The examination of Triton X 114 treated and at 37 °C sedimented microsomes (figure 1d) reveals large areas of extended membrane systems, most of which form whorls of 20 and more layers. Other regions clearly show long continuous membraneous structures. Microsomal vesicles could no longer be observed in this preparation; the ability to fuse completely among each other exists under these experimental conditions.

In addition, it should be noted that divalent cations as Ca^{++} or Mn^{++}, which have been shown to induce fusion of cells[16] and artificial membrane systems[17], are not required for fusion of microsomes.

The table shows that the sedimentation of microsomes at 37 °C had no apparent effect on the specific phospholipid content (per mg microsomal protein) and the qualitative composition of the microsomal phospholipids consisting of lysophosphatidyl choline, phosphatidyl choline, phosphatidyl ethanolamine, phosphatidyl serine + phosphatidyl inositol, and sphingomyelin. The values for microsomes given in the table are in good agreement with those previously found in our and in other laboratories[18–20]. Therefore, the fusion at 37 °C is surely not induced by lysophosphatides which arise from endogenous phospholipids by a phosphatide acyl-hydrolase.

More probable is, however, that an increase in the fluidity of the membrane lipids, as directly observed at the lipid phase transition (around 25 °C) by electron spin resonance, X-ray diffraction and NMR studies[12–14], is one of the prerequisites for the fusion of microsomal vesicles at 37 °C.

Helenius and Simons[21] have summarized evidence that when small amounts of detergent are added to biological membranes, some of it will be incorporated into the membrane. This is in agreement with sedimentation experiments carried out in our laboratory in order to study the relationship between fusion and solubilization of microsomal vesicles[22]. It is, therefore, reasonable to assume that incorporation of small amounts of detergent into the microsomal membranes without disrupting them, has a marked effect on the physical state of the membrane matrix. Furthermore, membranes containing detergent within the hydrophobic core should be more fluid than native membranes, because the viscosity of Triton X 114 (2.6 poise)[23] is lower than the apparent effective viscosity of the membrane fluid phase (3–10 poise)[24–27]. Consistent with this view, and in good agreement with our interpretation of the fusion of microsomes at 37 °C, is our observation that the ability of microsomal vesicles to fuse completely among each other exists in the presence of 0.03% (w/v) Triton X 114 (Triton/protein ratio of 2). However, the microsomal membranes are solubilized if the Triton X 114/protein ratio is increased to 4 (figure 2).

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Photoelectric properties of the 'yellow strips' of social wasps

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Summary. The yellow strips on the cuticle of social wasp workers become photoconductive following irradiation with light, the effect being perfectly reversible.

The influence of light on the behavior of social wasps has been studied by several investigators[2–7] and it is now well-known that sunlight plays a central role in the diurnal activity of these insects. We studied the photoelectric properties of the cuticle of various species of wasps collected from different countries, and, for comparative purposes, also the photoelectric properties of the honeybee cuticle. We concentrated mainly on the brown and yellow cuticular strips on the dorsal surface of the abdomen, because these are most frequently exposed to light. As is known[7], several yellow strips and spots occur on the cuticle of Vespinae and Polistinae. These are interspersed with brown or dark strips and together give the wasp its characteristic color. From an earlier study we suspected that the yellow strips are in some way connected with photoconduction because they shine in the darkness of the natural nest and also fluoresce under UV-illumination.

In the early pupal stages the yellow strips are not easily differentiated from the other strips, but become clearly distinguishable before eclosion. In *Vespa orientalis* and several other hornets, 2 of the abdominal segments, namely the 3rd and 4th, are especially suitable for photoconductivity determinations because their anterior half is brown and their posterior half is mostly yellow. In other species, the colored abdominal segments may differ in number, size, pattern, etc.

The photovoltaic potential and the photocurrent were measured with a Keithley digital electrometer Model 616 whose sensitivity is in the range of 10^{-1}–10^{-11} A and 10^{-2}–10^{+2} V and 10^{5}–10^{12} Ω. Hookup of the cuticle strips to the electrometer was accomplished via copper wire, 0.05–0.1 mm in diameter, both ends of which were smeared with a small amount of colloidal silver paint. Test insects were various hornets and wasps, both pupae and adults, and the measurements pertained to the tergites of the abdominal segments. The live insects were first anaesthetized with ether, while the dead insects were deep frozen or alcohol preserved. The source of light was a microscope incadescent bulb 50 W, 220 V white light. The photocurrent was also measured under irradiation with a laser He-Ne beam of 5 mW, Model 132, Spectra Physics.

Information on the smallest intensity at which measurable changes of current with irradiation occur was obtained through a Power Meter, Model 212, Coherent Radiation, Palo Alto.

The specimens were illuminated and the changes in current measured over a 2-min-period, both during, and 10–15 min after the exposure to light. The measurements were performed by applying a variable external bias from 0.05 V to 1.6 V. The current produced under prolonged irradiation (10–20 min) and the variation in the current by a further exposure to light darkness (30/30 sec) were also measured.

The current-voltage characteristics in the dark were likewise determined and it was found that, due to high resistance values (10^6–10^8 Ω), the rectifying properties were noticeable only when low voltages were applied.

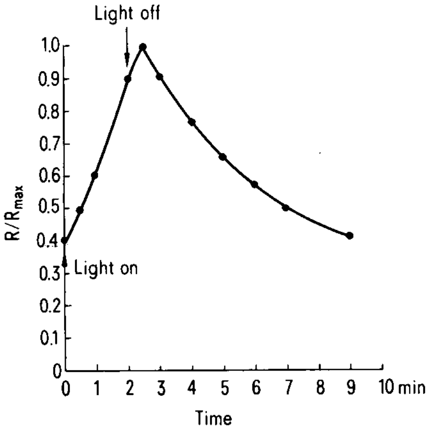

Fig. 1. The dependence of the ratio between the resistance at the initial value R and the maximal resistance R_{max} as a function of time, during and after irradiation with light on the yellow strip of a hornet worker (*Vespa orientalis*). Light is switched off after 2 min, and shortly afterwards, the resistance reverts to the initial value.

Effect of brief illumination. Short term (2 min) irradiation with or without the application of external bias of the cuticle invariably resulted in an increase of the resistance. Once the light was switched off, however, there was an essential difference between the yellow strips and the brown parts of the cuticle in that the current through the former but not through the latter increased again and after 10–20 min reverted to the starting level. The changes in the resistance with time following application of a voltage of 1.6 V to the 'yellow strip' of *Vespa orientalis* are presented in figure 1. The current varies slowly in the absence of light. The smallest, still detectable change in the current occurred at a white light intensity of 0.5 μW after 2 min of irradiation.

The resistance through the brown parts of the cuticle continued to increase following switch-off of the light and, only after a very long period (days), attained a saturation value or began to decrease. Such 'irreversible' change of the resistance in brown parts of the cuticle was observed also for hornet pupae and old queens.

Effect of prolonged illumination. During 10–20 min of illumination, the resistance in the yellow strips first increases to a maximal value, then decreases to a saturation value. The saturation of the resistance versus time in a measured yellow strip of *Vespa orientalis* is represented in figure 2. This sequence of events is typical only for the yellow strips of workers. In brown strips of all the tested species exposed to prolonged illumination, the resistance increases to a very high value and, although it drops again after the light is switched off, this requires a very long time and the maximal value reached is considerably higher than the starting value of the resistance of yellow strips.

In an attempt to understand the physical state prevailing in the yellow strips after prolonged illumination, the

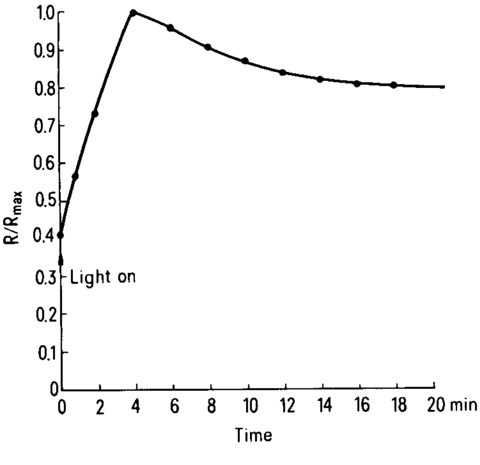

Fig. 2. The dependence of the ratio between the resistance and the initial value of the resistance as function of time, during prolonged irradiation of the yellow strip of a hornet worker.

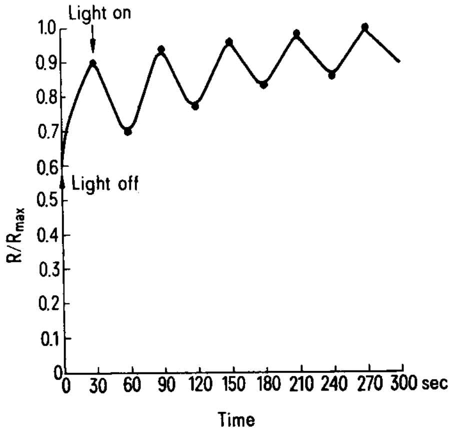

Fig. 3. The variation of the ratios between resistance and the initial value of the resistance as a function of time in the case of a yellow strip of a hornet worker after prolonged illumination, followed by switching the light off and on every 30 sec.

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strips were subjected to a series of brief (30 sec), alternate exposures to light and darkness. The variations in the resistance during such treatment are represented in figure 3, where they are clearly shown to be responsive (periodic) – the resistance increasing when the light is switched off, but decreasing when the light is switched on. Due to the high resistance values, there are also some slow irreversible changes, but essentially we have a reversible and typical photoconductive effect. With hornet males, pupae or young fertilized queens, as well as with honeybees exposed to the same procedure (i.e., prolonged illumination followed by brief, alternate light-darkness), there were occasional changes in the resistance of a periodic nature, but these were not consistent. In some instances the variation in resistance was periodic only for a few cycles of light-darkness, and then the resistance increased regardless of any further illumination. With living or recently killed workers, the saturation value of the resistance was attained more rapidly than with other specimens and likewise, decrease in resistance upon illumination was considerably higher and time of relaxation of the photocurrent was much shorter.

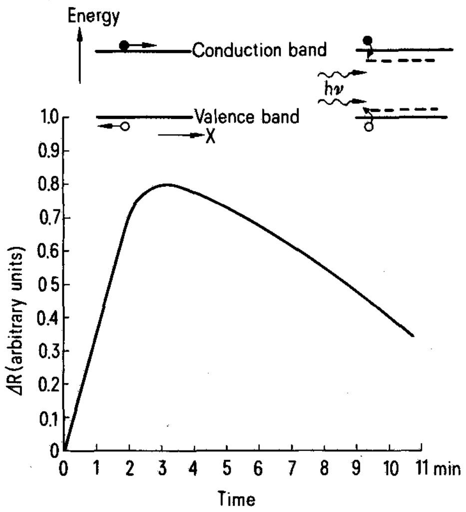

Fig. 4. Model for the reversible change of the current with irradiation and change of the current with time during and after switching off the light (see text).

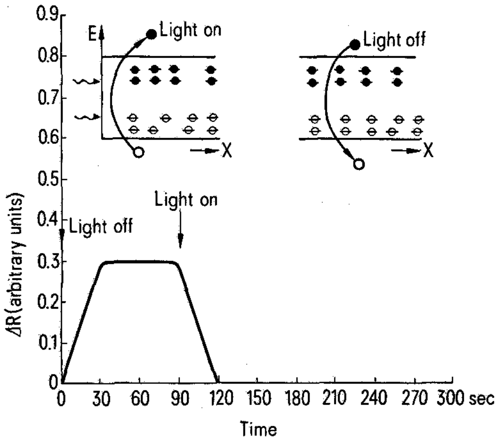

Fig. 5. Model for the reversible change in resistance after long irradiation with light (E = energy, X = distance through material). For explanation see text.

Interestingly, the nocturnally-active wasp *Apoica pallens*, although it lacks yellow strips on its dorsum, displayed a change of resistance with illumination which was very similar to that in wasps possessing yellow strips.

Irradiation with the light of a He-Ne laser also produced the afore-mentioned reversible changes of the resistance, but in this case, prolonged initial irradiation was unnecessary and the light of the laser was switched off every 10 sec rather than every 30 sec, since the longer exposure resulted in irreversible changes.

Discussion and physical model. Studies on the systematics of wasps at times base the distinction between related species on the color pattern of the wasp[7]. Results of the present study would seem to indicate that the cuticular yellow strips, insofar as their size, shape and relation to other colored spots on the cuticle are concerned, may be of functional importance to the daily activity of wasps, and that differences in yellow strip pattern between the species express also physical and physiological differences that may enable proper ecological adaptation of wasp population to their biotope and ambient climate. The fact that the cuticle of drones and queens, who usually do not engage in foraging, possess less prominent photoconductive properties than that of the workers, suggests that the yellow strips in workers may help them in some way in their orientation[8,9]. These must be associated with certain molecular changes brought about by light and leading to a reduction in the concentration of free carriers in the yellow strips. Such reduction may result from compositional changes imposed by photochemical reactions or from a rearrangement of molecular bondings. From the physical standpoint, what is important is that under illumination, some of the carriers contributing to the current disappear. The reduction in the number of carriers could be explained, on the basis of the semiconductor band theory[10], as an appearance of trap levels in the energy gap under illumination due to changes in the molecular structure. Indeed, similar changes have been noted in the optical absorption properties of some amorphous materials under irradiation with light[11,12]. As pertains to wasps, the process is represented schematically in figure 4. As can be seen, before the light is switched on, the free carriers in the conduction bands that contribute to the current are in a thermal equilibrium, but upon illumination, the photomolecular changes induce the appearance of trap levels in the energy gap and the photogenerate carriers and some of the equilibrium carriers are trapped, and consequently, the current decreases. Further irradiation with light will yield transition from the valence band into the conduction band and the generated carriers will produce a drop in the resistance. The relaxation in this case will be rapid and, upon switching off the light, the resistance will increase rapidly (figure 5).

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