J. Insect Physiol. Vol. 38, No. 1, pp. 37–48, 1992
Printed in Great Britain.

0022-1910/92 $5.00 + 0.00

PHOTOVOLTAIC EFFECTS IN THE ORIENTAL HORNET, *VESPA ORIENTALIS**

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(Received 18 June 1991; revised 2 August 1991)

Abstract—Photoelectric properties of the Oriental hornet (*Vespa orientalis*) cuticle and the pupal silk cocoon were studied. Exposure of a part of the cuticle to light caused a sharp increase in voltage, when measured between the illuminated and the dark part of the cuticle. The direction of this voltage was reversed if the other part of the cuticle was illuminated. This voltage was found to be linearly dependent on the intensity of the incident light for relatively low light intensities of a few mW/cm^2. However, this light-induced voltage was much higher if the light beam was directed at the back part of the cuticle strip than in the case where the front part of the cuticle strip was illuminated by the same light beam. The spectral dependence of this effect was also investigated and the maximum of the relative quantum efficiency was found in the spectral range of 360–380 nm. It appears that the cuticle might act as a biological solar cell. The dependence of photo current on the exposure time to light, as well as on environmental conditions, such as temperature and relative humidity was investigated in the pupal silk cocoon. Our results indicate that the cuticle as well as the cocoon act as convertors of light to electrial energy. At present we do not know the absolute efficiency of this conversion process, nor the biological applications of this effect.

Key Word Index: Social insects; hornet cuticle; pupal silk; spectral dependence of photovoltaic effect; photoelectric quantum efficiency; electrical resistance vs relative humidity

INTRODUCTION

The electrical properties of hornet cuticle have received considerable attention in our research of recent years. *Inter alia*, we have investigated the photoconductive properties (Croitoru *et al.*, 1978; Ishay and Croitoru, 1978) as well as the cuticular luminescence in various parts of the hornet body (Ishay *et al.*, 1987, 1988b). We have additionally studied hornet thermoconductive properties (Ishay *et al.*, 1982) and in this connection also a thermoelectric (Seebeck) effect (Shimony and Ishay, 1981), capacitance (Shimony and Ishay, 1984) and photovoltaic properties of the cuticle (Ishay *et al.*, 1988a).

The findings of these investigations point to the cuticle as behaving like one of the substances defined as an organic semiconductor (Gutmann and Lyons, 1967; Meier, 1974). The findings further show that the listed effects are particularly efficient at temperatures close to those associated with normal hornet functioning, i.e. at a temperature range between 20 and 40°C.

As is known, hornets comprise a group of social insects and as such their activity span is optimal only during the summer months, whereas from autumn to spring, there are no social activities and in fact only the fertilized queens remain alive. Our investigations so far have focused mainly on the cuticle of workers of the Oriental hornet, the latter being prevalent in the Mediterranean basin and the adjacent regions and active under conditions of Mediterranean summer (Ishay *et al.*, 1967). Other species of hornets are active either in tropical, equatorial or nearby regions (Van der Vecht, 1957, 1959; Matsuura and Yamane, 1990), or in temperate regions of the northern hemisphere (Kemper and Döhring, 1967; Wilson, 1971; Spradbery, 1973; Edwards, 1980; Akre *et al.*, 1981).

In previous studies we concentrated mainly on the cuticle of the adult hornet. In the present study, however, we also paid attention to the electrical

*This study includes a part of the Ph.D. thesis of A. Ben-Shalom.

properties of the silk cocoon enveloping the developing pupa. In the course of the investigation we thus measured both electrical voltage and current in the hornet cuticle and silk cocoon cap and the dependence of these two on the intensity of illumination. In the hornet cuticle we assessed also dependence of the light-induced voltage on the wavelength of the excitatory monochromatic light, while in the silk cocoon cap we evaluated the importance of environmental conditions.

MATERIALS AND METHODS

(a) Cuticle

The measurements were carried out on dead *V. orientalis* specimens frozen for long periods at $-20°C$. The specimens were attached to electrodes of $\phi = 0.08$ mm along the median line of the dorsum of the abdomen. For details see Ishay *et al.* (1990). The measured specimens were kept in a Faraday cage and the electrical measurements were carried out by a high resistance electrometer (up to $10^{14}\,\Omega$) Keithley (model 610A or 615). Light irradiation of the samples was with a 200 W high pressure mercury arc lamp or 150 W Halogen-Projection lamp. The incident light beam was focused with a quartz lens either on one of the points of attachment or simultaneously on both. The incident radiation flux was measured with a pyroelectric radiometer. For measurements of the spectral dependence of the effect, a grating monochromator as well as various optical filters were applied. The intensity of the incident light flashes varied for different wavelengths between 150 and 900 $\mu W/cm^2$.

(b) Silk cocoon cap

Cocoon caps were removed from hornet combs collected in the summer of 1989 in the Tel Aviv district. After their removal the silk caps were maintained in a sealed container at room temperature until use. Electrical properties, i.e. current and resistance were measured with a Keithley 617 programmable electrometer. To eliminate the influence of electrical and magnetic fields, the specimens to be measured were kept in a Faraday cage. Temperature and relative humidity were measured with a thermo-hygrometer (Hanna instruments 8564). The desired temperature levels were obtained with a variable-temperature incubator (Tutenour Model I-140, Jerusalem). Two electrodes were attached to the external (convex) and two to the internal (concave) surfaces of the silk caps. Irradiations of the samples were with a 20 W mercury beam passed through a 365 nm filter. The incident light flux in the external surface was about 100 $\mu W/cm^2$.

RESULTS

(a) Cuticle

Prior to any irradiation of the cuticle specimens, electrical measurements were performed in the dark. A voltage of few mV was recorded between the two electrodes. The polarity of the voltage was reversed by changing the direction of the electrodes. This internal voltage decayed with time when shortened by an external low resistance. However, the original voltage was restored after disconnecting the external resistance and storing the samples for several hours at a temperature of about 5°C in the dark. This "dark" voltage might be due to an electrochemical process. The internal resistance between the two points was also measured without applying any external electrical field. It was found to be on the order of 10–100 MΩ.

The exposure of the specimen to light pulses triggered the appearance of a voltage of the order of 10–100 mV between the two electrodes. This is shown in Fig. 1(A) for a strip of brown cuticle. A slight decrease both in the "light and dark" voltage levels was observed after repeated exposures to light pulses. However, after several pulses a steady "dark" level was reached. Keeping the samples for several hours at low temperature (about 5°C) in the dark, led to restoration of the original "dark" voltage level. As shown, the exposure of a specimen to an intense light beam resulted in a sharp increase in the measured voltage. The direction and the intensity of this light-induced voltage was found to depend on the position of the illuminating point (i.e. the electrode). When the light beam was focused on a posterior site, i.e. the back electrode, a considerably higher voltage was induced, and of an opposite direction, than that with a light beam focused on the front electrode. The results are given graphically in Fig. 1(B), where the a and b curves represent the voltages induced by 1-s flashes of polychromatic light, focused on the back electrode while the c and d curves are the corresponding voltages (lower and opposite) obtained with the light beam focused on the front electrode. It is worth mentioning that in a and b a "reverse" effect appeared which caused a slight decay in the light-induced voltage even during the illumination, whereas upon switching off the light a voltage of opposite polarity was recorded, which decayed slowly, to the original "dark" starting level. Such a "reversed" voltage was not detected in curves c and d (i.e. when the front electrode was illuminated). Curve e shows the light-induced voltage when both points (back and front electrode) were simultaneously illuminated by the same light beam. It can be seen that in this case the light-induced voltage had the same direction as in curves a and b but its intensity was approximately the difference between the voltages induced by separate illumination of each of the electrodes. The "reversed" voltage was in this case relatively high.

The spectral dependence. The specimens were irradiated by manochromatic light in the 250–700 nm spectral range. The recorded light-induced voltage was of the order of 10–100 mV. In Fig. 1(C) the relative quantum efficiency (η) of the light-induced voltage is given as a function of the wavelength (λ) of the incident light. The voltages induced by the various wavelengths are given in this figure as percentage of the maximal light-induced voltage. The results show maximal quantum efficiency in the 360–380 nm.

(b) Silk cocoon cap

Apart from the hornet cuticle, the hornet silk cocoon cap was also evaluated for its photoconductive properties. The silk cocoon caps comprise a protein material (Ochiai, 1960). Compared to cuticle it is relatively dry and therefore more easily amenable to repeated measurement. For measurement purposes, samples of silk cocoon were exposed to illumination at a fixed wavelength of 365 nm and an intensity of 100 $\mu W/cm^2$. This wavelength proved optimal also for the hornet cuticle (see above). Our experimental results showed that even in the absence of illumination there is a current flow between the electrodes amounting to several nA. The intensity of this current is enhanced as a result of illumination of the specimen, reaching saturation in about 2 min. Upon cessation of the illumination the flow diminishes within 4 min, attaining the starting level in the dark. The experimental time constant (τ) for the rise in current was about 18 s, and for the decrease—about 30 s. This response of the hornet silk cocoon caps is shown in Fig. 2(A) for a temperature of 26°C, and is clearly affected by the ambient temperature. In Fig. 2(B) we demonstrate an analogous dependence of the current on illumination and this at a temperature of 42°C. At specified conditions the time constant for a current increase is 60 s while the decay time constant is about 90 s. At the mentioned temperature, the increase in current following illumination is smaller than at 26°C.

The relative changes in the current as a function of temperature are shown in Fig. 2(C). As can be seen, the maximal increment (about 50%) occurred at about 25°C. The same figure also offers for comparison purposes the dependence of the current on the relative humidity and the temperature. It is noteworthy that in the dark the current on the silk cocoon cap also changed markedly with rise in the relative humidity. A particularly steep increase in the current was recorded at the relative humidity level of about 70%, the temperature kept constant at 32°C. This observation is implicit from Fig. 3(A). The present study assessed also the electric resistance of the silk cocoon as a function of the relative humidity. This correlation is shown in Figs 3(B) and (C), both at a constant temperature of 32°C.

DISCUSSION

Derivation and integration elements

As we have shown in previous studies (Ben-Shalom *et al.*, 1988; Ben-Shalom and Ishay, 1989; Benshalom-Shimony and Ishay, 1990a), hornet cuticle, and apparently also the silk cocoon of the pupa, comprises various substances that are arranged in a variety of morphological structures. It stands to reason that these various substances and structures possess different electrical properties, and in fact in previous studies we have established that the hornet cuticle and silk cocoon contain elements with different electric properties (Benshalom-Shimony and Ishay, 1990b; Ishay *et al.*, 1990). The described electrical properties were both the linear, passive types that occur in all types of material (e.g. capacitance, resistance, etc.) as well as non-linear, active properties (e.g. voltage and current formation, temperature and humidity dependence, preferred directionality of the conductance, etc.). From perusal of photomicrographs it is clear that size of the basic elements that determine the electrical properties is much smaller than that of the examined samples and even smaller than the size of the silver dots that served as contact points in our examinations. In such a situation, we are obviously unable to measure in a clear-cut fashion a single electrical property of a single element, but only the overall effect of all the elements and this would depend on the interconnections between these elements as well as between them and the measuring point. We need to take into account also that the measuring points are coarsely arranged (relative to size of the electric elements themselves) on the hornet cuticle or silk cocoon, and not necessarily at points that have physiological significance for functioning of the hornet. The situation is roughly analogous to measurement of the electric voltage in a domestic network, where one uses an instrument that does not connect to a socket but rather to a random spot on the wall of the room.

Nevertheless, one can create a simplistic model wherein the various elements arrange within an array of a single electrical circuit, just as we have done in our measurements of resistance and capacitance (Ben-Shalom *et al.*, 1988). By using such a model, we were able to explain to some extent the results we obtained but clearly it did not suffice to explain all the observed properties, being rather primitive in comparison to the complexity of the genuine linkages within the hornet cuticle or silk cocoon. As a stop-gap, however, it does come in handy in affording a general understanding and a qualitative picture of the electrical circuit.

As can be seen from our measurements on the effect of illumination both on the voltage as well as on the current as determined by electrodes placed upon the specimen, there are clearly photovoltaic, photoelectric or photoresistor elements in hornet cuticle and in the silk cocoon. At the same time, we note that this effect of illumination is not immediate but rather increases exponentially and decays after a while (also in exponential fashion). These phenomena are apparently influenced by capacitor and resistor elements present in cuticle and cocoon. Earlier (Ben-Shalom and Ishay, 1989) we demonstrated the existence of such elements and even measured their values. To assess how these elements could affect the shape of the measured voltage and current, we propose the existence of several possible ways of interlinking such elements, wherein each pattern of linkage comprises, in fact, a simple electric network which serves as a derivative or integrative circuit upon the voltage (or current) produced in the photoelectric element. If this is so, then the rate of voltage increase and decay is dependent on time constants within the derivative and integrative circuit and on the rates of illumination.

To simplify matters, we presume an electric source which is a photovoltaic cell hooked up to an in-serial resistor. It is clear that according to Thevenin's and Norton's equivalent circuit theorem (Diefenderfer, 1979) such a source can be converted to a current or voltage source (i.e. photoelectric cell) or, alternatively, to a source of fixed voltage or current, hooked up to a photoresistor. Our experiments were in fact undertaken on the voltage or the current and on the resistance (Ishay and Croitoru, 1978; Croitoru et al., 1978). In any event, we found that we could ignore the influence of the measuring instrument because in our voltage measurement, the internal resistance ($10^{12}\,\Omega$) is higher than that of the sample (10^4–$10^7\,\Omega$), whereas in current measurement, the voltage burden on the instrument (<1 mV) is smaller than the voltage measured on the specimens surface (tens to hundreds of millivolts). The basic model constructed by us, including the derivative and integrative circuit(s), is shown in Fig. 4. As can be seen, in this circuit, the source of photovoltaic voltage is hooked up to an internal resistor (R_1), to a capacitor (C_1) which integrates the electric signal, to an additional capacitor (C_2), and finally to an external resistor (R_2) which comprises the resistance between the two points on which measurements are made. In the case of current measurement the resistor is the one between the capacitance element and the measured

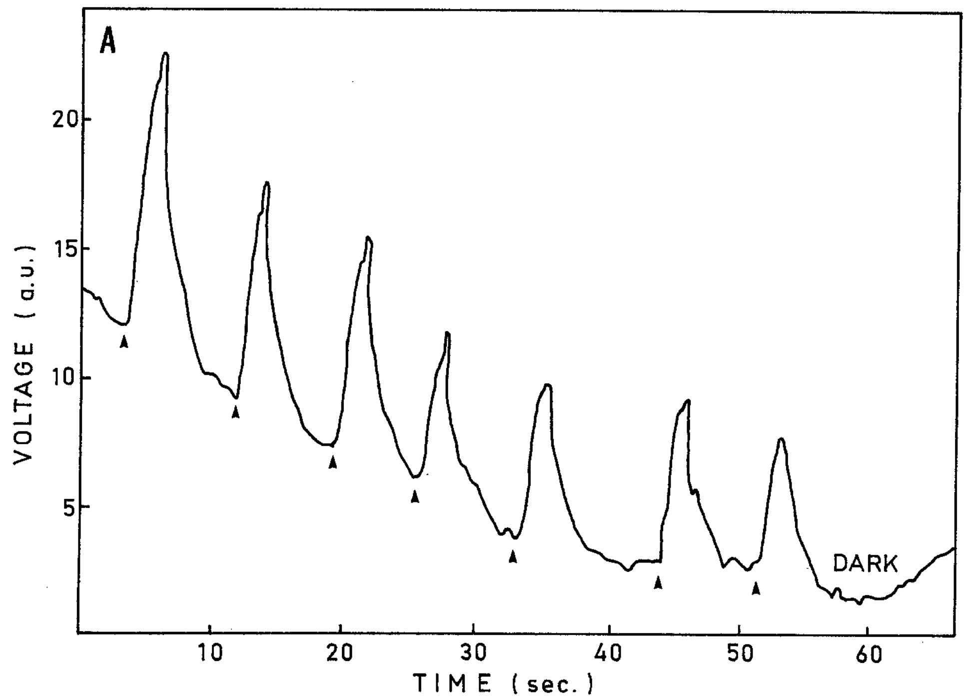


Fig. 1(A)

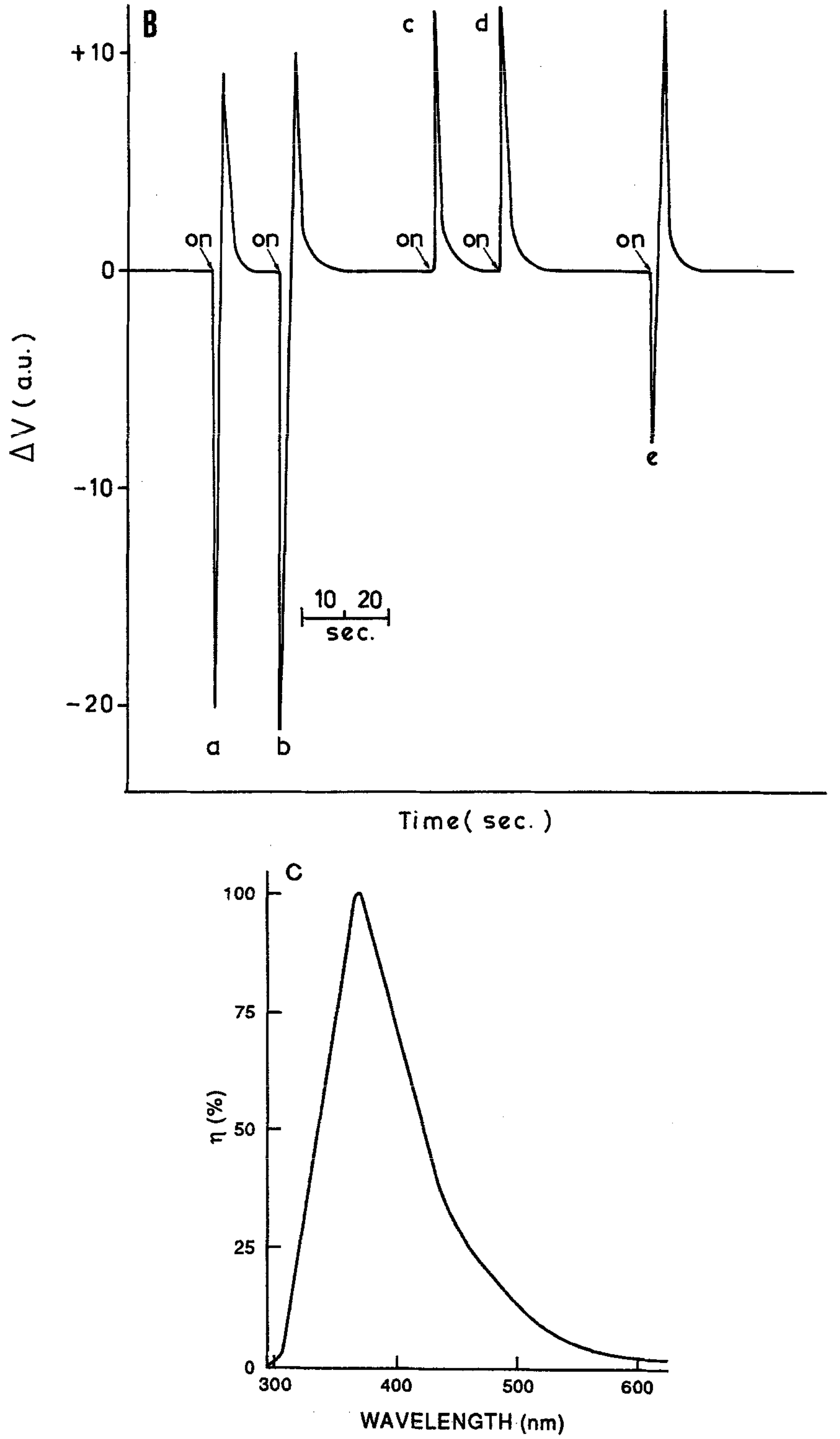
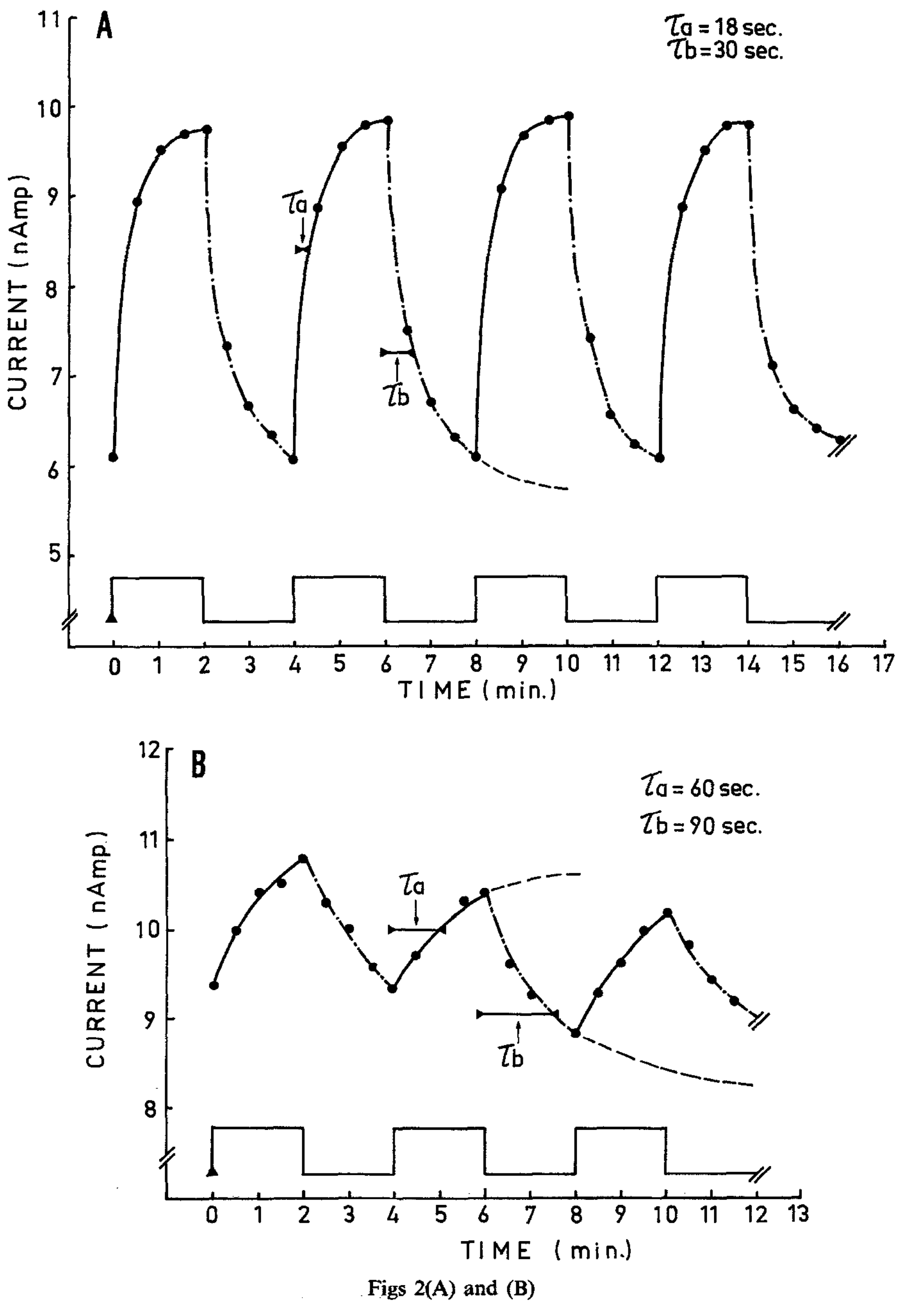


Fig. 1. Photovoltaic effect of hornet cuticle. (A) The results of exposure of a specimen to light pulses. The electrodes were connected to the strip of brown hornet cuticle. For details see text. a.u., arbitrary units. Arrow head = light on. (B) The direction and intensity of the light-induced voltage on the hornet cuticle. In a and b the light beam was focused on the back electrode (BE); in c and d the beam was focused on the front electrode (FE) and in e the beam was on both electrodes. For details see text. (C) The spectral dependence. The relative quantum efficiency (η) of the light induced voltage in the brown cuticle is given as a function of the wavelength (λ) of the incident light. The obtained result is an average of more than 10 various samples.

point while the measured current is that current which flows through said resistor as a result of the voltage gradient upon it.

We carried out a number of simulations wherein we altered the voltage source in the circuit in similar fashion to the way we changed the source of illumination in the experiment (i.e. on–off illumination at a given rhythm) and we found that the electric voltage obtained on the external resistor (R_2) appears, from a quantitative standpoint just the same as in the experiment [see Fig. 5 as compared to Fig. 2(A)]. The values which we used for R_1, C_1, R_2, C_2 were those typical for hornet cuticle or a silk cocoon. It was clear to us that R_1 needed to be much smaller than R_2 in value because it is also physically smaller besides being closer to the voltage source (the photovoltaic element).

It needs re-emphasizing that the preferred modes of linkage are simplified and "degenerate" models of the true electric circuit inherent in cuticle or silk cocoon, wherein the number of elements is considerably larger (being in the order of the ratio between size of the element—tens to hundreds of microns—and the size of the measured specimen—several millimeters). In the genuine circuit, the effects of the derivative and integration elements may be consider-



Figs 2(A) and (B)

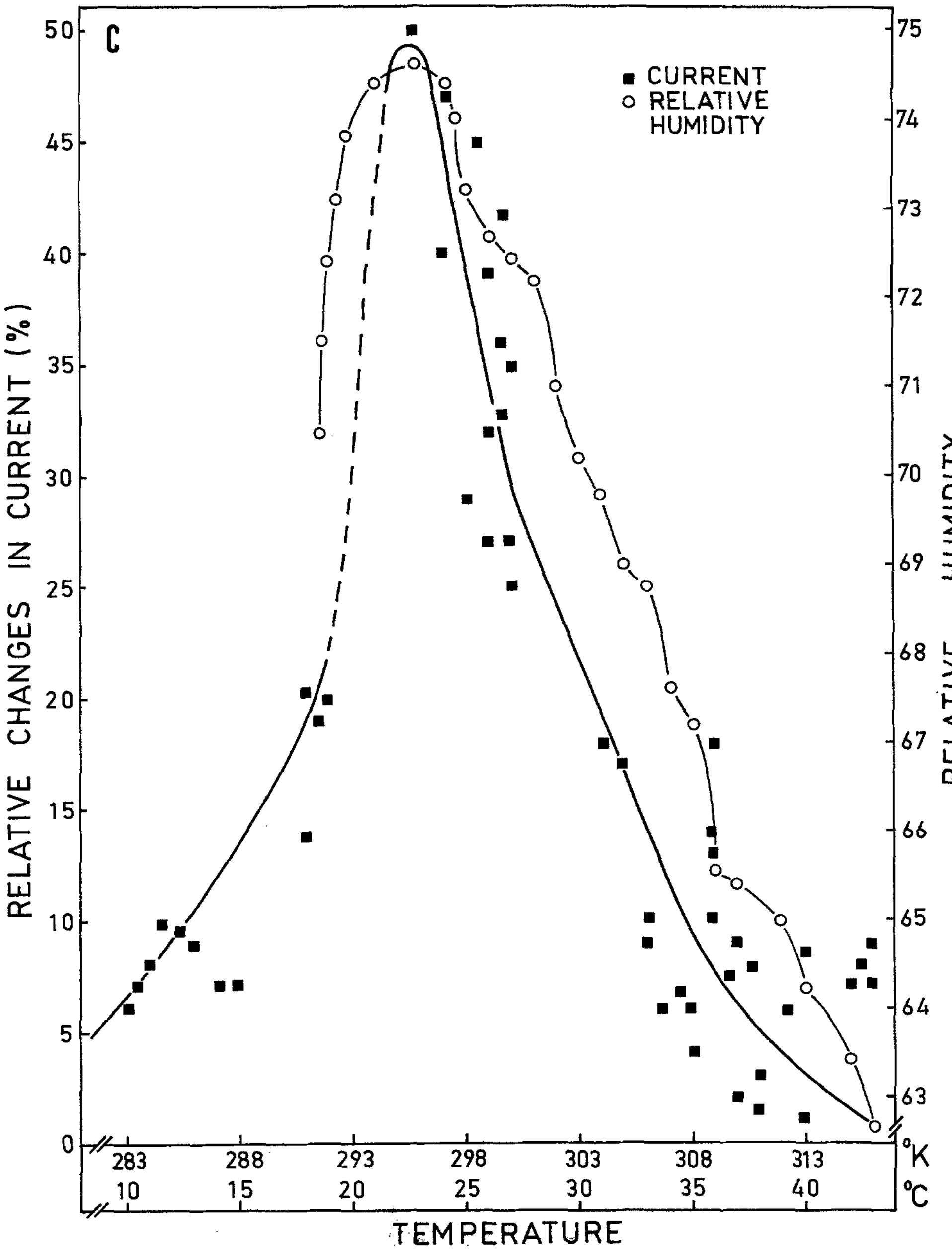
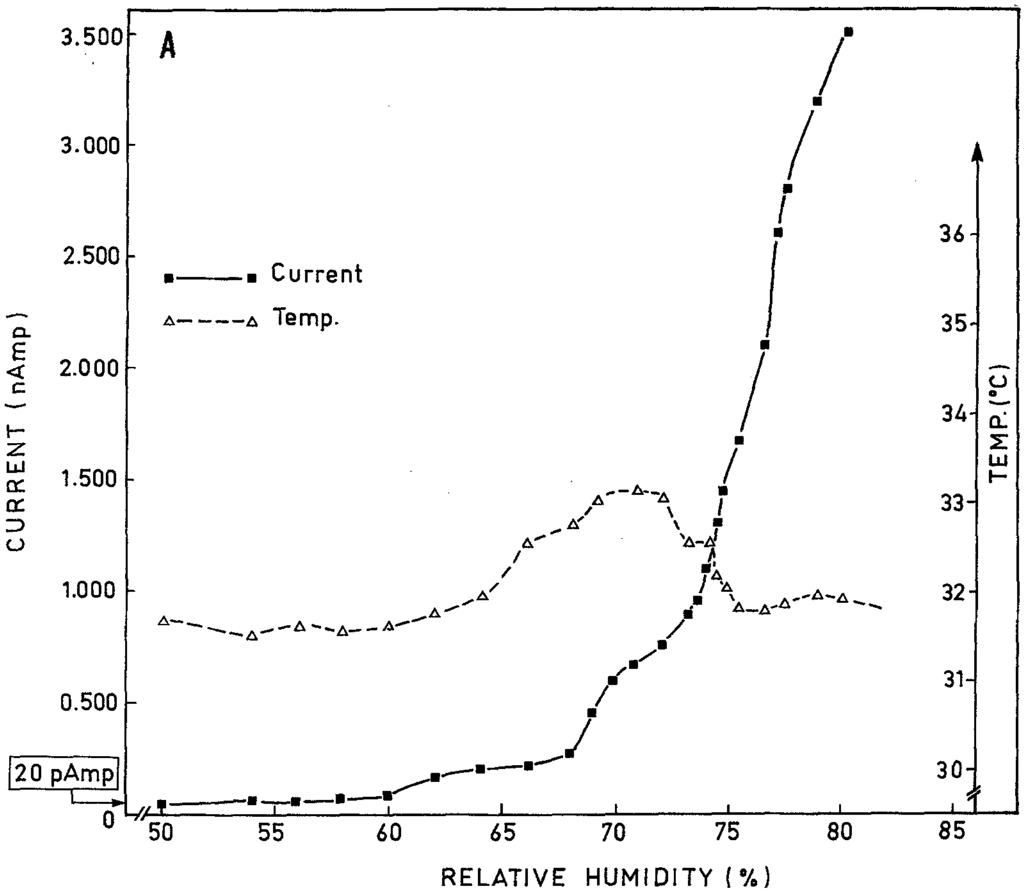


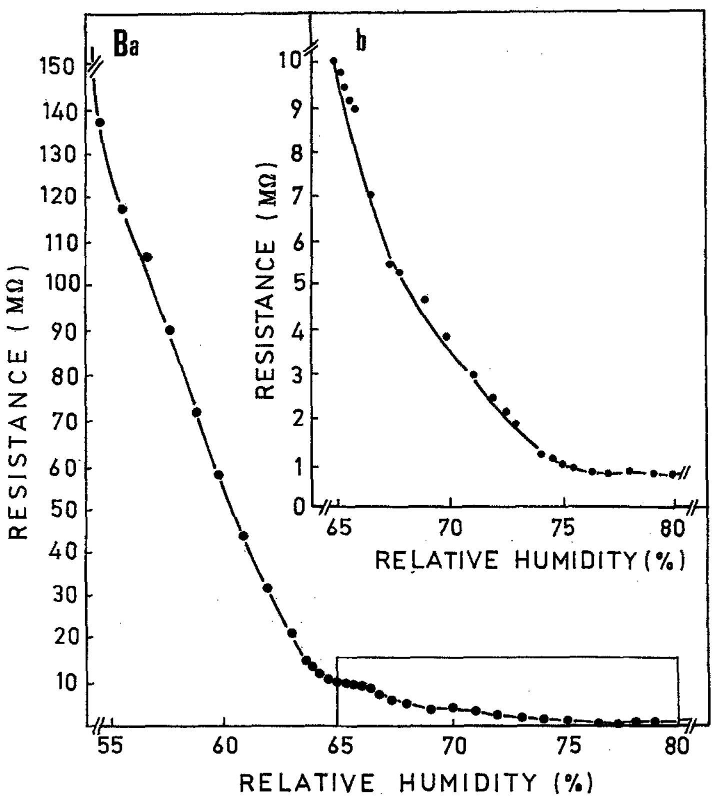
Fig. 2. Dark current and photoelectric effect of hornet cocoon silk. (A) The results of exposure of the silk cocoon cap to intermittent light of 365 nm and intensity of 100 $\mu W/cm^2$. The light pulses induce a current flow between the electrodes of up to several nAmperes. The time constant (τ) for the rise in current (τa) was about 18 s, while that for current decay (τb) was about 30 s. The sample was measured at 26°C. (B) Same measurement as in (A) but at 42°C. The solid line represents the actual measured results; the broken line is an extrapolation of the measured line to the point where it may reach saturation or complete decay. (C) The relative changes in current as a function of temperature and humidity. As can be seen the maximal increment occurred at about 25°C and 75% r.h. For details see text, the solid lines represent the range of obtained results, the broken line is an interpolation.

ably more complex than the simplified model which we constructed.

Influence of humidity

As we have seen, humidity exerts a very strong effect on the resistance of the silk cocoon. We should note that this property is typical for a large number of organic materials and is being utilized to manufacture components that serve as sensors in electronic humidometers. The effect of humidity on the resistance of a commercial sensor manufactured by Phys-Chemical Research Corp. is shown in Fig. 6. In this sensor, interestingly, the relative change in the resistance is less than four orders of magnitude in


A
Current
Temp.
CURRENT (nAmp)
3.500
3.000
2.500
2.000
1.500
1.000
0.500
20 pAmp
0
TEMP.(°C)
36
35
34
33
32
31
30
50
55
60
65
70
75
80
85
RELATIVE HUMIDITY (%)


Ba
b
RESISTANCE (MΩ)
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
55
60
65
70
75
80
RELATIVE HUMIDITY (%)
RESISTANCE (MΩ)
10
9
8
7
6
5
4
3
2
1
0
65
70
75
80
RELATIVE HUMIDITY(%)

Figs 3(A) and (B)

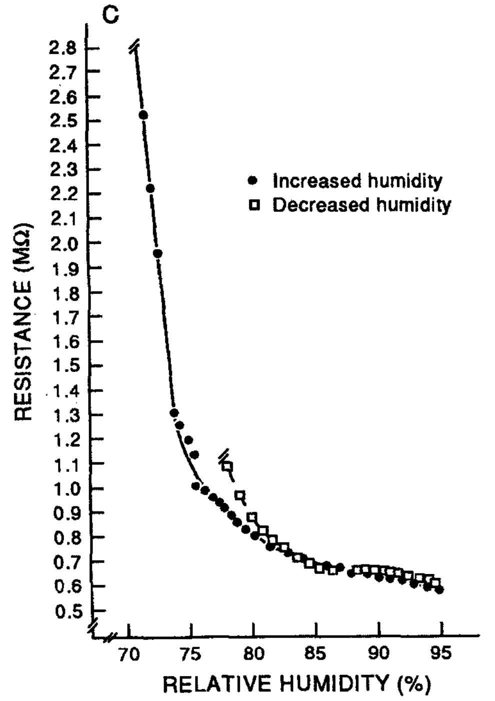


Fig. 3. (A) The (dark) changes in current as a function of changes in relative humidity. Increase in current is induced by increase in relative humidity. The steepest increase was found at and around 75% r.h. (B) The changes in electrical resistivity as a function of changes in relative humidity. a, the relative humidity range was between 55–80%; b, enlargement of the range between 65–80% r.h. All measurements were performed in a dark chamber. (C) Same as (B) but relative humidity was between 70–95%. As can be seen the effect is reversible—the resistance decreasing with increase in relative humidity and increasing with decreased humidity.

the range between 5–100% r.h., whereas in the silk cocoon the relative change is very much higher [see Fig. 3(b) curves a and b for comparison]. Even in a narrower range of humidity changes we see that while the commercial component changes its resistance by about a half order of magnitude per each 10% change in the relative humidity, in the silk cocoon the change in resistance is by more than one order of magnitude. In fact within the range of biological activity, that is at about 65%, the change amounts even to one and

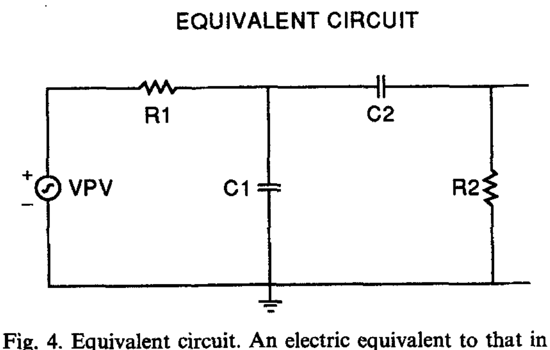


Fig. 4. Equivalent circuit. An electric equivalent to that in hornet cuticle and in the silk cocoon, where R_1 and C_1 are respectively the resistors and capacitors of the integration and R_2 and C_2 are the resistors and capacitors of the derivation and VPV is the photovoltaic source. $R_1 = 10^6\,\Omega$, $C_1 = 10^{-4}$ F, $R_2 = 10^8\,\Omega$, $C_2 = 10^{-4}$ F.

a half orders of magnitude. This finding points to the high sensitivity of hornet silk cocoon to humidity and to a possible inherent commercial/industrial potential.

Our present results on hornet cuticle show that the intensity of the light-induced voltage and its polarity depend on where on the cuticle the illumination occurs [see Figs 1(A) and (B)]. In Fig. 1(A) a monotonic decrease in the level of the "dark" voltage occurs after repeated exposure to light pulses. This is probably due to a reversed voltage caused by a secondary overlapping effect. This secondary effect starts already during the illumination period and develops at a slower rate than does the primary light-induced effect. The opposite voltage, stemming from the secondary effect, after the light is switched off, but decays slowly after a few seconds to the original "dark level" [Fig. 1(B) curves a, b and e]. This brief period of a few seconds is apparently needed to re-attain a thermal equilibrium. Exposure to light pulses of the same intensity but of a larger duration caused a notable reversal effect already during the illumination phase, following which a stronger and opposite "dark" voltage and a much longer time were required in order to reach the original "dark" level. In contrast to the primary

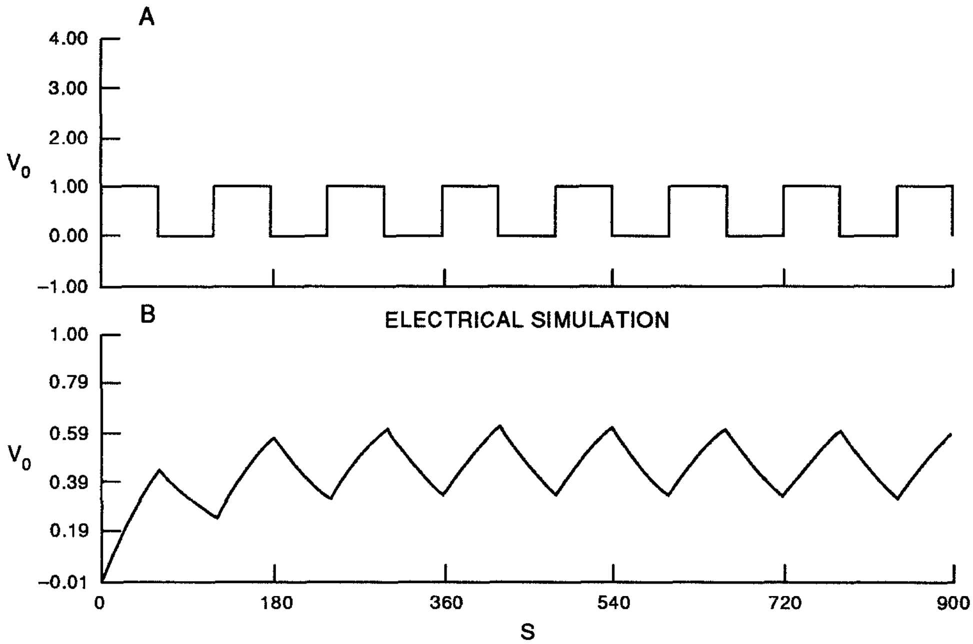


Fig. 5. Electric simulation. Simulation of the measured voltage in the electric circuit shown in Fig. 4. (A) The voltage produced from the photovoltaic cell as a function of time. (B) The voltage measured on the resistor R_2 (of Fig. 4) as a function of time. V_0, voltage in arbitrary units; S, time in s.

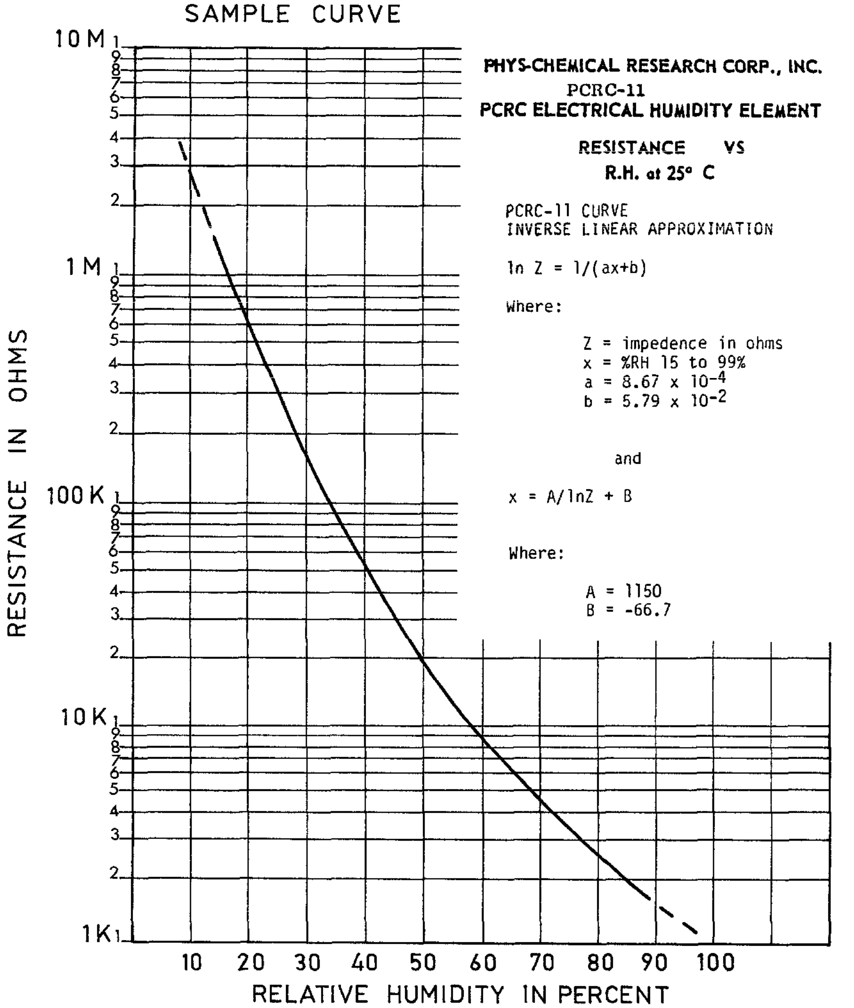


Fig. 6. Commercial humidity element sensor data. Resistance vs relative humidity (cf. Figs 3(A–C) and also see text).

effect, the secondary effect induces a polarity of voltage which apparently is independent of which of the two electrodes is illuminated, and can also occur by illuminating the front electrode [Fig. 1(B) curves c and d]. In the latter instance, however, the effect may be indistinguishable from the overlapping primary light-induced effect, because then both voltages are in the same direction. In this case also after switching off the light, a low decay of the voltage to the original "dark" level is observed.

The secondary effect may possibly be due to the heating of the area by the absorbed radiation. This conclusion is supported by our finding that the secondary effect was more pronounced when the light of longer wavelength was used for the illumination and was markedly abrogated by using a heat-absorbing filter (corning 1-75), which transmits visible and near ultraviolet light down to about 350 nm, but absorbs the infrared part of the radiation.

The primary light-induced voltage observed in the cuticle is due to a photovoltaic effect. This is consistent with previous findings that the cuticle of the hornet behaves like an organic semiconductor and on the area measured acts as a diode (Ben-shalom and Ishay, 1989). This explains the observed marked difference between the voltage induced by the illumination of the back electrode and that induced by front electrode. The total effect thus appears to be a combination of a photovoltaic effect and a heating effect, both caused by the same absorbed radiation.

The above two effects differed not only in terms of direction but also in their dependence on the wavelengths of the illumination. Thus, while the aforementioned warming effect was induced primarily by long wavelengths, i.e. ones in the region of red and infrared the most productive irradiation for the photovoltaic effect was in the range of ultraviolet light, i.e. at about 370 nm.

It is noteworthy that in previous investigations we found this spectral range to be influential also in inducing luminescence (Ishay *et al.*, 1987, 1988b) and photoconductivity (Croitoru *et al.*, 1978) in the cuticle. We note further that Rosenberg (1962) also found this spectral range to be the most efficient in β-carotene in a state of isomerized glass, and this both for a photovoltaic effect as well as for photoconductivity. Interestingly, in another organic material, namely anthracene, the photovoltaic effect is maximal also in a similar spectral range of 360–390 nm (Gutmann and Lyons, 1967).

We plan to pursue this line of research further in order to try and ascertain whether indeed optic energy (particularly that in the near ultraviolet range) which converts in part to electric energy, is utilized by the hornet for its biological activities.

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