A further proof of polarization vision of *Notonecta glauca* and a note on threshold intensity for eliciting the plunge reaction

R. Schwind

Zoology Institute, University of Regensburg, D–8400 Regensburg (Federal Republic of Germany), 11 July 1984

Summary. Polarized UV light from a platform on the ground can attract backswimmers and elicit plunge reactions. Threshold intensity is independent of the overall UV-intensity in the surrounding space. Unpolarized UV light attracts the animals only when the intensity is higher than that of the surroundings. These results show that polarized UV light can be discriminated from unpolarized UV light independently of intensity.

Key words. Polarization vision; water insect; visual orientation; UV vision.

Natural linearly polarized light can be used by some insects for orientation. Bees and ants, for example[1–4], can adjust their course relative to the pattern of polarized light in the sky, which is brought about by scattering of the sunlight in the atmosphere. In addition to polarization through atmospheric scattering natural light can also be linearly polarized by reflection on water surfaces. The e-vector of this polarized light is orientated horizontally. Experiments with flying water bugs, *Notonecta glauca* (Insecta, Hemiptera); backswimmers, have shown that UV-light polarized by reflection on water surfaces plays an important role for the detection of water. A surface of the laboratory floor that emits polarized UV light can cause flying backswimmers to fly downwards until they contact the surface[5]. In descending, many of the animals exhibit the 'plunge reaction' normally seen over a water surface[6]; that is, they close their wings and dive head-first. This reaction was observed only when the bugs were flying over the polarizing film covering the luminous platform on the floor in a direction such that the e-vector of the polarized light was perpendicular to the median plane of the animal, as would be the case over water.

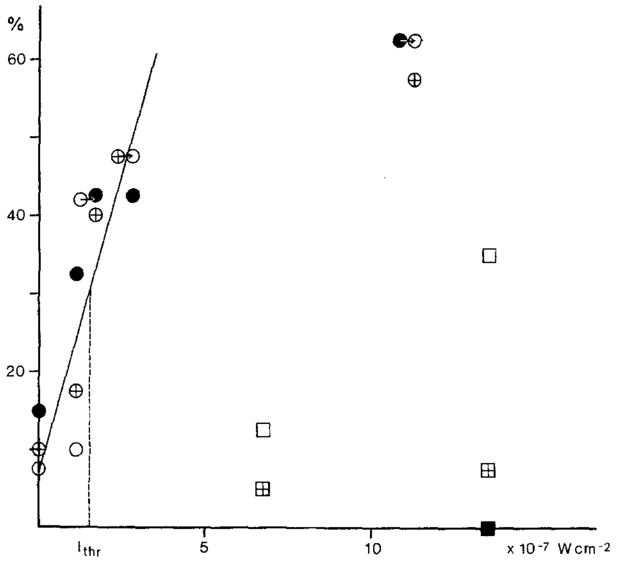
Neither polarized nor unpolarized visible light without a UV component caused the animals to fly downwards. In preceding experiments it was found, however, that unpolarized UV light could also elicit flight to the surface on the floor, though relatively high intensities were required. The experiment described here was done to determine whether the threshold intensity eliciting downward flight depends on the intensity of the UV light in the entire surroundings of the animal (i.e. the UV component of the light from the ceiling of the room). Different results were obtained with polarized and unpolarized UV light. These show more clearly than the preceding experiments did that polarized UV light (with horizontal e-vector) and unpolarized UV light are different stimulus qualities for the animal.

Materials and methods. Backswimmers of both sexes were used in the experiments. The animals flew within a flight room. The ceiling illumination was diffused by a layer of translucent drafting paper. On the floor there was a platform measuring 1 m^2 with a translucent surface that emitted diffuse UV-light with an emission maximum at 360 nm and a half-height width of 40 nm. This light was produced by D.C. supplied, UV-emitting fluorescent tubes (Osram, Type L40/W73). The light of the surface was linearly polarized by a polarization film (Käsemann, Type PW84), covering the entire luminous surface. The arrangement of the flight room was described previously[5]. For the experiments described here the lighting above the drafting-paper ceiling was modified so that various numbers of UV-emitting fluorescent lamps could be switched on in addition to the daylight fluorescent lamps already present. The light intensity was measured with a calibrated Optronic radiometer/spectroradiometer (Mod 730/730A–735).

Results and discussion. The figure demonstrates that polarized UV light at a given intensity from the surface of the platform P on the floor of the room always elicited about the same number of landings on P, regardless of the intensity of the UV component of the ceiling light, which was set at 5×10^{-7} (open circles), 10×10^{-7} (circles with a cross) or 50×10^{-7} W/cm^2 (filled circles). That is, elicitation of the flight to P by polarized light does not depend on the relative intensities of the light from P and from the ceiling, but requires only that the polarized UV light from P exceed a certain threshold intensity, independent of the intensity of the surroundings.

Different results were obtained with unpolarized UV light. When the UV light emitted from P was unpolarized, the number of flights to P (squares in the figure) depended on the ratio of the intensities of the platform and ceiling lights. P emitting unpolarized light was approached only when the UV intensity of the ceiling light was lower than that of the light from P, so that P was the brightest surface in the room. The result shows that unpolarized UV light elicits only the positive phototactic behavior exhibited by many insects, in which they approach the most intense (UV) light source.

When the UV intensity of the ceiling light was several times greater than that of the light from P (filled symbols), the phenomenon of 'polarization vision' of *Notonecta* was revealed most clearly. Polarized UV light was just as effective in eliciting flight to P as it was with the lower ceiling-light intensities, whereas unpolarized light attracted none of the animals even when its



Effectiveness of a luminous platform P on the floor of a flight room in causing flying backswimmers to land, Ordinate: percentage of animals that ended their flight by landing on P rather than elsewhere on the floor. Abscissa: intensity of the UV light emitted by the test surface. Round symbols (○⊕●): reactions to polarized light from P; square symbols (□⊞■): reactions to unpolarized UV light. The UV content of the ceiling light varied as follows: 5×10^{-7} W/cm^2 for the open symbols (○□), 10×10^{-7} W/cm^2 for the symbols with a cross (⊕⊞), and 50×10^{-7} W/cm^2 for the filled symbols (●■).

The regression line (continuous line) was calculated from only the data represented by the open circles and the circles with a cross. With the highest ceiling-light intensity tested (filled symbols) the intensity of the UV light reflected from the polarizing film and polarized in the process is no longer negligibly small, but is near the threshold intensity for eliciting the flight to P. n = 40 for each data point.

intensity was relatively high. Polarized UV light (with horizontal e-vector[5]) is thus distinguished from unpolarized UV light in an intensity-invariant manner. In the field the intensity of the UV component of the sky light is always several times higher than the intensity of the UV light reflected from water surfaces. It is therefore plausible that the dive into the water, the plunge reaction, is elicited exclusively by the polarized component of the reflected UV light.

The threshold intensity I_{thr} was found to be 1.5×10^{-7} W/cm^2. The UV light with which this result was obtained had $\lambda_{max} = 360$ nm, with a half-height width of 40 nm. The experiments employed animals that had been illuminated before the test with incandescent-bulb light containing little UV. Control animals, illuminated for half an hour before the flight by two additional 40-W UV fluorescent lamps, did not have higher thresholds. That the intensities naturally encountered by the animal are above this level is demonstrated by measuring the intensity of P in the laboratory at I_{thr} and that of an outdoor water surface on a cloudless summer afternoon through a Schott UG11 filter in combination with a Käsemann P-UV2 polarization filter with horizontal direction of transmission; the transmission properties of this filter combination correspond approximately to the absorption properties of the UV retinula cells of *Notonecta* with horizontal analyzer direction[7]. The results indicate that the light reflected from the water surface at an angle of for example 30° from the vertical is 100 times as intense for the UV receptors with horizontal analyzer as the polarized light in the laboratory at I_{thr}.

1 von Frisch, K., Experientia *5* (1949) 142.
2 Vowles, D. M., Nature *165* (1950) 282.
3 Waterman, T. H., in: Handbook of sensory physiology, vol. VII/6B, p. 281. Ed. H. Autrum. Springer, Berlin, Heidelberg, New York 1981.
4 Wehner, R., A. Rev. Ent. *29* (1984) 277.
5 Schwind, R., J. comp. Physiol. *A 154* (1984) 53.
6 Schwind, R., J. comp. Physiol. *A 155* (1984) 319.
7 Schwind, R., Schlecht, P., and Langer, H., J. comp. Physiol. *A 154* (1984) 341.

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Cerebrovascular reactivity to CO_2: modulation by arterial pressure[1]

J. D. Lifson, E. H. Rubinstein, O. U. Scremin and R. R. Sonnenschein[2]

Departments of Physiology and Anesthesiology and The Brain Research Institute, University of California School of Medicine, Los Angeles (California 90024, USA), 13 July 1984

Summary. Cerebrovascular reactivity to CO_2 (CO_2R), measured in halothane-anesthetized rabbits, decreased as arterial pressure was increased either pharmacologically or mechanically. On the other hand, hypotension, induced by bleeding, led to an increase in CO_2R. These responses were unaffected by denervation of baroreceptors.

Key words. cerebral blood flow; arterial pressure; CO_2 reactivity; baroreceptors; halothane; rabbit.

We previously reported[3] that halothane-anesthetized rabbits whose mean arterial pressure (MAP) is at or above 70 mm Hg show less cerebral vasodilatation in response to hypercapnia than do those whose MAP is at a lower level. The present experiments were designed to test whether this difference in CO_2 reactivity (CO_2R) was causally, rather than coincidentally, related to MAP, and to investigate the possible role of arterial baroreceptors in the response. Accordingly, CO_2R was tested when MAP was altered by both pharmacological and mechanical means, and the role of the baroreceptors was assessed by testing before and after section of the sinus and vagus nerves.

Methods. Male New Zealand rabbits weighing 2.5–3.5 kg were initially anesthetized with 3.5% halothane in O_2 administered by mask, and then maintained on 1% halothane throughout the experiment. A femoral artery and an auricular vein were cannulated for recording of MAP and administration of drugs, respectively. The animals were tracheostomized, paralyzed by a continuous i.v. infusion of pancuronium bromide at 0.4 mg/h and mechanically ventilated to achieve an initial end-tidal CO_2 ($ETCO_2$) of approximately 3%, as measured by a Beckman LB-2 gas analyzer. From this low value, $ETCO_2$ was set at the desired level by adding CO_2 to the inspired gas mixture. Respiratory anesthetic concentration was monitored continuously with a mass spectrometer or with a Beckman infrared LB-2 analyzer with a suitable pick-up head.

Internal carotid blood flow (ICBF) was measured with a 1.0–1.5 mm noncannulating electromagnetic flowmeter probe and a Biotronex 410 flowmeter. The probe was placed on the left common carotid artery after ligation of the external carotid artery and any extracerebral branches from the internal carotid. A hydraulic occluder[4] was placed around the artery distal to the flow probe to provide mechanical zero calibration. The detailed procedure, as well as a validation of ICBF in the rabbit as an estimation of cerebral blood flow, is described elsewhere[5]. Mean ICBF, MAP and respiratory CO_2 concentration were recorded continuously on a Grass Model 5 Polygraph.

MAP was adjusted downwards by bleeding from the arterial line, or upwards either by i.v. infusion of phenylephrine (0.3–2.5 $mg \cdot kg^{-1} \cdot h^{-1}$) or by inflation of a no. 5 Swan-Ganz catheter advanced through the femoral artery into the thoracic aorta. In the latter case, MAP was recorded through the large lumen at the tip of the catheter just above the level of the occlusion.

Before measurements of ICBF were taken, a 1-h stabilization period was allowed after completion of all surgical procedures. The dependence of CO_2R on MAP was calculated for each animal as follows. First, CO_2R was determined at the resting, undisturbed level of MAP by varying $ETCO_2$ in steps between 3

Dependence of cerebrovascular reactivity to CO_2 (CO_2R) on mean arterial blood pressure (MAP)

Groups	Intact A		B		Denervated C	
	Slope	Intercept	Slope	Intercept	Slope	Intercept
Mean	−0.15	24.5	−0.19	27.6	−0.15	31.7
SE	0.03	0.97	0.02	2.4	0.05	2.9
n	6	6	7	7	6	6

Mean values represent the average of slopes or intercepts of the regressions of CO_2R ($\Delta\%$ ICBF/$\Delta\%$ $ETCO_2$) on MAP (mm Hg) in the three experimental groups. MAP was lowered by bleeding in all groups; it was elevated by phenylephrine infusion in groups A and C and by an intra-aortic balloon in group B. Baroreceptors were denervated by severing cranial nerves IX and X at the neck in group C. All three slopes were significantly different from zero; neither the slopes nor the intercepts differed significantly from each other.