tegration, F. D. Carlson, Ed. (Prentice-Hall, Englewood Cliffs, N.J., 1968), p. 17. The cell nomenclature by the above authors has been used throughout this paper. The modifications used here are an extension of the nomenclature, for example, LC1 and LD1 cells.

3. I. Kupfermann and E. R. Kandel, *Fed. Proc.* **27**, 277 (1968).
4. B. Peretz and F. Strumwasser, *ibid.* **28**, 333 (1969).
5. B. Peretz, *Amer. Zool.* **8**, 779 (1968). The genital nerve has been renamed the ctenidio-genital nerve because the largest branch of this nerve, the ctenidial nerve, posterior to the genital ganglion innervates the gill. The other branch terminates in the gonad. All along its path the ctenidio-genital nerve gives off small branches to the reproductive tract structures. This is the case in *Aplysia californica* and in *A. dactylomela.*
6. During SGM the afferent vessel contracts, moving the entire gill toward the dorsal surface of the body wall (Fig. 1A). Two rows of pinnules, fingerlike projections, which are sites of gaseous exchange between the blood and sea water, separate. The pinnules bend away from the midline of the gill and expose the efferent vessel which carries the blood toward the auricle of the heart (*7*). As the gill returns to the rest position, the efferent vessel appears to contract. The branchial nerve also innervates the gill (*7*). When it is the only nerve connecting the ganglion to the periphery, it elicits gill movements clearly distinguishable from those described above; the pinnules clump together, similar to a fan being closed. The entire gill then moves rostrad, pivoting about the afferent vessel.
7. N. B. Eales, *Proc. Trans. Liverpool Biol. Soc.* **35**, 183 (1921).
8. F. Strumwasser, in *Circadian Clocks*, J. Aschoff, Ed. (North-Holland, Amsterdam, 1965), p. 442; and in *Invertebrate Nervous Systems*, C. A. G. Wiersma, Ed. (Univ. of Chicago Press, Chicago, 1967), p. 291.
9. Interneuron I, L10 (*1*), was inhibited during SGM; its activity did not contribute to the movements. This cell does not have a process in the ctenidio-genital nerve but does have one in the pericardial nerve (*13*).
10. G. Bittner, *J. Gen. Physiol.* **51**, 731 (1968).
11. Neuron R15, presumed to be neurosecretory (*2*) and having no observable effects on the gill, may have long-term influence, for example, metabolic effects on muscle in the gill which could regulate gaseous exchange over circadian intervals. Neuron L11, a nonsecretory cell, could control the activity of cilia in the gill.
12. I. Kupfermann, *Physiol. Behav.* **3**, 179 (1968); F. Strumwasser, in *The Neurosciences, A Study Program*, C. G. Quarton, T. Melnechuk, F. O. Schmitt, Eds. (Rockefeller Univ. Press, New York, 1967), p. 516.
13. Anatomical descriptions of this ganglion have treated the genital and pericardial nerves as separate trunks [see Eales (*7*) and Strumwasser (*8*)]. Frazier *et al.* (*2*) have considered the nerves as a single trunk. These nerves do have overlapping constituents, for example R15. However, there are cells, for example L12 and L13, each of which has a process in only one of the nerves; L12 has one in the genital nerve, and L13 has one in the pericardial nerve. The pericardial nerve, when stimulated, did not elicit gill movements.
14. M. Jouvet, in *The Neurosciences, A Study Program*, G. C. Quarton, T. Melnechuk, F. O. Schmitt, Eds. (Rockefeller Univ. Press, New York, 1967), p. 529; E. V. Evarts, in *ibid.*, p. 545; W. Dement, *Electroencephalogr. Clin. Neurophysiol.* **10**, 291 (1958).
15. E. V. Evarts, *J. Neurophysiol.* **31**, 14 (1968).
16. *Aplysia dactylomela* also shows SGM which appear correlated with activity like that of interneuron II. The movements appear to be the same as those observed in conjunction with gill movements and were like their counterparts in *A. californica.*
17. I. Kupfermann and E. R. Kandell, *Science* **164**, 847 (1969).
18. I thank F. Strumwasser for encouragement, support, and comments. I also thank J. J. Gilliam for technical assistance. Supported in part by PHS special fellowship 7 FO3 GM-32, 521-03, grant NB 07071, and NASA grant NGR 05-002-031.

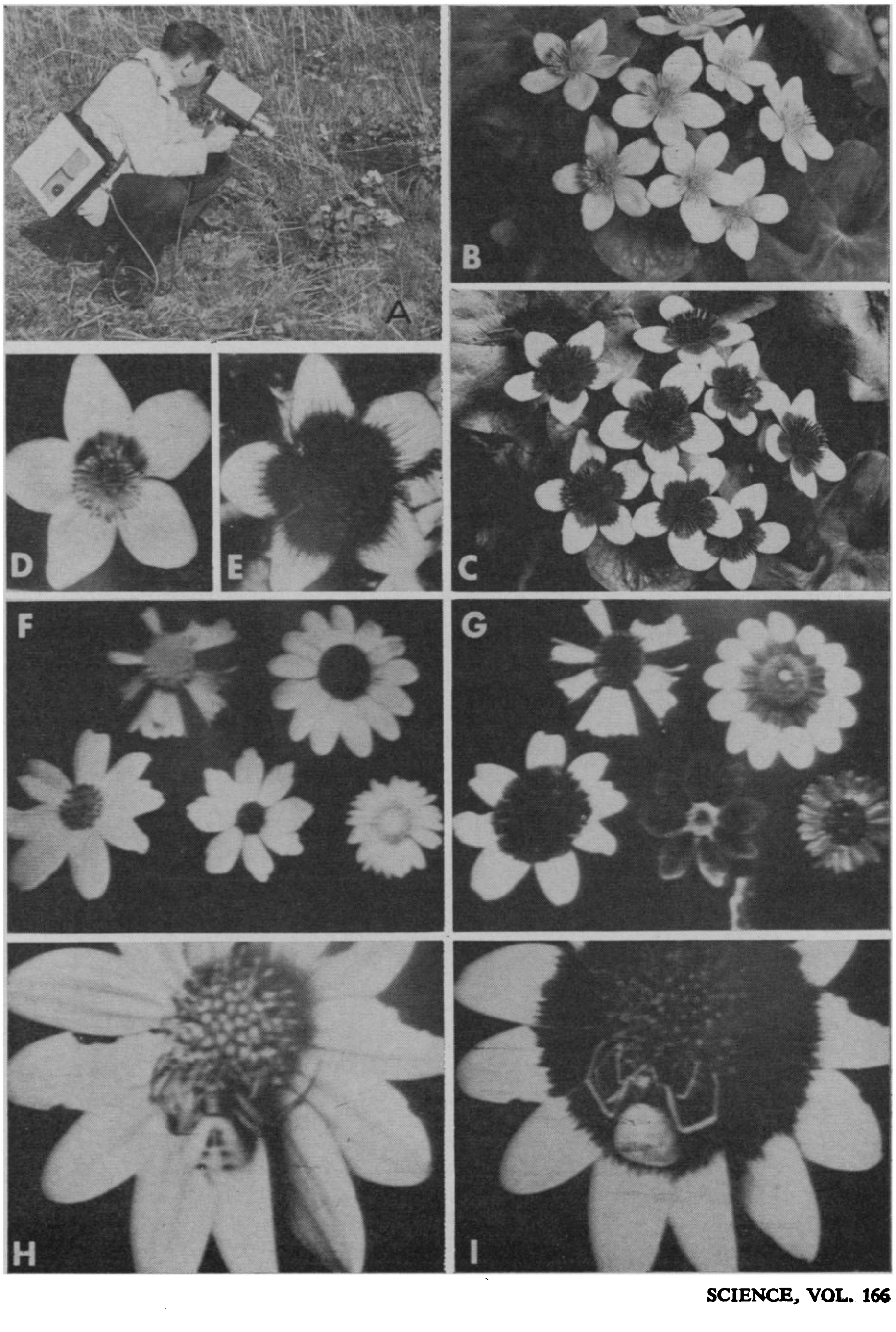
* Present address: Department of Physiology and Biophysics, University of Kentucky Medical School, Lexington 40506.

14 April 1969; revised 11 August 1969

Ultraviolet Video-Viewing: The Television Camera as an Insect Eye

Abstract. *A television camera, like the eyes of some insects, is sensitive to ultraviolet light. When equipped with an appropriate ultraviolet-transmitting lens, such a camera can be used for the direct examination of ultraviolet reflection patterns (for example, on flowers, butterflies) that are invisible to us, but visible to insects.*

Honeybees and certain other insects, unlike man and possibly all vertebrates, are visually sensitive and behaviorally responsive to ultraviolet light (*1*). Objects such as flowers may possess ultraviolet reflection patterns, invisible to us, but visible and significant to pollinating insects (*2*). The demonstration of such "hidden" ultraviolet patterns, whether on flowers or sometimes, as in the case of butterflies (*3*), on the insects themselves, has hitherto relied on the use of special photographic techniques, all somewhat elaborate, and unsuited for direct examination of subjects in motion (*2–5*). An ordinary television camera, by virtue of its intrinsic sensitivity to ultraviolet light (*6*), providing only that it is equipped with an ultraviolet-transmitting lens, can serve as an appropriate "eye" by which the ultraviolet patterns of nature may be directly observed. Portable video units are particularly suitable since both video camera and tape recorder can be carried by one individual in the field (Fig. 1A). We have used a Sony



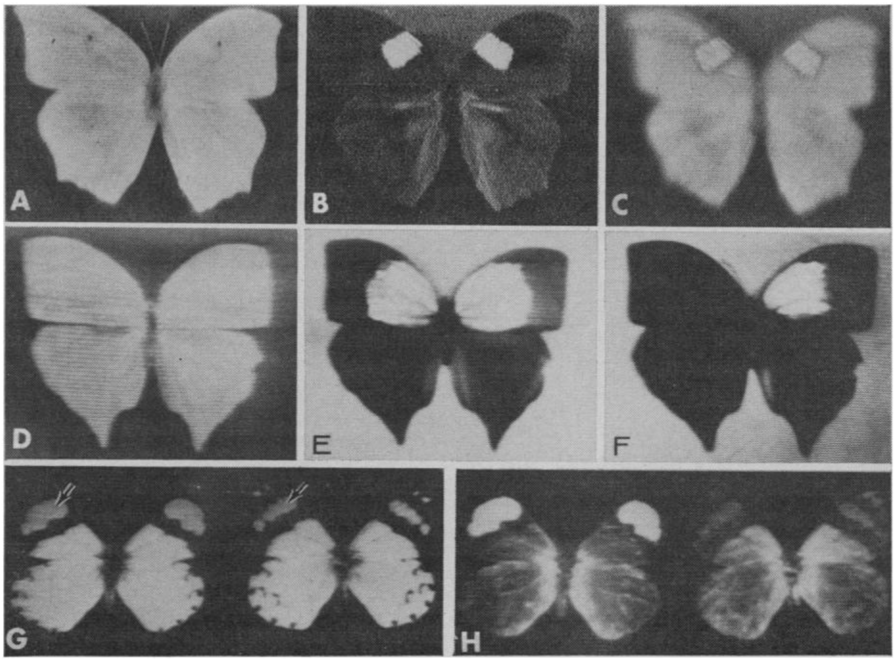


Fig. 2. Ultraviolet reflection patterns in butterflies (neotropical Pieridae). A–C, *Anteos clorinde* (male), seen in visible light (A) and in the ultraviolet (B). If an ultraviolet-transmitting lens that is not color-corrected for ultraviolet is used, the visible and ultraviolet images are separately discernable even in a composite view, since they do not focus on the same plane; in C, for example, the focus is on the ultraviolet patches, which are sharply highlighted against the unfocused visible part of the image. D–E, *Phoebis rurina* (male), a yellow butterfly (D), is brilliantly ultraviolet reflectant at the bases of the forewings (E); the reflectance is a directional iridescence (oblique illumination from one side causes only the patch of the opposite side to "light up," as in F). G–H, *Eroessa chilensis*, a black and white butterfly with orange wingtips (G, arrows) is sexually dimorphic in that it reflects ultraviolet from the orange markings of the male only (H). All pictures are video images.

VCK 2400, outfitted with a Zeiss-Jena *f*/4, 60-mm ultraviolet lens, which transmits well in the near ultraviolet (330 to 400 nm), to which insects are sensitive. The camera is simply aimed at a particular object, the lens is capped with an ultraviolet-transmitting filter (for example, Zeiss UG 2; Corning C.S. 7-39), and the ultraviolet image of the object appears as a visible picture on the monitor screen of the camera. Sunlight provides proper lighting for outdoor viewing while a "blacklight" (for example, Fluorescent General Electric BLE 1800B) may be used in the absence of sunlight indoors. Quantification of reflectance characteristics is accomplished, as in photography (*2*, *5*), by viewing the object in comparison with a precalibrated ultraviolet-reflecting gray scale. Observations can be recorded on video tape, and replayed for examination on conventional monitors. We have used the technique in the study of various problems involving flower ecology and ontogeny, and insect mimicry, camouflage, phylogeny, and behavior. Isolated observations, in part corroborative of earlier photographic findings of others (*2*–*5*), are noted here.

To the uninitiated, the first ultraviolet view of a meadow in mixed bloom is unforgettable. Evenly tinted flowers, which to the naked eye appear to lack the usual central or radial color markings that direct an alighted pollinator to its goal (nectar guides) (*2*), are suddenly revealed to possess such markings in the ultraviolet (Fig. 1, B–E). Other flowers, visibly patterned, are additionally adorned in the ultraviolet. Flowers that appear similar to us, such as many composites, and that grow intermingled and in seeming competition with one another, may in the ultraviolet be grossly dissimilar, and to insects, presumably, distinguishable (Fig. 1, F–G). Mature flowers may differ in the ultraviolet (as they often do in the visible) from their own buds, indicating that even in the same plant competitive interference may be prevented, in part at least, by a disparity in image. Flowers that are pollinated by birds (we have examined many species of Gesneriaceae) or by bats (*Hylocereus* sp.), as anticipated, lack ultraviolet nectar guides or other special ultraviolet markings. Ultraviolet patterns are often preserved in pressed flowers, and video-viewing is therefore applicable to the study of herbarium specimens.

Fig. 1 (opposite page). A, Ultraviolet video-viewing of marsh marigolds *Caltha palustris* in the field. Video-camera and video-tape recorder (Sony VCK 2400) are battery-operated and portable. B–E, Marsh marigolds, as seen by man, are uniformly yellow (B, D); in the ultraviolet (C, E) they are shown to have darkly absorbent centers. F–G, Sympatric, yellow-petaled Compositae from Florida (clockwise from upper left: *Helenium tenuifolium*, *Rudbeckia* sp., *Heterotheca subaxillaris*, *Coreopsis leavenworthii*, *Bidens mitis*) as seen in visible light (F) and in the ultraviolet (G). H–I, Yellow crab spider *Misumenoides formosipes* on yellow flower *Viguiera dentata*, in visible (H) and ultroviolet light (I). Panels D to I are actual video-images as they appear on a monitor screen. Direct ultraviolet photography yields a sharper image (C), but the technique is much more laborious.

Animals that appear well camouflaged in the visible spectrum need not be similarly camouflaged in the ultraviolet. Crab spiders, whose visible color characteristically matches that of the floral heads upon which they stalk their insect prey, are sometimes sharply conspicuous against their background when viewed in the ultraviolet (Fig. 1, H–I). They are evidently well concealed from the ultraviolet-insensitive eyes of predaceous birds or lizards, but potentially detectable by approaching insect prey. Whether this potential detectability operates to the detriment of the spider's feeding efficiency is not known. It is clear, however, that crab spiders are not simply "aggressively mimetic" in the sense that they seek concealment solely from intended prey.

Striking ultraviolet patterns also occur in butterflies, notably in the family Pieridae (Fig. 2, A–C), where sexual dimorphism is sometimes only barely apparent to us, but pronounced in the ultraviolet (*3*). The reflectant markings characteristically found on the males of these insects are due to interference color (*7*), and they often appear as directionally iridescent patches (Fig. 2, D–F), comparable, for example, to the shiny blues of the tropical *Morpho* butterflies, but purely ultraviolet. We have observed male pierids in the field (*Phoebis argante* in Panama; *Eurema lisa* and *Colias eurytheme* in Florida) and have seen the brilliant ultraviolet flicker that they emit in flight. Since flickering stimuli are important in butterfly behavior (*8*), and since pierids have color vision (*9*) and are electrophysiologically (*10*) and behaviorally (*5*) sensitive to ultraviolet light, their ultraviolet reflectant patches undoubtedly play a communicative role. In one species, which is similarly marked with orange in both sexes, a pronounced sexual dimorphism becomes apparent when the same markings are viewed in ultraviolet (Fig. 2, G–H). One is tempted to conclude that the orange is an aposematic display aimed by both sexes at enemy birds, while the ultraviolet disparity provides the basis whereby the insect communicates sexually within its "private" visual domain.

Ultraviolet video-viewing is an exciting teaching aid. Any closed circuit television can be adapted for this technique by merely outfitting it with a proper lens and filter.

T. EISNER, R. E. SILBERGLIED*
D. ANESHANSLEY, J. E. CARREL
H. C. HOWLAND
Section of Neurobiology and Behavior,
Division of Biological Sciences,
Cornell University,
Ithaca, New York 14850

References and Notes

1. K. von Frisch, *The Dance Language and Orientation of Bees* (Harvard Univ. Press, Cambridge, Mass., 1967), and references therein.
2. K. Daumer, *Z. Vergl. Physiol.* **41**, 49 (1958).
3. G. A. Mazokhin-Porshnyakov, *Insect Vision* (Plenum Press, New York, 1969), and references therein.
4. F. E. Lutz, *Ann. N.Y. Acad. Sci.* **24**, 181 (1924).
5. J. Crane, *Zoologica* **39**, 85 (1954).
6. *Reference Data for Radio Engineers* (International Telephone and Telegraph Corporation, New York, ed. 4, 1956), p. 423.
7. R. E. Silberglied, thesis, Cornell Univ. (1969).
8. D. B. E. Magnus, *Proc. Int. Congr. Entomol. 10th* **2**, 405 (1958).
9. D. Ilse, *Z. Vergl. Physiol.* **8**, 658 (1928).
10. C. T. Post and T. H. Goldsmith, *Ann. Entomol. Soc. Amer.*, in press.
11. Supported in part by the Bache Fund of the National Academy of Sciences and by Cornell University. We thank the directors and staff of the Archbold Biological Station, Lake Placid, Florida; the Smithsonian Tropical Research Laboratory, Barro Colorado Island, Canal Zone; and the Rocky Mountain Biological Station, Crested Butte, Colorado, for help and hospitality. The Gesneriaceae were supplied by H. Wiehler; the flowers were identified by W. J. Dress and P. A. Hyypio, and the spider by C. D. Dondale.

* Present address: Biological Laboratories, Harvard University, Cambridge, Mass.

26 September 1969

■

Ponzo Perspective Illusion as a Manifestation of Space Perception

Abstract. *The Ponzo perspective illusion, a special case of space perception, is influenced by contextual factors, texture, stereopsis, and familiarity in addition to perspective cues. The importance of familiarity is demonstrated by cultural differences obtained with photographs of natural settings which emphasize depth cues.*

It has been suggested that the Ponzo perspective illusion (Fig. 1A) represents the operation of cues which normally subserve the perception of depth in three-dimensional space (*1*). Specifically, converging lines in the retinal image are ordinarily associated with distance and signal the organism to correct for the diminishing retinal image size of distant objects, that is, size constancy. When one views the Ponzo figure, this same cue falsely indicates depth and produces a size illusion. The hypothesis that the basis of this illusion is simply a manifestation of a normal mechanism of size perception has an intuitive and logical appeal. Whereas it would be an oversimplification to equate the illusion with space perception and size constancy, it would also seem unreasonable to limit the generality of this interpretation by concentrating solely on the perspective cue. Space perception and size constancy are complex phenomena involving various monocular and binocular cues as well as cognitive factors. If the Ponzo illusion is a special case of size and depth perception, it should be subserved by a number of the same cues which are common to two- and three-dimensional viewing situations. Further, this communality of function implies that space and size perception and the illusion should be sensitive to the same sort of experimental manipulations. We now present empirical evidence in support of this hypothesis.

Figure 1B illustrates a scene rich in depth cues which also contains the geometric elements that make up the Ponzo illusion (Fig. 1A). In these figures, the two horizontal lines are the same length, but presumably, because of the context in which they are viewed, the observer "corrects" for the assumed distance of the upper line resulting in an overestimation. In the first phase of a three-phase study of factors influencing this phenomenon, 24 subjects (students at the Pennsylvania State University) viewed the actual scene illustrated in Fig. 1B from the point at which the photograph was taken (*2*). In the second phase, 72 different subjects from the same population viewed the four two-dimensional stimuli illustrated in Fig. 1. In the third phase, 20 students native to Guam (University of Guam) were tested with the two-dimensional stimuli. Similar instructions were employed in all phases to obtain comparable judgments throughout the study (*3*).

In all cases the upper board or line was constant in length, while the lengths of the lower boards or lines were presented in random order. For all observation conditions, the equality value was determined by interpolation as the midpoint of the region at which the subject's responses changed. The magnitude of the overestimation or illusion is the percentage overestimation of the upper line or board.

For the actual scene, the length of the upper line was consistently overestimated, that is, matched by the lower line whose value was on the average 45.4 percent greater than would be predicted from the dimensions of the visual angle or retinal image (100 percent overestimation corresponds to size constancy). This value is comparable to data obtained in size-constancy experiments in which instructions, similar to those given in this study, were utilized (*4*). It should be noted also that the overestimation is three or four times greater than is reported for the abstract Ponzo figure which typically ranges from 10 to 15 percent for adult observers.

Reduction of cues by elimination of stereopsis was achieved either by observing the actual scene monocularly with the subject's head held steady, or by viewing the two-dimensional photographs of the same scene. In both cases, the extent of the visible field was equated. Similar results were obtained under both conditions. The overestimation for monocular observation of the actual scene was 34.7 percent, while the value for the photograph was 31.4 percent. Similarly, inversion of the real scene or the photograph further reduced the overestimation. Inversion was accomplished by rotating the photograph and by viewing the real scene monocularly through a Dove prism. The value for the actual scene inverted was 17.7 percent, and for the inverted photograph, 12.6 percent. A repeated-measures analysis of variance indicated that there were significant differences between the binocular upright, monocular upright, and monocular inverted conditions in the natural setting situation ($F = 48.4$, d.f. $= 2$ for 36 subjects, $P < .01$). An independent-measures analysis of variance indicated a significant difference between observations of the upright and inverted photograph ($F = 25.6$, d.f. $= 1$ for 46 sub-