showing strong motion dependent responses.

The role of noise in polarization artefacts has been extensively studied, proving the incorrect assumption of black objects being intrinsically more polarized even though they may appear so to an observer. A new de-noising algorithm has also been developed for visualizing the correct polarization information in a visual scene (QR8, QR10, QR12; Bristol lab).

**Summary, outlook and perspectives**

Our collaborative efforts have greatly expanded our knowledge and understanding of polarization vision, specifically concerning the architecture of the compound eye of horseflies. The photoreceptor anatomy and spectral characteristics of the Ljubljana work-horse fly *Tabanus bromius* are now unravelled into exquisite detail. The study of the higher order processing in the neural network will be the challenge of the coming years. And how this results in the polarization-dependent behavior will be the next level. Present hypotheses concerning the involvement of the central photoreceptors in specific eye areas can now be well tested. Two further themes of high interest are understanding when polarization provides an information benefit for task specific behaviours and whether or not polarization vision in different arthropods follows the same rules. This last topic will be intensely pursued in the new grant, provided to the same team joined by the Wernet-group in Berlin.

**Publications (since 2015)**
**London group**

*Papers in peer-reviewed journals*

Yue X., Huang J.V., Krapp H.G., Drakakis E.M.: An implantable mixed-signal CMOS die for battery-powered in vivo blowfly neural recordings. Microelectronics Journal 74, 34-42, (2018).

Longden K.D. Wicklein M., Hardcastle B.J., Huston S.J. and Krapp H.G.: Spike interval coding of translatory optic flow and depth from motion in the fly visual system. Current Biology 27(21), 3225-3236.e3 (2017).

Swart P., Wicklein M., Sykes D., Ahmed F., and Krapp H.G.: A quantitative comparison of micro-CT presentations in Dipteran flies. Scientific Reports 6: 39380, doi: 10.1038/srep39380 (2016).

Hardcastle B.J. and Krapp H.G.: Evolution of gaze stabilization. Current Biology 26(20), R1010-1021 (2016).

Krapp H.G.: How a fly escapes the reflex trap. Nat Neuroscience 18:1192-1194 (2015)

Mokso R., Schwyn D.A., Walker S.M., Doube M., Wicklein M., Müller T., Stampanoni M.,

Taylor G.K., Krapp H.G.:  Four-dimensional in vivo X-ray microscopy with projection-guided gating. Scientific Reports 5, doi: 10.1038/srep08727, (2015).

*Peer-reviewed conference publications*
Huang J.V., Wei Y., and Krapp H.G.: Active collision free closed-loop control of a biohybrid fly-robot interface. In: Biomimetic and Biohybrid Systems, *Living Machines*, Springer, pp. 213-222 (2018).

Huang J.V. Krapp H.G.: Neuronal distance estimation by a fly-robotic interface. In: Biomimetic and Biohybrid Systems, *Living Machines*, Springer, pp. 204-215 (2017).

Huang J.V., Wang Y., and Krapp H.G.: Wall-following in a semi-closed-loop fly-robotic interface. In: Biomimetic and Biohybrid Systems, *Living Machines* 2016, Lecture Notes in Computer Science, vol 9793. Springer, pp. 85-96 (2016).

Huang J.V. and Krapp H.G.: Closed-loop control in an autonomous bio-hybrid robot system based on binocular neuronal input. In: Biomimetic and Biohybrid Systems, *Living Machines* 2015, Springer, ISBN: 978-3-319-22978-2 (Print) 978-3-319-22979-9 (Online), pp. 164-174 (2015).

*Book chapter*
Krapp H.G.: Optic flow processing. In: Encyclopedia of Computational Neuroscience. Jaeger D. and Jung R (eds.), Springer, Berlin, Heidelberg, DOI. 10.1007/978-1-4614-7320-6_332-1 (2015).

*Manuscripts submitted to peer-reviewed Journals*
Varennes, L. P., Krapp, H.G. and Viollet, S.: A novel setup for 3D chasing behavior analysis in free flying flies. Journal of Neuroscience Methods (under review).

Huang, J.V., Wei, Y. and Krapp H.G.: Biohybrid Fly-Robot Interface system performs active collision avoidance in corners. Journal of Bioinspirations and Biomimetics, Special issue on 'Active Perception and Bioinspired Sensing' (under review).

## Ljubljana group

*Papers in peer-reviewed journals*
Ilić M., Meglič A., Kreft M., Belušič G.: The fly sensitizing pigment enhances UV spectral sensitivity while preventing polarization-induced artifacts. Frontiers in Cellular Neuroscience, 12, 34 (2018).

Belušič G., Šporar K., Meglič A.: Extreme polarisation sensitivity in the retina of the corn borer moth *Ostrinia*. Journal of Experimental Biology 220, 2047-2056 (2017).

Belušič G., Ilić M., Meglič A., Pirih, P.: A fast multispectral light synthesiser based on LEDs and a diffraction grating. Scientific Reports 6, 32012 (2016).

*Conference abstracts*
Chen P-J., Belušič G., Matsushita A., Arikawa K.: Examination of the histamine hypothesis for a mechanism underlying photoreceptor spectral opponency in the *Papilio* butterfly. In: ICN 2018: conference abstracts, International Congress of Neuroethology, 15-20 July 2018, Brisbane., p. 20.

Belušič G., Meglič A., Ilić M.: Spectral tuning of polarization vision in the retina of female horseflies. In: Phototransduction, UK Workshop 2016, Firth Hall, 31st August - 2nd September 2016, p. 25.

Pirih P., Ilić M., Meglič A., Arikawa K., Belušič G.: A fast multispectral light synthesiser based on LEDs and a diffraction grating. In: Phototransduction, UK Workshop 2016, Firth Hall, 31st August - 2nd September 2016, pp. 53-54.

Belušič G., Ilić M., Horvat K., Pirih P.: LED-based tunable light source for visual electrophysiology. Documenta ophthalmologica, ISSN 0012-4486, 2015, vol. 130, suppl. 1, p. 31.

*Invited lecture at a conference*

Belušič G., Ilić M., Wehling M.F., Pirih P., Kreft M., Meglič A.: Horsefly polarotaxis is mediated by a segregated ommatidial subtype with spectrally imbalanced photoreceptors, leading to colour-induced polarization artifacts. In: ICN 2018: conference abstracts, International Congress of Neuroethology, 15-20 July 2018, Brisbane, p. 20. http://www.icn2018.com/downloads/ICN2018-Abstract-Book.pdf.

*Manuscripts submitted to peer-reviewed journals:*

Šporar K., Ketkar D.M., Gür B., Ramos-Traslosheros G., Seifert M., Santiago I.J., Ilić M., Belušič G., Pecot M.Y., Silies M.: A luminance sensitive pathway in *Drosophila* facilitates motion detection in low light conditions. Cell (under review)

**Groningen group**

*Papers in peer-reviewed journals*

Kooi CJ van der, Dyer AG, Stavenga DG (2015) Is floral iridescence a biologically relevant cue in plant-pollinator signaling? New Phytol 201:18-20

Stavenga DG, Leertouwer HL, Osorio DC, Wilts BD (2015) High refractive index of melanin in shiny occipital feathers of a bird of paradise. Light Sci Appl 4, e243

Balmakou A, Podalov M, Khakhomov S, Stavenga D, Semchenko I (2015) Ground-plane-less bidirectional terahertz absorber based on omega resonators. Optics Lett 40:2084-2087

Stavenga DG, Matsushita A, Arikawa K (2015) Combined pigmentary and structural effects tune wing scale coloration to color vision in the swallowtail butterfly *Papilio xuthus*. Zool Lett 1:14

Wilts BD, Matsushita A, Arikawa K, Stavenga DG (2015). Spectrally tuned structural and pigmentary coloration of birdwing butterfly wing scales. J Roy Soc Interface 111:20150717.

Kooi CJ van der, Pen I, Staal M, Stavenga DG, Elzenga JTM (2016) Competition for pollinators and intra-communal spectral dissimilarity of flowers. Plant Biol 18:56-62

Stavenga DG, van der Kooi CJ (2016) Coloration of the Chilean Bellflower, *Nolana paradoxa*, interpreted with a scattering and absorbing layer stack model. Planta 243: 171-181

Giraldo MA, Stavenga DG (2016) Brilliant iridescence of *Morpho* butterfly wing scales is due to both a thin film lower lamina and a multilayered upper lamina. J Comp Physiol A 202:381-388

Kooi CJ van der, Elzenga JTM, Staal M, Stavenga DG (2016) How to colour a flower: on the optical principles of flower coloration. Proc R Soc B 283:20160429.

Stavenga, DG, Otto JC, Wilts, BD (2016). Splendid coloration of the peacock spider *Maratus splendens*. J Roy Soc Interface 13:20160437.

Wilts, BD, Giraldo MA, Stavenga, DG (2016). Unique wing scale photonics of male Rajah Brooke's birdwing butterflies. Front Zool 13:36

Giraldo MA, Yoshioka S, Liu C, Stavenga DG (2016). Coloration mechanisms and phylogeny of *Morpho* butterflies. J Exp Biol 219:3936-3944

Wardill TJ, Fabian AT, Pettigrew AC, Stavenga DG, Nordström K, Gonzalez-Bellido PT (2017) A novel interception strategy in a miniature robber fly with extreme visual acuity. Current Biol 27:854-859

Wilts, BD, Wijnen B, Leertouwer HL, Steiner U, Stavenga, DG (2017) Extreme refractive index wing scale beads containing dense pterin pigments cause the bright colors of pierid butterflies. Adv Opt Mat 5: 1600879.

Kooi CJ van der, Elzenga JTM, Dijksterhuis J, Stavenga DG (2017) Functional optics of glossy buttercup flowers. J Roy Soc Interface 14:20160933.

Stavenga DG, Kooi CJ van der, Wilts, BD (2017) Structural coloured feathers of mallards act by simple multilayer photonics. J Roy Soc Interface 14:20170407.

Wilts, BD, Vey AJ, Briscoe AD, Stavenga DG (2017). Longwing (*Heliconius*) butterflies combine a restricted set of pigmentary and structural coloration mechanisms. BMC Evol Biol 17: 226.

Hsiung B-K, Siddique RH, Stavenga DG, Otto JC, Allen MC, Liu Y, Lu Y-F, Deheyn DD, Shawkey MD, Blackledge TA (2017) Rainbow peacock spiders inspire miniature superiridescent optics. Nature Communications 8: 2278

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Giraldo MA, Parra JL, Stavenga DG (2018). Iridescent colouration of male Anna's hummingbird (*Calypte anna*) caused by multilayered barbules. J Comp Physiol A 204:965-975.

Freyer P, Wilts BD, Stavenga DG (2018). Reflections on iridescent neck and breast feathers of the peacock, *Pavo cristatus*. J Roy Soc Interface Focus, 9:20180043

Kooi CJ van der, Elzenga JTM, Staal M, Stavenga DG (2019) Vividly coloured poppy flowers due to dense pigmentation and strong scattering in thin petals. J Comp Physiol A (2019). https://doi.org/10.1007/s00359-018-01313-1

**Bristol group**

*Papers in peer-reviewed journals*

Temple, S.E., Roberts, N. W. and Misson, G. P. 2019 Haidinger's brushes elicited at varying degrees of polarization rapidly and easily assesses total macular pigmentation. Journal of the Optical Society of America A 36: B123-B131

Marshall, N.J., Powell, S.B., Cronin, T.W., Caldwell, R.L., Johnsen, S., Gruev, V., Chiou, T.H.S., Roberts, N.W. and How, M.J., 2019. Polarisation signals: a new currency for communication. Journal of Experimental Biology 222, jeb134213

Fleming, J.F., Kristensen, R.M., Sørensen, M.V., Park, T-Y. S., Arakawa, K., Blaxter, M., Rebecchi, L., Guidetti, R., Williams, T.A., Roberts, N.W., Vinther, J. and Pisani, D. 2018 Molecular palaeontology illuminates the evolution of ecdysozoan vision. Proceedings of the Royal Society B 285, 20182180

Daly, I.M., How, M.J., Partridge, J.C. and Roberts N.W. 2018. Complex gaze stabilization in mantis shrimp. Proceedings of the Royal Society B 285, 20180594

Tibbs, A.B., Daly, I.M., Bull, D.R. and Roberts, N.W., 2018. Noise creates polarization artefacts. Bioinspiration & Biomimetics 13, 015005

Tibbs, A.B., Daly, I.M., Roberts, N.W. and Bull, D.R., 2018. Denoising Imaging Polarimetry by Adapted BM3D Method. Journal of the Optical Society of America A 35, 690-701

Foster, J.J.,Temple, S.E., How, M.J., Daly, I.M., Sharkey, C.R. Wilby, D. and Roberts N.W.. 2018. Polarization Vision: Overcoming Challenges of Working with a Property of Light We Barely See. The Science of Nature. 105, 27

Innes C. Cuthill, William L. Allen, Kevin Arbuckle, Barbara Caspers, George Chaplin, Mark Hauber, Geoffrey E. Hill, Nina Jablonski, Chris D. Jiggins, Almut Kelber, Johanna Mappes, Justin Marshall, Richard Merrill, Daniel Osorio, Richard Prum, Nicholas W. Roberts, Alexandre Roulin, Hannah Rowland, Thomas Sherratt, John Skelhorn, Michael P. Speed, Martin Stevens, Mary Caswell Stoddard, Devi Stuart-Fox, Laszlo Talas, Elizabeth Tibbetts and Tim Caro. 2017 The biology of color. Science 357: eaan0221

Feller, K.D., Jordan, T.M. Wilby, D. and Roberts, N.W. 2017 Selection of the intrinsic polarization properties of animal optical materials creates enhanced structural reflectivity and camouflage. Phil. Trans. R. Soc. B 372, 20160336

Maxwell, D.J., Partridge, J.C., Roberts, N.W., Boonham, N. and Foster, G.D. 2017 The effects of surface structure mutations in *Arabidopsis thaliana* on the polarization of reflections from virus-infected leaves. PLoS ONE 12: e0174014

Daly, I.M., How, M.J., Partridge J.C., Temple S.E., Marshall N.J., Cronin T.W. and Roberts, N.W. 2016 Dynamic polarization vision in mantis shrimps. Nature Communications 7:12140

Maxwell, D.J., Partridge, J.C., Roberts, N.W., Boonham, N. and Foster, G.D. 2016 The effects of plant virus infection on polarization reflection from leaves. PLoS ONE 11:e0152836

Wang, X., Gao, J., Fan, Z., Roberts, N.W. 2016 An analytical model for the celestial distribution of polarized light, accounting for polarization singularities, wavelength and atmospheric turbidity. Journal of Optics 18:065601

Jordan, T.M., Wilby, D., Chiou, T-H., Feller, K.D., Caldwell, R.L., Cronin, T.W., Roberts, N.W. 2016 A shape-anisotropic reflective polarizer in a stomatopod crustacean. Scientific Reports 6:21774

Iwasaka, M., Mizukawa, Y., Roberts, N.W. 2016 Magnetic control of the light reflection anisotropy in a biogenic micro-guanine crystal platelet. Langmuir 32: 180-187

How, M.J., Christy, J., Temple, S.E., Hemmi, J.M., Marshall, N.J., Roberts, N.W. 2015 Target detection is enhanced by polarization vision in a fiddler crab. Current Biology. 25, 3069–3073

Temple, S.E., McGregor, J.E., Miles, C., Graham, L., Miller, J., Buck, J., Scott-Samuel, N.E., Roberts, N.W. 2015 Perceiving polarization with the naked eye: characterization of human polarization sensitivity. Proceedings of the Royal Society B, 282, 20150338

*Organization of an invited International Symposium on Processing the Polarization of Light at the 2018 International Congress of Neuroethology, Brisbane, Aus.*

Invited talks were:
***Gregor Belusic*** Horsefly polarotaxis is mediated by a segregated ommatidial subtype with spectrally imbalanced photoreceptors, leading to colour-induced polarization artifacts (see above)
***Basil El Jundi*** Integration of Celestial and Wind information in the Dung Beetle's Compass.
***Jan Hemmi*** Characterizing the sensitivity of polarization vision in invertebrates using ERGs.
***Nicholas Roberts*** New directions for studies of how animals use the polarization of light.

*Manuscripts submitted to peer-reviewed journals:*
Daly I.M., Meah, R.J. and Roberts N.W. How 2019 *Haematopota pluvialis* perceive the polarization of light (*under review*)

Daly I.M., Meah, R.J. and Roberts N.W. 2019 The mild benefit of stripes as protection against biting flies is due to limited visual acuity (*under review*)

Daly I.M., How, M.J., Partridge, J.C. and Roberts N.W. 2019 A method for tracking the three-dimensional rotation of a rigid body in the aquatic environment (*under review*)

Smithers, S.P., Roberts N.W. and How, M.J. 2019 Parallel processing of polarization and intensity information in fiddler crab vision (*under review*)

## Joint publications

*Papers in peer-reviewed journals*

Pirih P., Ilić M., Rudolf J., Arikawa K., Stavenga D. G., Belušič G.: The giant butterfly-moth *Paysandisia archon* has spectrally rich apposition eyes with unique light-dependent photoreceptor dynamics. *Journal of Comparative Physiology A*, 204, 639-651 (2018).

Stavenga D. G., Leertouwer H. L., Meglič A., Drašlar K., Wehling M. F., Pirih P., Belušič G. Classical lepidopteran wing scale colouration in the giant butterfly-moth *Paysandisia archon*. PeerJ, 6, e4590 (2018)

Stavenga D.G., Meglič A., Pirih P., Koshitaka H., Arikawa K., Wehling M. F., Belušič G.: Photoreceptor spectral tuning by colorful, multilayered facet lenses in long-legged fly eyes (Dolichopodidae). *Journal of Comparative Physiology A*, 203, 23-33, (2017).

Stavenga D. G., Wehling M. F., Belušič G.: Functional interplay of visual, sensitizing and screening pigments in the eyes of *Drosophila* and other red-eyed dipteran flies. *The Journal of Physiology*, 595, 5481-5494 (2017).