

Permotipula cannot be one of the direct ancestors of the recent Diptera. As already outlined by Tillyard [3], the elongated median cell is a specialization of *Permotipula* as is the three-branched radial sector (there are extant Diptera with Rs being still four-branched, see also [4], and which are thus more primitive with respect to this character). A further autapomorphy of *Permotipula* is the reduction of the second anal vein.

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A Variety of Insects are Attracted to Water by Reflected Polarized Light

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As was shown in laboratory experiments, backswimmers in flight (*Notonecta glauca*) recognize bodies of water by the polarized, reflected (UV-)light [1–3]. Very simple field experiments employing different reflecting (or non-reflecting) surfaces now demonstrate that a large variety of insect species are attracted to bodies of water by the polarized light they reflect.

The main clue came from an experiment carried out on the very last two warm days in October, 1988. Three different testing surfaces, each a little over 1 m² in size, were laid on the ground near the Zoology Institute of the University of Regensburg. The first was a dull black cloth (B); the second, a black cloth of the same material covered by a pane of glass (BG); the third, a sheet of aluminum foil also covered by a pane of glass (AG). After a mere 1.5 h of observation (4–4:30 PM, Oct. 15; 3–4 PM, Oct. 18) 19 water beetles had landed on BG [11 *Laccobius* sp. (Hydrophilidae), 5 *Helophorus* sp., 1 *Limnebius* sp. (Hydraenidae), 1 *Hydroporus palustris*, 1 *Agabus bipustulatus*

(Dytiscidae)]. Nothing had landed on B and nothing on AG.

The experiments were resumed the following spring with an improved arrangement: a film of water flowed across each glass surface and automatically swept the insects landing there into a collecting receptacle. Only B needs to be watched. The number of species and of individuals captured has risen greatly. It includes water-dwelling beetles (Coloepoptera) and bugs (Hemiptera); also bugs of the family Gerridae. For example, during the 2 h from 3:30 to 5:30 PM on March 28, BG netted 99 water insects of many species. Just one (probably accidentally) was caught in AG and not one was observed to land on B.

These experiments demonstrate that neither the dark appearance of some ponds nor the brightness of reflecting water surfaces suffice to attract the insects to land on them. Otherwise they would have landed on the dull dark surface of B or on the bright surface of AG where the intensity of reflected light is higher than from the other two

surfaces at wavelengths visible to insects.

The most satisfactory explanation for the large number landing on BG is that all these water insects recognize bodies of water by the polarized light reflected from their surfaces. In the case of BG, the polarized light from the surface is only slightly “diluted” with nonpolarized light coming up from beneath the transparent covering, because the dull dark cloth beneath the glass hardly reflects any wavelength visible to the insects. Here, the degree of polarization is high. Aluminum, on the other hand, reflects the entire spectrum, including UV, but it is nonpolarizing. Therefore, in case of AG, the polarized light from the glass or the water film is strongly “diluted” by nonpolarized light from the background. The degree of polarization is too low to be considered by flying water insects.

The same conclusion can be drawn from the behavior of certain Nematocera. These oviposit on BG but not on B or AG.

Two further testing surfaces were also devised for automated collection in a film of flowing water. One was a sheet of white plastic reflecting at wavelengths from 400 to > 800 nm and covered with a pane of glass (WG). The other was a sheet of yellow plastic reflecting at wavelengths from 500 to > 800 nm, also glass-covered (YG). The different preferences displayed by different groups of insects demonstrate differences in polarization vision. One

group lands on WG, on YG, and on BG. The three surfaces have only polarized UV undiluted by nonpolarized UV light in common, suggesting the polarization systems of these insects is coupled with their UV systems. In addition, there appears to be another group landing both on YG and on BG. Still another accepts BG exclusively. The latter polarization system may require

wavelengths longer than 500 nm. Identification of the material is in progress. A quantitative evaluation will be presented soon.

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Automatic Gain Control in Movement Detection of the Fly

Implications for Optomotor Responses

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Walking or flying insects try to follow a stripe pattern, rotating around their vertical body axis (optomotor response) [1, 2]. Similarly, if a stripe pattern is moving up and down in front of a fly, the animal turns its head up and down. Such head movements, as shown in

Fig. 1 b, c demonstrate that the “gain” of this optomotor response is not constant but variable, depending upon the stimulus paradigm. This can be interpreted as being due to an automatic gain control mechanism in the movement detection system of the fly. Im-

plications for optomotor responses will be discussed.

At the onset of the experiments illustrated in Fig. 1 b, a striped pattern was moved upwards and downwards with reversal of direction every 4.3 s (Fig. 1 b, tracks A). Head-bending follows this motion stimulus, as can be seen in the upper tracks, whereby the movement of the head was relatively slow. Head movement to the onset of the same motion stimulus is much faster if motion of the pattern lasts for only 1.5 s, followed by a phase in which the pattern is stationary for 3 s, then moves for 1.5 s in the opposite direction, etc. As can be seen in the tracks B, the amplitude of the head-bending to this short stimulus has roughly the same amplitude as to the longer lasting stimuli (tracks A). If the duration of a short stimulus (track B) would have been increased, the amplitude of the head tilt transiently would be larger than shown in Fig. 1 b, upper track B.

The different angular velocities of head movement to the onset of the same motion stimulus indicate that, following onset of the stimulus, an internal signal must be generated, different in amplitude in the two stimulus paradigms. The difference can be interpreted as being due to a gain control element G (Fig. 2). The gain of the unit G is assumed to be modified by the signal of the motion detectors via the filter C. The results in Fig. 1 b can be modelled by assuming that the gain in case B is about twice that of case A. The filter C is a complicated element properties of which will be described in more detail elsewhere (Kirschfeld and Reitmajer, in prep.). If the contrast frequency of the stimulus is constant as in the example shown, it acts as a low pass filter with a time constant in the order of a few seconds. Furthermore, gain control is

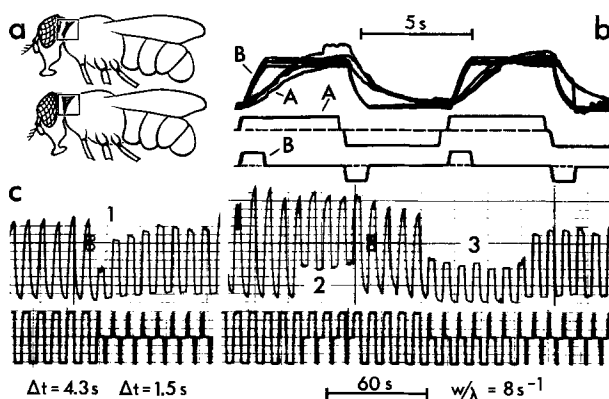


Fig. 1. a) Alignment of the aperture for monitoring head movement of the fly *Musca*. The light flux, passing the rectangular aperture indicated, changes with the head position and is measured by a photomultiplier. Red light, invisible to the fly, was used. b, c) *Upper tracks*: head position of *Musca* ♀ (rotation around transverse axis). The maximal amplitudes correspond roughly to 10 to 15° head pitch. This is far from any mechanical stop which occurs only at an angle of $\approx 30^\circ$ [15]. Although the head was free to move, the situation corresponds practically to an open-loop condition since angular velocity of the head pitch ($\approx 10^\circ/\text{s}$) is much slower than angular velocity of the pattern movement ($\approx 80^\circ/\text{s}$). The *two lower tracks* in (b) and the *lower track* in (c) indicate the periods of movement of the striped pattern (pattern wavelength $\lambda = 10^\circ$). Movement from dorsal to ventral is indicated by the upper position of the line, from ventral to dorsal by the lower position. Qualitatively same results have been found by all 12 flies observed. Quantitatively there was considerable variability in the degree of change of the gain between different flies