21 Polarization-Sensitive Optomotor Reaction in Invertebrates

If a cylindrical pattern of vertical black and white stripes is rotated around an animal, it usually displays a turning reaction. The tendency for the animal to turn in the direction of motion of a pattern is called "optomotor response", which demonstrates that the animal is able to detect the movement of the optical environment on the basis of brightness cues. This behaviour serves to stabilize the animal's orientation with respect to the environment, and helps it to maintain a straight course during locomotion. The optomotor reaction of insects to black-and-white (B&W) patterns has been intensively studied (e.g. Hassenstein and Reichardt 1956; Hassenstein 1959; Varjú 1959). Studies of the dependence of motion perception on the wavelength of light demonstrated, that the visual subsystem performing directionally-selective movement detection is usually colour-blind (e.g. Kaiser and Liske 1974; Kaiser 1974, 1975; Tinbergen and Abeln 1983; Lehrer et al. 1990; Srinivasan and Guy 1990; Schaerer and Neumeyer 1994).

If this visual subsystem is sensitive to polarization, it is to be expected that an optomotor response can also be elicited by movement of stripes of linearly polarizing filters with alternating orientations of their transmission axes. The strength and phase difference of the optomotor response to rotating B&W patterns should depend on the orientation of the transmission axis of a polarizing filter positioned between the animal and the pattern. Such experiments with crabs, honeybees, flies, backswimmers and waterstriders have shown that depending on the orientation of the polarization-sensitive microvilli system in the eyes of these animals, optomotor responses can be elicited by different E-vector patterns. In this chapter first the published results are briefly surveyed. Then the results of the experiments performed by Horváth and Varjú (2003) are presented, who studied the polarization sensitivity of the optomotor response of the backswimmer *Notonecta glauca* and the waterstrider *Gerris lacustris*.

21.1 Crabs

Korte (1965) observed polarization-induced optomotor response in the European fiddler crab *Uca tangeri*. According to Kirschfeld (1973b, p. 291), optomotor response can be elicited in the crabs *Carcinus* with white, blue or orange light, if the alternating E-vectors of the moving polarization pattern are parallel and perpendicular to the dorso-ventral plane of the eyes. However, if the E-vector directions were $\pm 45^{o}$ with respect to the dorso-ventral plane, optomotor response was not observed.

21.2 Honeybees

De Vries and Kuiper (1958) investigated the optomotor reaction of honeybees *Apis mellifera* to a moving pattern of stripes of linear polarizers with alternating vertical and horizontal E-vectors. In this experiment the bees did not show optomotor response to the E-vector contrast, since the polarization-insensitive lateral and frontal eye regions were stimulated. In *Apis mellifera* the optomotor response appeared only when the E-vectors were oriented $\pm 45^{o}$ from the dorso-ventral plane of the eyes (Kirschfeld 1973a). In this reaction the blue- and/or UV-sensitive receptors participate. Alternating parallel and perpendicular E-vectors in the frontal eye region did not elicite optomotor response.

21.3 Flies

Kirschfeld and Reichardt (1970) recorded optomotor reactions under open-loop conditions of walking houseflies *Musca domestica* as a function of the E-vector orientation of the stimulus light and found a sinusoidal modulation of the strength of the response. The E-vectors of the stimulating white, blue or orange light had to be $\pm 45^{o}$ from the dorso-ventral plane of the eyes to produce this reaction. Alternating E-vectors parallel and perpendicular to the dorso-ventral plane in the lateral eye region produced no optomotor response. Using electrophysiological recordings and optomotor experiments, McCann and Arnett (1972) studied the spectral and polarization sensitivity of wild-type adult *Musca domestica*, *Calliphora erythrocephala* and *Phaenicia sericata*.

Polarization sensitivity of the optomotor response in flying fruitflies *Drosophila melanogaster* was investigated by Heisenberg (1972) in an experiment, in which a rotating cylinder composed of two polarizing filters with E-vectors $\pm 45^{o}$ to the vertical was used as a stimulus. Repeating the optomotor experiment of Kirschfeld and Reichardt (1970) with *Drosophila*, Wolf et al. (1980) studied thoroughly the polarization sensitivity of course control and optomotor reaction of fruitflies. They found that polarization sensitivity is mediated by the peripheral retinula cells R1-R6 in the ommatidia. Although the

amplitude of the optomotor response of walking *Drosophila* was a sinusoidal function of the E-vector orientation, the phase and amplitude did not reflect directly the polarization sensitivity of the photoreceptors mediating the reaction. This suggests that *Drosophila* has an inner representation of the E-vector orientation, which is abstracted from the alignment of the dichroic microvilli. According to the original interpretation of Kirschfeld and Reichardt (1970), the modulation of the optomotor response due to the change of E-vector orientation should correspond to the change in the perceived brightness and thus to the polarization sensitivity of the receptors. Obviously, this is not the case in *Drosophila*, for which the polarization sensitivity estimated on the basis of the optomotor response is PS = 20-60, values considerably larger than typical PS-values in insect photoreceptors.

In a closed-loop situation, in which the fruitflies were illuminated from above by linearly polarized light and were allowed to turn the orientation of the E-vector relative to their body axes by their yaw torque, the animals could maintain their optomotor balance, i.e. they could use the polarization to fly straight. Above a rotating polarizer covering a fraction of the visual field with an angular diameter of 45^{o} just underneath the animal, *Drosophila* showed a significant optomotor response at 550 nm.

In the opinion of Wolf et al. (1980), at least under clear skies flying *Drosophila* could use the celestial polarization pattern for orientation. The threshold of the degree of linear polarization is about 15%. Since polarization sensitivity is not restricted to the dorsal part of the eye, *Drosophila* seems to possess polarization-sensitive receptors in most, if not in all, parts of its visual field. It might utilize polarization sensitivity to distinguish different surface properties on the ground, when searching for or trying to avoid water, distinguishing wet and dry surfaces which is a vital function for such a small insect. Alternatively, also with its ventral eye region *Drosophila* could use a polarization pattern for course control. Note, that Wolf et al. (1980) suggested as first that an animal could use the polarization sensitivity of its ventral eye region for water detection. This capability was later demonstrated by Schwind (1983a) in the backswimmer *Notonecta glauca*.

Considering the polarization sensitivity of the R1-R6 retinula cells in flies, there is a controversial problem. On the one hand, the polarization sensitivity of receptors mediating the optomotor response has been demonstrated for both *Musca* (Kirschfeld and Reichardt 1970) and *Drosophila* (Heisenberg 1972; Wolf et al. 1980; Coombe et al. 1989). On the other hand, it was argued that due to neural superposition in the dipteran *lamina ganglionaris* behavioural responses mediated by retinula cells R1-R6 should be almost invariant to the rotation of the E-vector of polarized light (Kirschfeld 1971). Each of these six cells, which superimpose their activity onto the same monopolar cells in the lamina, differ in their preferred E-vector direction by about 60^{o} from the neighbouring cells. Thus polarization sensitivity should be lost at the level of the lamina if the six retinula cells contribute equally to the activity of the monopolar cells. In light of this argument Kirschfeld (1973c) suggested that receptors R1-R6 may not be involved in the polarization-sensitive optomotor response. However, this is not the case in *Drosophila*. Coombe et al. (1989) have shown that although the optomotor

response of *Drosophila*, mediated unambiguously by the retinula cells R1-R6, is strongly polarization sensitive, the large monopolar neurons in the lamina are not sensitive to polarization.

21.4 Rose Chafers

Mischke (1984) investigated the polarization sensitivity of the optomotor reaction in the African rose chafer *Pachnoda marginata*. The lateral middle regions of the superposition eyes were stimulated by different oscillating (6 Hz) patterns containing intensity and/or colour and/or E-vector contrasts. The scarab beetle showed optomotor response exclusively to intensity contrasts. Mischke concluded, that *Pachnoda* is insensitive to polarization contrasts and was surprised, because the related scarab beetle *Lethrus* can orient menotactically by means of polarization (Frantsevich et al. 1977). Since in the experiment of Mischke the dorsal rim area of the eye of *Pachnoda marginata* was not stimulated, only the polarization insensitivity of the lateral middle eye regions can be concluded.

21.5 Optomotor Reaction to Over- and Underwater Brightness and Polarization Patterns in the Waterstrider *Gerris lacustris*

Waterstriders (Gerrids) have trichromatic colour vision (Hamann and Langer 1980; Bartsch 1991) and polarization sensitivity (Bohn and Täuber 1971; Bartsch 1995). The high polarization sensitivity of their photoreceptors to vertically and horizontally polarized light is not restricted to a special eye region or to a distinguished spectral region. One of the functions of this polarization sensitivity is to find the aquatic habitat by means of the partially and horizontally polarized light reflected from the water surface (Schwind 1991). This task requires a ventral polarization-sensitive eye region. Schwind (1985b) proposed that this ventral polarization-sensitive visual pathway is UV-sensitive in Gerrids. The high polarization sensitivity in the whole eye of waterstriders (Bartsch 1991, 1995) raises the question of its functional significance in the dorsal and lateral eye regions.

Waterstriders compensate for displacement and rotation of their body due to water flow or wind by two distinct types of behaviour (Junger and Varjú 1990; Junger 1991; Junger and Dahmen 1991):

1. To compensate for linear displacement they periodically jump against the direction of drift such that they maintain in average their position relative to the surroundings over a long time.
2. For rotation they compensate by a precisely combined rotation of the head and body, such that the gaze is stabilized in space.

Both behaviour types are visually controlled. With this in mind, the function of the polarization sensitivity of the lateral and dorsal eye regions in waterstriders could be to enhance the contrast of objects in the optical environment used for motion detection. The optical environment of waterstriders, composed of the water surface below the animal, the vegetation on the shore and the sky above the animal, is rich in polarization patterns with different degrees and angles of polarization, which could serve for contrast enhancement. To test whether these polarization patterns can be exploited for motion detection, Horváth and Varjú (2003) investigated the optomotor response of *Gerris lacustris* to different polarization patterns and compared it with the optomotor reaction to B&W patterns.

Male and female *Gerris lacustris* were collected from ponds and kept in a watertank. They were fed on wingless *Drosophila* from a culture. Before an experiment the animals were narcotised by CO_2 for some seconds. Then they were fixed by a wax drop on their pronotum to a 2 mm long vertical piece of a needle, which was glued to one end of a horizontal thin plastic stripe of about 2.5 cm length and 5 mm width. The other end of the stripe was adjusted by a holder to a proper height above the water surface. In this way the animals on the water surface were allowed to roll, pitch and raise to some degree in order to accommodate themselves, but were prevented from yaw and displacement of their body. On the head of the animal a pin, a hair of about 1 cm length of a shaving brush, was fixed by a wax droplet. The function of this pin was to display the head orientation during video recording (Fig. 21.1).

The animals were placed in the centre of a plexi cylinder (diameter 9.4 cm, height 12 cm), which was connected to a second one by a silicone tube (Fig. 21.1A). After the system was filled half with water, the water level in the first cylinder could be changed by lowering or raising the second cylinder. For stimulation of the ventral and dorsal eye regions a horizontal disc consisting of 12, e.g. black and white, sectors was oscillated sinusoidally with an amplitude of 5^o and a frequency of 1 Hz around its vertical symmetry axis immediately below (Fig. 21.1B) and above the animal (Fig. 21.1C). Ventrally and dorsally, this disc occupied a cone with an aperture of 120^o and 90^o, respectively (Fig. 21.2). The black and white sector pattern B&Wsec (Fig. 21.2) consisted of matt black and thin semitransparent white paper providing a brightness contrast of 80%. The polarizing sector pattern POLsec consisted of sectors cut from a neutral density linearly polarizing filter (HN32, Polaroid) with the transmission axes of adjacent sectors perpendicular to each other (Fig. 21.2).

For stimulation of the lateral eye region $\pm 30^o$ from the horizontal direction (Fig. 21.2) a vertical cylindrical pattern holder with two different patterns, one on the top and another below, composed of 12 segments in a panoramic arrangement, was sinusoidally oscillated around the animal (Fig. 21.1A). Two pattern holders with four different patterns were used (Fig. 21.2). In an experiment one of the two patterns on a given pattern holder was occluded by a cylindrical matt black occulter, which could be vertically lowered and raised (Fig. 21.1A). The water level with the animal on it was adjusted in such a way, that the non-occluded stimulus pattern on the holder was seen by the animal at 0^o–30^o above the horizon.

Due to reflection at the water surface the animal could also see the mirror image of the pattern at 0^o–30^o below the horizon (Fig. 21.2). A change between the two stimulus patterns could be achieved by cautiously lowering or raising the water level together with the animal within 10-15 seconds without larger disturbance of the animal. This was important, because thus reactions of the animal to two different patterns could be recorded while the physiological state of the animal did not change. The experiments were performed in white, green and blue light. In the latter two cases cylindrical colour filters (Käsemann, Germany) were used around the animal (Fig. 21.1A). The intensity of light emitted by the white lamps was adjusted in such a way that the intensities transmitted by these two colour filters were the same (Fig. 21.3).

The oscillation of the stimulus patterns and the reactions of the animals were video recorded from above or below through tilted plane and conical mirrors (Fig. 21.1). After a frame-by-frame analysis, the orientations φ of the stimulus pattern and the pin fixed onto the head of the animal were determined as a function of time. The resulting stimulus and response data were fitted by sinusoid functions with amplitude A, from which the closed-loop gain $g_c = A_{response}/A_{stimulus}$ and the closed-loop phase difference $\Delta\varphi_c = \varphi_{response} - \varphi_{stimulus}$ were determined. Then the open-loop gain $g_o = g_c/[1+g_c^2-2g_c cos\Delta\varphi_c]^{1/2}$ and the open-loop phase difference $\Delta\varphi_o = arc\ tan(sin\Delta\varphi_c/cos\Delta\varphi_c - g_c)$ were calculated.

The stimulation of the ventral eye region of *Gerris* from nadir angle 0^o to $\pm60^o$ (Fig. 21. 2) in white light did not induce optomotor reaction for both the B&Wsec and POLsec patterns, although about 30% of the ommatidia look into these directions and see the underwater world (Varjú and Horváth 1989; Dahmen 1991; Horváth 1995a). This corresponds to the finding that *Velia caprai* does not respond to underwater brightness stimuli at all (Meyer 1970, 1971). When the dorsal eye region of *Gerris* from zenith angle 0^o to $\pm45^o$ (Fig. 21.2) was stimulated in white light, a weak optomotor response (with an open-loop gain $g_o = 25\pm3\%$ and phase difference $\Delta\varphi_o = 62^o\pm5^o$ averaged for 8 animals) was elicited by the B&Wsec pattern but none by the POLsec pattern.

Stimulating the lateral eye region between 0^o and 30^o above the horizon and because of reflection at the water surface also from 0^o to 30^o below the horizon in white light, *Gerris* exhibited an optomotor response to the B&W pattern (Fig. 21.4A) and the vhPOL pattern (Fig. 21.4B), but it did not respond to the ±45POL pattern (Fig. 21.4C) and the vvPOL pattern (Fig. 21.4D). The vvPOL pattern was used as a control to test whether the small inevitable brightness contrast at the borders of adjacent polarizing filters elicited a response. As we can see in Fig. 21.4D, there was no such a reaction, even if the amplitude of the stimulus was sometimes quite large. The spatial resolution of the compound eyes of *Gerris* (Dahmen 1991) was apparently not high enough to perceive the low brightness contrast at the borders of the polarizing filters. The optomotor response to the vhPOL pattern (Fig. 21.4B) is, therefore, exclusively due to the E-vector contrast.

As we mentioned, in the experiments waterstriders could also see the mirror image of the vhPOL pattern (Fig. 21.2). The intensity of vertically polarized light reflected from the water surface is slightly smaller than that of horizontally

polarized light, because the reflectivity of water is slightly smaller for vertical polarization (Guenther 1990). Thus after reflection the vhPOL pattern should have been partially transformed to a brightness pattern with a weak contrast. Using the same experimental setup (Fig. 21.1A), Horváth and Varjú (2003) repeated the experiment without water beneath the animals and with a double-height vhPOL pattern stimulating the lateral eye region at $\pm 30^{o}$ from the horizon. Then the average gain and phase difference of the optomotor response to this modified vhPOL pattern were the same as in the original case. Thus, the weak brightness contrast in the mirror image of the vhPOL pattern did not affect the optomotor response of *Gerris*.

The open-loop gain and phase difference of the optomotor response of *Gerris* to vhPOL and B&W patterns in white, green and blue light averaged over 8 animals are shown in Fig. 21.5 together with their standard deviations. In Fig. 21.6A the open-loop gain of responses to the B&W pattern in white, green and blue light is plotted versus that to the vhPOL pattern. The strongest response is found in white light, the weakest in blue. The ratio $gain_{B\&W}/gain_{vhPOL}$ is relatively constant independently of colour and physiological state of the animal (the latter varied only slightly between subsequent stimulations). Figure 21.6B shows the average open-loop gains for the three different light fields. The open-loop gain ratio, as indicated by the regression line, is $gain_{B\&W}/gain_{vhPOL} = 2.564$. It is clear from Fig. 21.5B that waterstriders followed the lateral stimuli with the smallest delay in white light and with the largest delay in blue light, furthermore the phase difference for the vhPOL pattern was always larger than that for the corresponding B&W pattern.

In order to interpret the above findings, we refer to the ultrastructure of the ommatidia in *Gerris lacutris* shown in Fig. 21.7. Since the light sources used in the optomotor experiments did not emit UV light and the polarizing filters did not transmit UV light, the UV-receptors could not be involved in the registered optomotor responses of *Gerris*. This and the result that waterstiders did not respond to ventral rotating brightness or polarization patterns suggest that self-rotation is detected by a visual pathway, which is separate from that mediating polarotactic water detection. The contrast of the vhPOL pattern is

$$C_{vhPOL} = (PS-1)/(PS+1) \approx 75\% \qquad (21.1)$$

both for the green and blue receptors due to the similar *PS*-values of about 7. The intensity of the stimulating green and blue light was adjusted to be the same (Fig. 21.3). In his electrophysiological recordings Bartsch (1991, 1995) found a great variation of the absolute sensitivity. Nevertheless the blue receptors tend to be slightly more sensitive than the green ones. If the blue receptors contributed remarkably to the optomotor response, a similar or even a somewhat higher gain could be expected for the blue compared to the green stimuli used in the experiments of Horváth and Varjú (2003). Instead, they found a gain ratio

$$gain_{B\&W}{}^{green}/gain_{B\&W}{}^{blue} = 2.82. \qquad (21.2)$$

The green receptors were also stimulated by the blue light used in the experiments (Fig. 21.3). The ratio of the amounts of green and blue light absorbed by the green receptor (calculated from the spectral sensitivity of the green receptor and the equal transmitted light intensity of the green and blue filters, Fig. 21.3) is

$$I_{green}/I_{blue} = 1.58. \quad (21.3)$$

Although nothing is known about the relation between stimulus intensity and gain of the optomotor response of *Gerris*, comparison of the ratios given in Eqns. (21.2) and (21.3) suggests that the blue receptor may not contribute to the optomotor reaction, otherwise the gain ratio $gain_{B\&W}{}^{green}/gain_{B\&W}{}^{blue}$ should be less than 1.58. Thus, the optomotor response of *Gerris* are mediated by the R1-R6 green receptors, and the motion-sensitive visual pathway is colour-blind. This agrees well with the findings that in many insect species the primary input to the optomotor pathway is via receptors R1-R6 (Coombe et al. 1989), and in honeybees and butterflies, for example, the optomotor response is green sensitive (Kaiser 1974; Kaiser and Liske 1974; Horridge et al. 1983). For waterstriders, living in an optical environment dominated by green foliage on the shore, green receptors seem to be optimal to the task of detecting self-motion (e.g. compensation for drift and rotation of the body), or motion of dark objects (e.g. enemies) against a green background.

Since in *Gerris* the ±45POL pattern did not elicit optomotor response, whereas the vhPOL pattern did (Fig. 21.4), all rhabdomeres involved in this reaction should have either horizontal or vertical microvilli in the normal posture of the animal. This conclusion is in accordance with the anatomical findings of Schneider and Langer (1969) and with the electrophysiological findings of Bartsch (1991, 1995).

21.6 Optomotor Response to Over- and Underwater Brightness and Polarization Patterns in the Backswimmer *Notonecta glauca*

The backswimmer *Notonecta glauca* is polarization sensitive and detects water by means of the horizontally polarized light reflected from the water surface (Schwind 1983a,b, 1984a,b, 1985a,b). Both of its above- and underwater optical environments are rich in polarization patterns:

- viewing from water through the Snell window, the celestial polarization pattern is seen, which is modified by refraction polarization (see Chapter 15.3);
- the foliage on the shore reflects strongly polarized light, which also can be seen through the Snell window;
- the light scattered in turbid water is strongly polarized.

The last phenomenon was demonstrated by Horváth and Varjú (2003) in the following way: A small aquarium was filled with turbid water from a pond with a dense growth of green-yellowish phytoplankton inhabited by backswimmers. The middle part of the aquarium was illuminated by a vertical, slightly divergent white light beam of an incandescent lamp. The polarization of light scattered by the suspended particles in water was measured by video polarimetry from the side. Figure 21.8 shows the obtained polarization patterns. The light scattered by the suspended phytoplankton is strongly polarized, and its E-vector is horizontal, i.e. perpendicular to the incident light beam. Thus, in small turbid ponds the spatial distribution of scattering polarization is quite similar to that in lakes and seas.

In turbid waters the characteristic strongly polarized ring at 90^o from the refracted sun light (see Fig. 15.1) develops within some centimetres around a backswimmer, the light intensity progressively decreases due to absorption, and the brightness contrasts are significantly reduced due to scattering (Lythgoe 1979). In such a contrast-poor, dimly lit, turbid optical environment the mentioned highly polarized ring around backswimmers could be well exploited for orientation. In their natural habitat backswimmers are often hanging upside-down at the water surface in such a way that the angle of their longitudinal body axis is 31^o from the surface. In this position they precisely compensate for passive translations and rotations of their body induced by water flow or wind. In this behaviour they rely mainly on visual cues (Blanke and Varjú 1995; Blanke 1996). To elucidate whether the overwater and underwater polarization patterns can be exploited for motion detection in backswimmers, Horváth and Varjú (2003) investigated the optomotor response of *Notonecta glauca* to different above- and underwater polarization patterns and compared it with the optomotor reaction to B&W patterns.

Backswimmers *Notonecta glauca* were collected from ponds, and were placed in the centre of a vertical plexi cylinder (diameter: 9.5 cm, height: 12 cm) half-filled with water. Translation of the animal's body was prevented by means of a small water-filled plexi cylinder (diameter: 3 cm, height: 6 cm) within the large one. In the small cylinder the animal could rotate freely around the vertical axis. The stimulation of the ventral, dorsal and lateral eye regions happened in white light with the same apparatuses and patterns used in the optomotor experiments with waterstriders (Fig. 21.1). Figure 21.9 shows the angular extensions of the stimuli within the visual field of *Notonecta*. The patterns were sinusoidally oscillated with 5^o amplitude and 0.2 Hz frequency. The orientation of the longitudinal body axis and the angular position of the stimulus pattern were evaluated frame by frame, from which the closed- and open-loop gains and phase differences were calculated.

Stimulation of the dorsal and ventral eye regions of *Notonecta* induced optomotor reaction only to the B&Wsec pattern. To the ventral B&Wsec pattern there were only weak responses (g_o = 7±2.7%, $\Delta\varphi_o = 43^o \pm 21.7^o$). The responses were relatively strong (g_o = 54±28.7%, $\Delta\varphi_o = 33^o \pm 18.3^o$) to the dorsal B&Wsec pattern. Backswimmers did not respond to the ventral and dorsal POLsec patterns.

The open-loop gain and phase difference of the optomotor response of *Notonecta* to lateral B&W, vhPOL and vvPOL patterns are shown in Fig. 21.10.

Stimulating the lateral eye region, backswimmers exhibited strong optomotor responses to the B&W pattern and a considerably weaker reaction to the vhPOL pattern. The optomotor responses to vvPOL and ±45POL patterns were the same and very weak. The vvPOL pattern was used to control the weak response induced by the small inevitable brightness contrast at the border lines between adjacent polarizing filters. Although the response to the vvPOL pattern was very weak, it was not zero, like in the case of waterstriders. Due to the higher spatial resolution of their compound eyes (Schwind 1978, 1980, 1983b) backswimmers could perceive the low brightness contrast at the borders of the polarizing filters. In order to obtain the real gains of the optomotor response of *Notonecta* to the vhPOL and ±45POL patterns, the gain of this "border response" to the vvPOL pattern must be subtracted from them. After this subtraction we obtain that *Notonecta* did not respond to the ±45POL pattern, while its response to the vhPOL pattern was weak, but definitely significantly larger than zero. Backswimmers followed the lateral B&W stimulus pattern with shorter delay than the vhPOL pattern (Fig. 21.10B).

The responses to overwater lateral stimulations were always slightly weaker than those for the corresponding underwater stimulations. Due to total-reflection of light at the water surface, backswimmers could also see the mirror image of the underwater stimulus pattern at 0^o-30^o above their horizon (Fig. 21.9). Thus, the underwater stimulus patterns were doubled in their vertical angular extension. On the other hand, because of refraction of light at the water surface the apparent vertical angular extension of the overwater stimulus patterns was compressed to about 8^o. These two effects explain, why backswimmers had a weaker optomotor response to overwater patterns in comparison with that to underwater ones.

According to Schwind (1985b), in the ommatidia of *Notonecta glauca* the six peripheral rhabdomeres R1-R6 are open and grouped around the two central fused rhabdomeres R7 and R8 (Fig. 21.11). In the medial eye region, with optical axes from 60^o ventrally to 80^o dorsally from the horizontal direction, the microvilli of the central rhabdomeres are horizontal. In the ventral eye region, 70^o or more ventrally from the horizontal, the microvilli of receptors R7 and R8 are horizontally and vertically aligned. We call this part of the eye the "ventral POL-area". Both in the dorsal and ventral eye regions, receptors R1-R6 are green sensitive. In the dorsal eye region, cells R7 and R8 are either UV or blue sensitive, while in the ventral POL-area they are exclusively UV sensitive. In the normal resting position, like in our experiments, the direction of the longitudinal body axis of *Notonecta* is 30^o relative to the water surface with head down. In this position the visual field of the animal is subdivided in three different regions (Schwind 1985b):

- the ventral POL-area looks into the air through the Snell window;
- the eye region directly below the ventral POL-area looks at the region of total reflection on the water-air interface;
- the remaining part of the eye looks at the underwater world.

In our optomotor experiments the light sources did not emit UV light, and the polarizing filters did not transmit UV light. Therefore in the ventral POL-area only the peripheral green receptors R1-R6 were stimulated, while in the lateral and dorsal eye regions also the central blue receptors. Thus, in the optomotor response of *Notonecta* to overwater stimuli the green receptors of the ventral part of the eye must have been involved. Since it is very unlikely that in the other eye regions the motion perception would be mediated by another receptor type than in the ventral POL-area, we conclude that in backswimmers only the green-sensitive visual pathway is responsible for motion detection, which is distinct from the UV-sensitive pathway involved in polarotactic water detection. In blowflies, droneflies, honeybees and goldfishes (Kaiser and Liske 1974; Tinbergen and Abeln 1983; Srinivasan and Guy 1990; Schaerer and Neumeyer 1994), for example, the visual subsystem performing directionally-selective movement detection responds also only in the green.

Since the microvilli of the central receptors R7 and R8 in the ventral POL-area of *Notonecta* are always vertical or horizontal (Fig. 21.11), the contrast of the vhPOL pattern is $C_{vhPOL}^{blue} = (PS-1)/(PS+1) \approx 75\%$. In *Notonecta PS*-values are unknown, therefore $PS = 7$ measured in waterstriders (Bartsch 1991, 1995) was assumed for the blue receptors of *Notonecta*. Because the B&W pattern provided a contrast of about $C_{B\&W} = 90\%$, the ratio of the contrast of the vhPOL and B&W patterns is $C_{vhPOL}^{blue}/C_{B\&W} = 0.83$.

On the other hand, the effective contrast of the vhPOL pattern perceived by the green-sensitive visual pathway is reduced, because the microvilli orientations of the peripheral green receptors are slightly disordered (Fig. 21.11). The perceived contrast of the vhPOL pattern is $C_{vhPOL}^{green}(\beta) = |cos2\beta|(PS-1)/(PS+1)$ for a green receptor, where β is the angle of the microvilli axis measured from the vertical. In the ventral POL-area of the *Notonecta* eye the mean values of β for the peripheral green receptors R1-R6 are (Fig. 21.11) $\beta_1 = 56^o$, $\beta_2 = 15^o$, $\beta_3 = 71^o$, $\beta_4 = 68^o$, $\beta_5 = 20^o$, $\beta_6 = 30^o$, and the relative cross-sections of the corresponding rhabdomeres are $A_1 = 0.17$, $A_2 = 0.83$, $A_3 = 0.83$, $A_4 = 1$, $A_5 = 1$, $A_6 = 0.17$ (Schwind 1985b). Supposing that the contribution of the green receptors to the effective contrast is proportional to their cross-section and to the perceived contrast, the average effective contrast of the vhPOL pattern is $C^*_{vhPOL}^{green} = {}_{n=1}\Sigma^6 A_n C_{vhPOL}^{green}(\beta_n)/ {}_{n=1}\Sigma^6 A_n = 56\%$. From here the ratio of the contrasts of the vhPOL and B&W patterns perceived by the green receptors is $C^*_{vhPOL}^{green}/C_{B\&W} = 0.62$. The contrast of the vhPOL pattern perceived by both the blue and green receptors is, thus lower than that of the B&W pattern. This is in accordance with our findings that backswimmers responded stronger to the B&W stimulation. In the case of the ±45POL stimulation the green-sensitive subsystem perceived a considerably reduced contrast, and this is the reason why *Notonecta* possessed practically no optomotor reaction in this situation.

The role of the UV-sensitive ventral POL-area in the eye of *Notonecta* in water detection is well understood (Schwind 1985b). In the opinion of Schwind (1983b), the special pattern of the central microvilli in the ventral part of the eye might not be related to the ability of the animal to orient itself by polarization below the

water surface. On the other hand, our results suggest the functional significance of polarization sensitivity of the lateral eye region in the optomotor reaction to polarization patterns in the green range of the spectrum. Horváth and Varjú (2003) proposed that the function of this polarization sensitivity may be a slight contrast enhancement for motion perception in the course of compensation for passive drift and rotation of the body of *Notonecta*. They admitted that the relatively disoriented microvilli structure of the peripheral green receptors (Fig. 21.11) is not ideal for this task, because the effective polarization sensitivity of this subsystem is not as good as it could be. The consequence is that the effective contrast of polarization patterns perceived by the green-sensitive visual pathway is generally reduced in comparison with the contrast perceived by the UV- or blue-sensitive central receptors. In spite of this, in *Notonecta* the motion perception is mediated by the green receptors, perhaps because in the aquatic habitat of backswimmers brightness and polarization contrasts occur mainly in the visible, especially in the green part of the spectrum, e.g. foliage on the shore, water plants and phytoplankton in water.

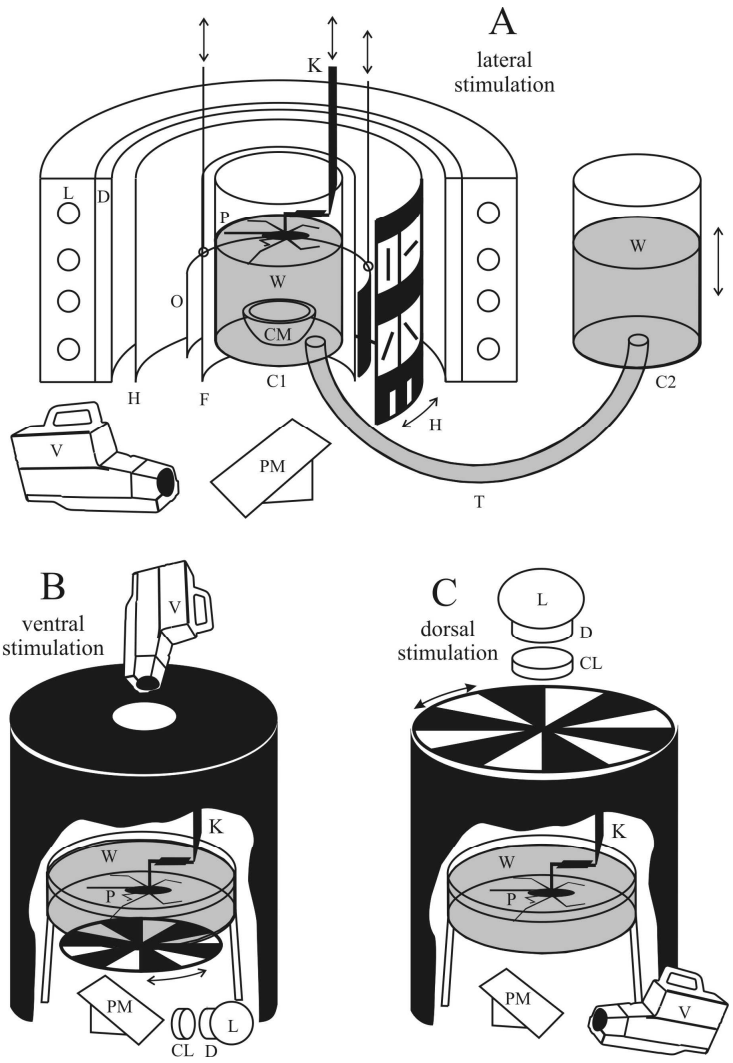

Fig. 21.1. Schematic diagrams of the arrangement of the optomotor experiments for stimulation of the lateral (A), ventral (B) and dorsal (C) eye regions in waterstriders *Gerris lacustris*. V: video camera; W: water; PM: plane mirror; P: pin (on the head of the animal); CM: conical mirror; T: tube; C1: first plexi cylinder (fixed); C2: second plexi cylinder (vertically moveable, to alter the water level in C1); H: oscillating cylindrical holder with two different stimulus patterns above (in a given experiment only one of them is visible to the animal) and a black and white stripe pattern below (invisible to the animal); O: occulter (vertically moveable by strings, to occlude one of the two stimulus patterns on the holder); F: colour filter (green or blue); K: moveable keeping (to change the vertical position of the animal following the change of the water level); L: incandescent lamps emitting white light; D: diffusor (white milky plexi glass); CL: condensor lens. (After Fig. 27.1 of Horváth and Varjú 2003).

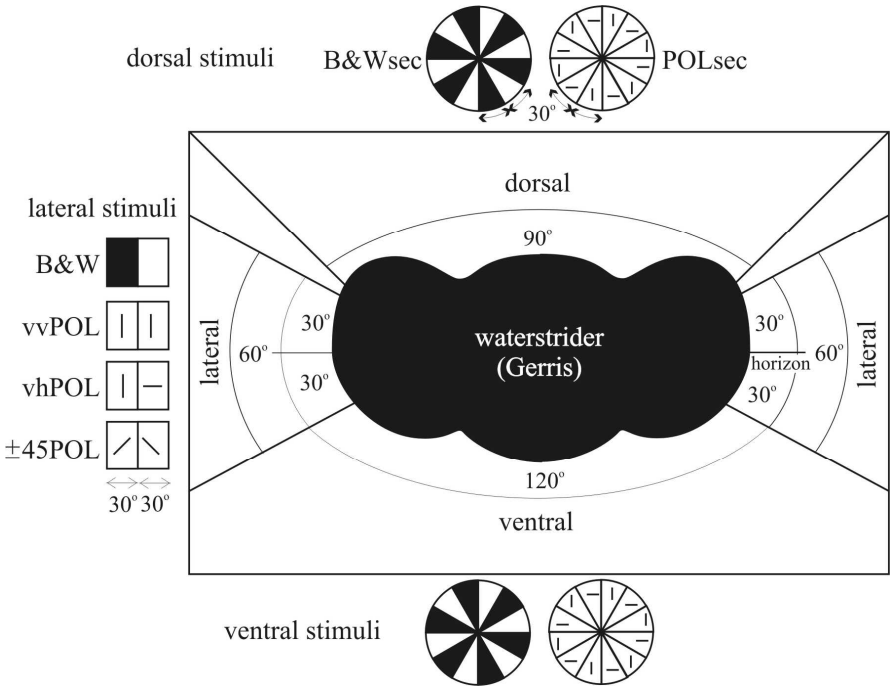

Fig. 21.2. Frontal view of the visual field of the eyes of *Gerris lacustris* (black: eyes and head) showing the different eye regions stimulated by various patterns. One of the two patterns on a given cylindrical pattern holder (Fig. 21.1A) stimulate the lateral eye region ±30° from the horizon due to the mirror image of the pattern at the water surface. The symbols outside the rectangle represent the different stimuli. B&Wsec: horizontal disc with alternating black and white sectors; POLsec: horizontal disc composed of sectors of linearly polarizing filters with alternating orthogonal transmission axes; B&W: vertical alternating black and white stripes; vvPOL: vertical stripes of polarizers with vertical transmission axes; vhPOL: vertical stripes of polarizers with alternating vertical and horizontal transmission axes; ±45POL: vertical stripes of polarizers with transmission axes alternating ±45° to the vertical. The orientation of the transmission axes of the polarizers is shown by bars. (After Fig. 27.2 of Horváth and Varjú 2003).

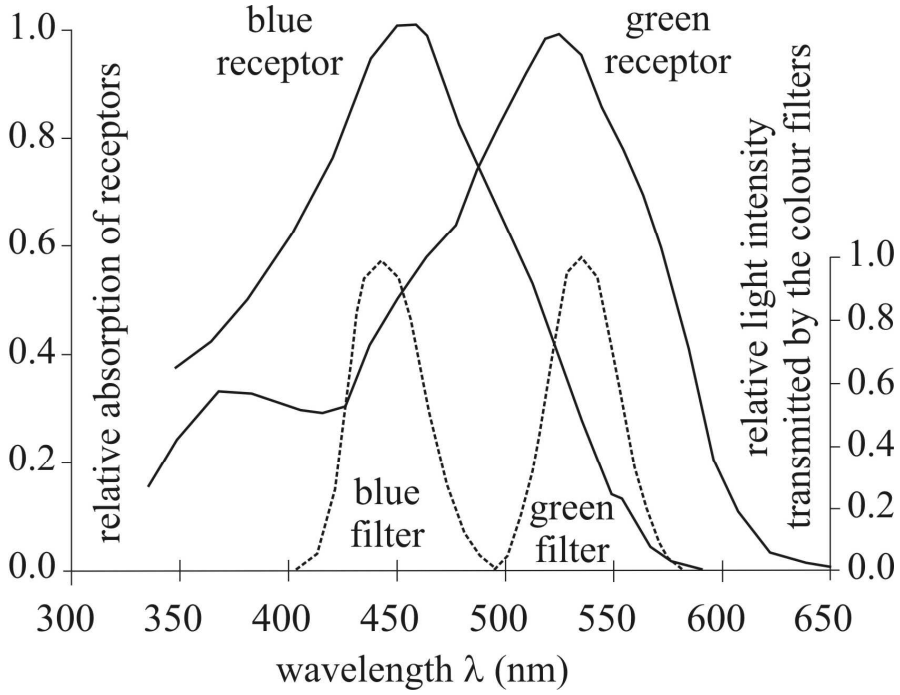

Fig. 21.3. Relative light intensities (dashed lines) transmitted through the blue and green filters versus wavelength λ used in the optomotor experiments, as well as the relative absorption curves $A(\lambda)$ (continuous lines) of the blue and green receptors R1-R6 in the eye of *Gerris lacustris*. (After Fig. 27.3 of Horváth and Varjú 2003).

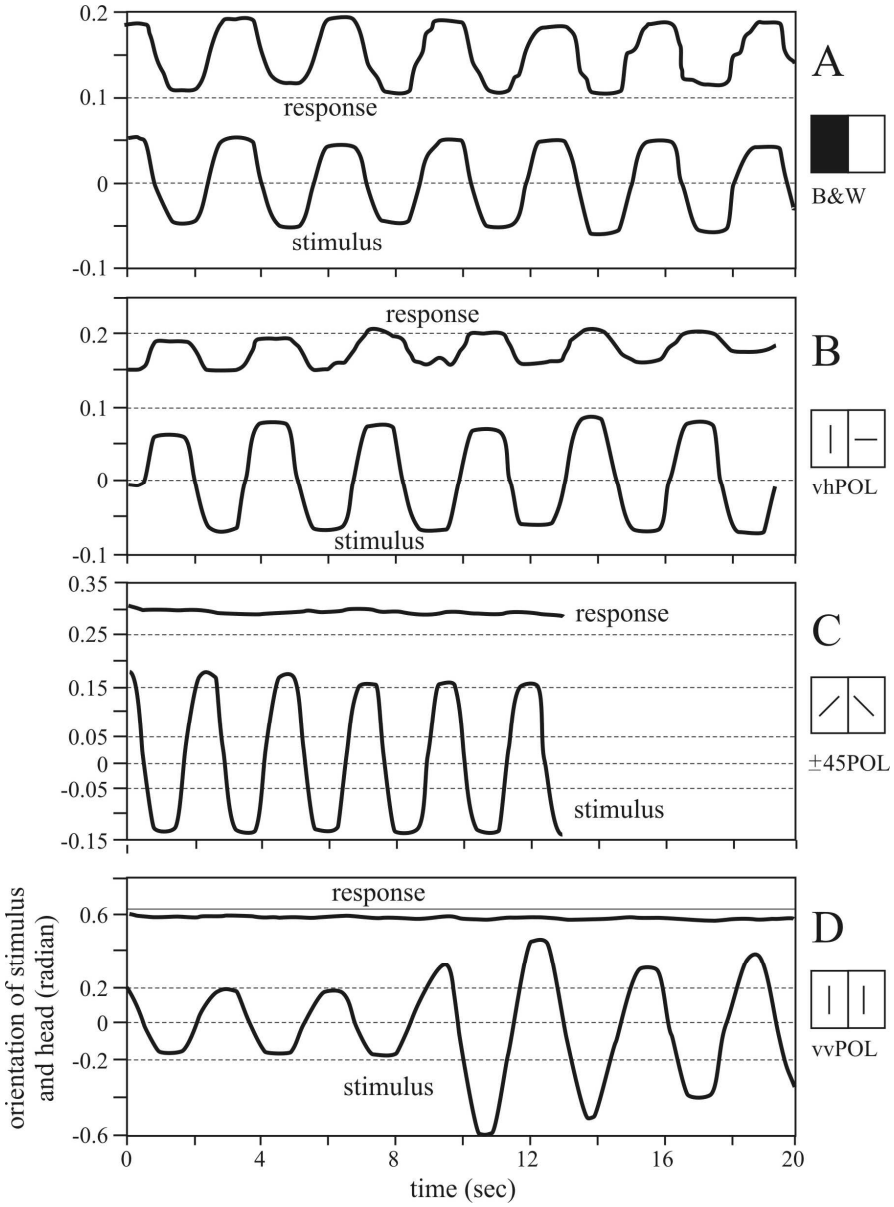

Fig. 21.4. Typical examples of the optomotor response of *Gerris lacustris* for different lateral stimuli in white light. The stimulus type is indicated by its symbol defined in Fig. 21.2. The abscissa is the time (measured in second) and the ordinate is the oscillating orientation (in radian) of the stimulus and the head. The response is practically zero to the ±45POL and vvPOL stimuli. (After Fig. 27.4 of Horváth and Varjú 2003).

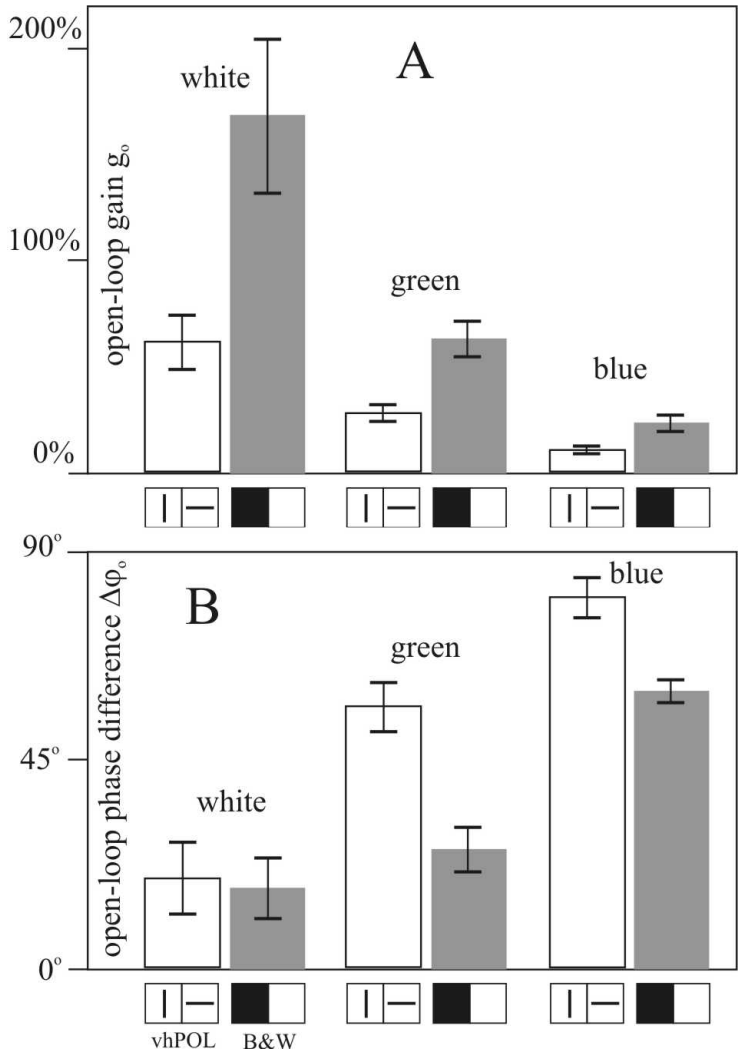

Fig. 21.5. The open-loop gain g_o (A) and phase difference $\Delta\varphi_o$ (B) of the optomotor response of *Gerris lacustris* to the vhPOL (white columns) and B&W (grey columns) stimulus in white, green and blue light averaged over 8 animals. The bars show the standard deviations. (After Fig. 27.5 of Horváth and Varjú 2003).

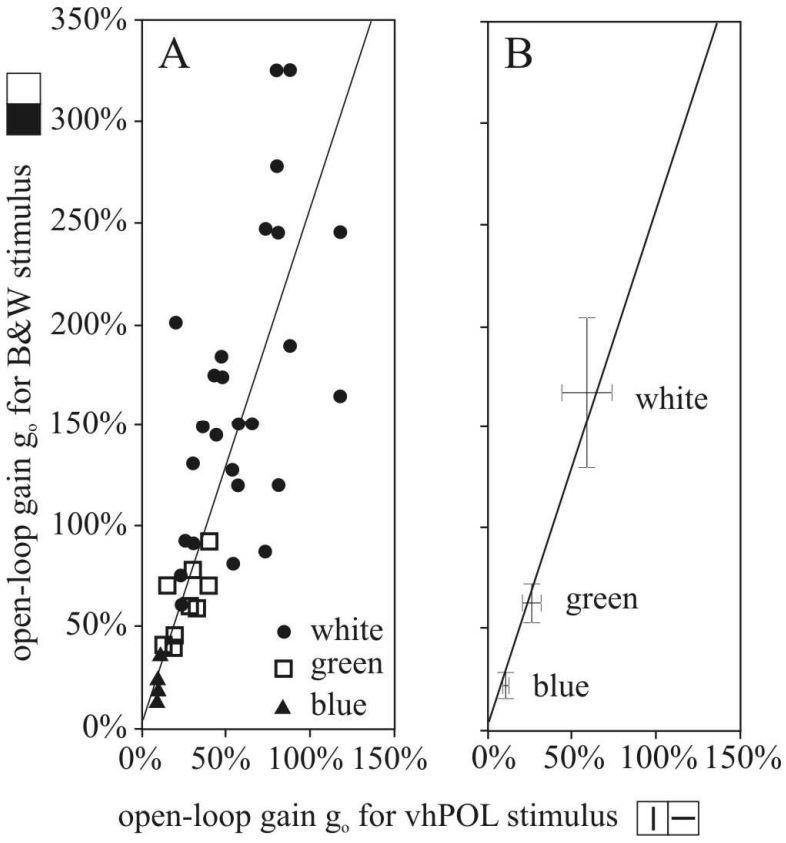

Fig. 21.6. A: The open-loop gain g_o for B&W stimulus versus g_o for vhPOL stimulus of the optomotor response of *Gerris lacustris* in white (dots), green (rectangles) and blue (triangles) light for 8 animals. Every symbol represents two subsequent optomotor responses to vhPOL and B&W stimuli. B: The average of the above-mentioned data. The horizontal and vertical bars show the standard deviation of the open-loop gains for the vhPOL and B&W stimuli, respectively. The slop of the regression line passing through the origin and fitted to the data points is $gain_{B\&W}/gain_{vhPOL} = 2.564$. (After Fig. 27.6 of Horváth and Varjú 2003).

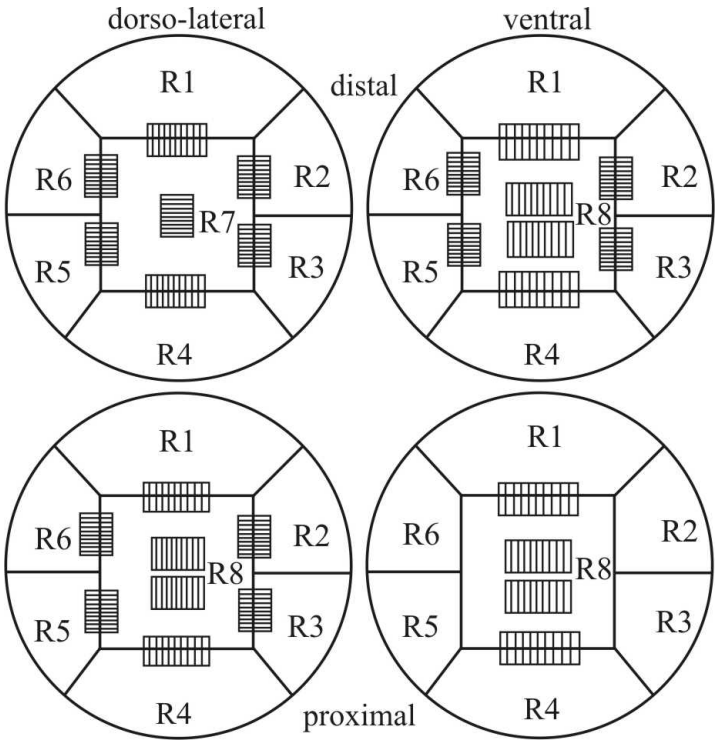

Fig. 21.7. Schematic cross-section of the ommatidium in different regions of the compound eye of the waterstrider *Gerris lacustris*. The hatched areas represent the microvilli of retinula cells R1-R8 and their orientation in the open rhabdom. (After Fig. 18.2 of Horváth and Varjú 2003).

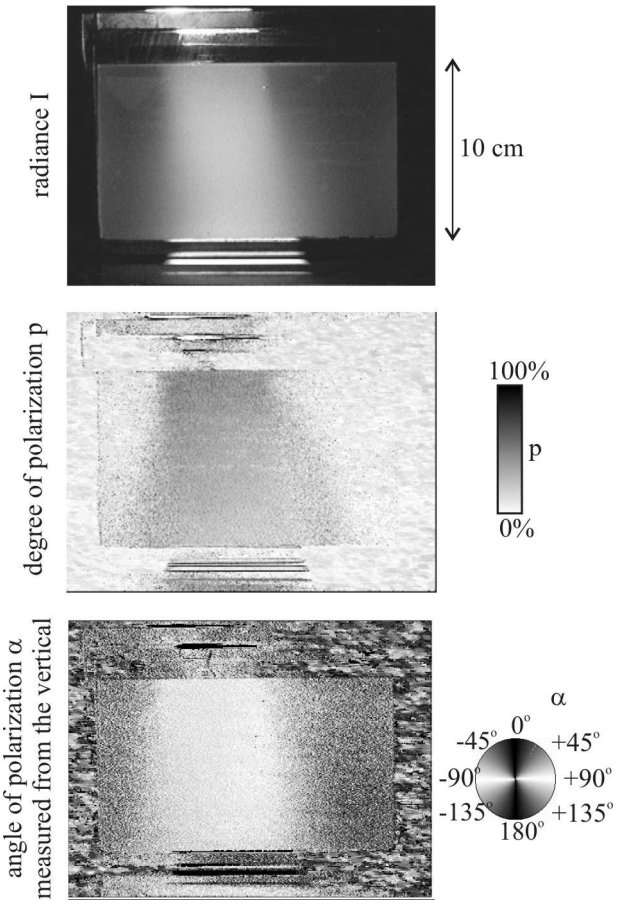

Fig. 21.8. Scattering-polarizational characteristics of turbid water in an aquarium, the middle part of which was illuminated by a slightly divergent vertical white light beam and the polarized light scattered by suspended particles in water was measured from the side by video polarimetry at 550 nm in such a way that the optical axis of the video camera was horizontal (perpendicular to the incident light beam). Demonstration of the strong scattering polarization of light within some centimetres in turbid water with a dense growth of green-yellowish phytoplankton from a pond inhabited by backswimmers *Notonecta glauca*. (After Fig. 27.7 of Horváth and Varjú 2003).

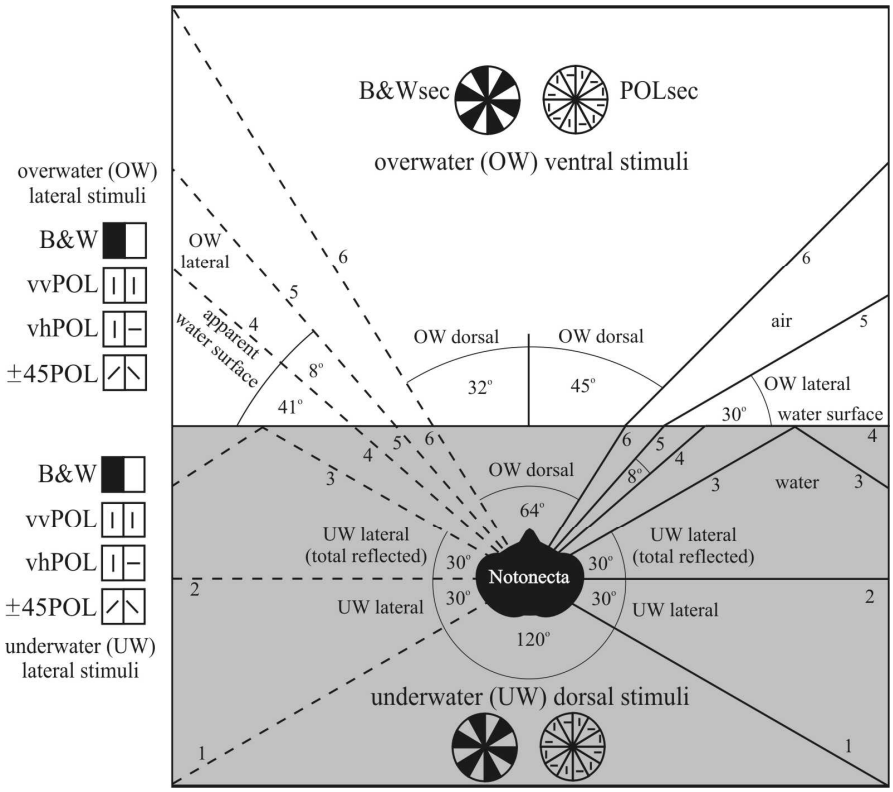

Fig. 21.9. Frontal view of the visual field of the eyes of *Notonecta glauca* (black: eyes and head) showing the different eye regions stimulated by various patterns. The patterns on the cylindrical pattern holder (Fig. 21.1A) stimulate the lateral eye region ±30° from the horizon due to total reflection at the water-air interface. The symbols outside the rectangle represent the different stimuli, which are the same as in Fig. 21.2. At the right hand side of the figure the incident, refracted and reflected rays of light from the borders of the different stimulus patterns are traced by continuous lines, while at the left hand side the dashed lines show the corresponding directions of view perceived by the eye of *Notonecta*. (After Fig. 27.8 of Horváth and Varjú 2003).

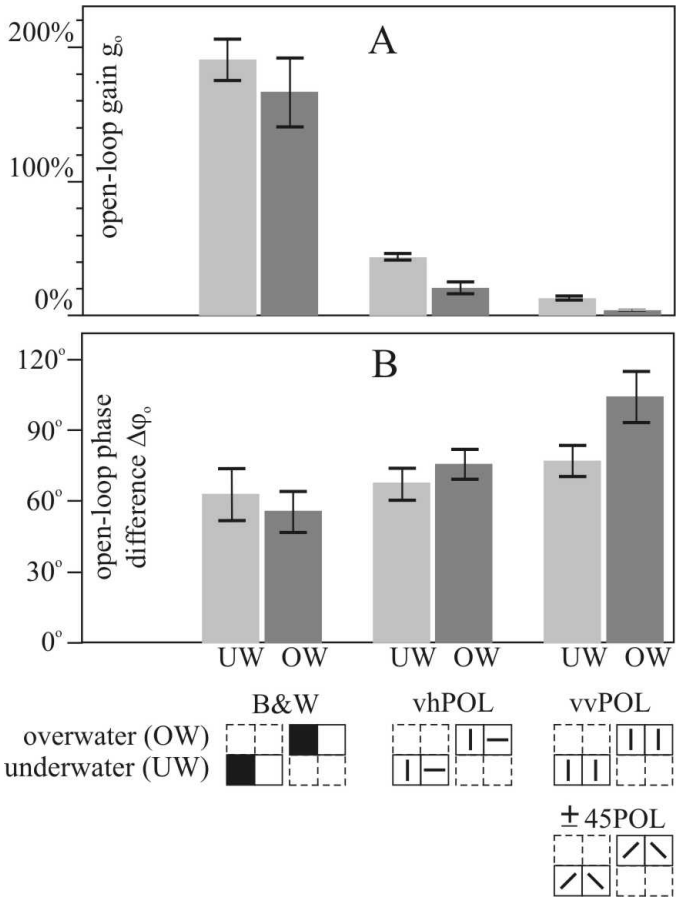

Fig. 21.10. The open-loop gain g_o (A) and open-loop phase difference $\Delta\varphi_o$ (B) of the optomotor response of *Notonecta glauca* to the B&W, vhPOL and vvPOL patterns stimulating the lateral eye region under (UW) and over (OW) the water surface. Columns: average data obtained with 8 animals. Bars: standard deviations. (After Fig. 27.9 of Horváth and Varjú 2003).

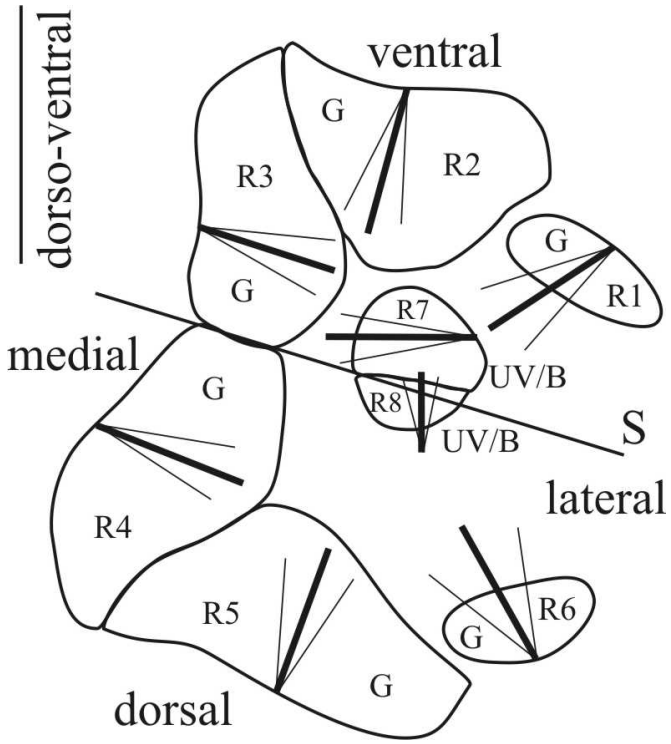

Fig. 21.11. Schematic representation of the cross-section of rhabdoms in the ventral POL-area of the compound eye of *Notonecta glauca* with the average orientations of the microvilli (thick bars) and their standard deviations (thin bars). These ommatidia look immediately above the water surface through the Snell window at its margin. The contours of retinula cells R1-R8 are also shown. Vertical bar at left: orientation of the dorso-ventral plane of the animal. S: average direction of the symmetry axis of the rhabdoms. G: green receptor, UV/B: ultraviolet or blue receptor. (After Fig. 18.4 of Horváth and Varjú 2003).