Early experimental psychology.

Vitalism (final causes, infallibile and unexplainable instincts, the animal is driven by purposes that do not require further explanations; subjective aspects; deHaan, McDougall, EC Tolman, ES Russell; 1930-1950)

Mechanicism (heritage of the mechanicistic philosophy; emphasis on the physical causes; rejection of the subjective aspects of behavior).

1900-1930 Loeb (tropisms), Pavlov (conditioned reflexes):
behavior as chain of reflexes,
rejection of instinct.

1910-1970. J.B. Watson, E.L. Thorndike, K.S. Lashley, B.F. Skinner.
Behaviorism (angloamerican):
great emphasis on learning.
only ‘objective’ (measurable) factors are considered:
input-output, Skinner cages, organism as a ‘black box’,

Little consideration for apparently more subjective aspects, such as attention, will, etc.

Behavioral studies in the field and ethology.

Innate behavioral modules: Reaumur (‘700), Spalding (1873), Fabre (circa 1900)

Darwin (1872): phylogenetic analysis of behavior.

Jennings, Whitman, Heinroth (1895-1920).

Innate behavioral modules that characterize certain systematic groups like morphology does.

Ethograms (in the field and in captivity).

W. Craig (1918).

Appetitive behavior (variable)

Consummatory action (more stereotyped).

J. von Uexküll (1920-1940).

Experimentation on the organism-environment relation;
the animal perceives only part of the surrounding environment.

K. Lorenz and N. Tinbergen (1940).

Omology of ethograms; phylogenetic analysis.
Function and selective advantage of a behavior.

Initial interpretation: reflex chains (influence of experimental psychology).
Subsequent interpretation: endogenous modules and instincts (influence of neurophysiology, von Holst).

Imprinting: sensitive developmental stages for learning and stabilization of behavior.

Great development of neurophysiology between the beginning of the XX century and the Seventies.

Behavioral physiology and neuroethology (since the seventies of the XX century).

Sensory reception and elaboration, motivating mechanisms, orientation and navigation.

Control of complex behavioral sequences, neuromuscular systems, etc.

Studies can be at the cell level, but interpreted in the context of the organism's activity.

P. Weiss, R.W. Sperry, E. von Holst, T.H. Bullock, K.D. Roeder, D.H. Hubel, T. Wiesel, J.P. Ewert, Wehner ecc.

Endogenous generators of rhythms and modules.
Endogenous generators of motivation.

Cellular mechanisms of memory and learning, simple nervous networks (e.g. *Aplysia* or leech): E. Kandel and many others.

Supplementary bibliography on orientation and navigation.

Hill et al. *Animal Physiology* (Chapter 18 and references therein). Sinauer, 5th edition 2022.

Manning & Stamp-Dawkins, *An introduction to animal behavior,* 2012 (Italian ed. Boringhieri)

Eibl-Eibesfeldt, *Ethology* (Italian: *I fondamenti dell'etologia*, Boringhieri 1987)

Berthold, *Le migrazioni degli uccelli*. Boringhieri 2003.

Johnsen & Lohmann, The physics and neurobiology of magnetoreception, *Nat Rev Neurosci* 6: 703-712, 2005.

Mouritsen et al. Cryptochromes and neuronal activity markers colocalize in the retina of migratory birds during magnetic orientation. *PNAS* 101: 14294-14299, 2004.

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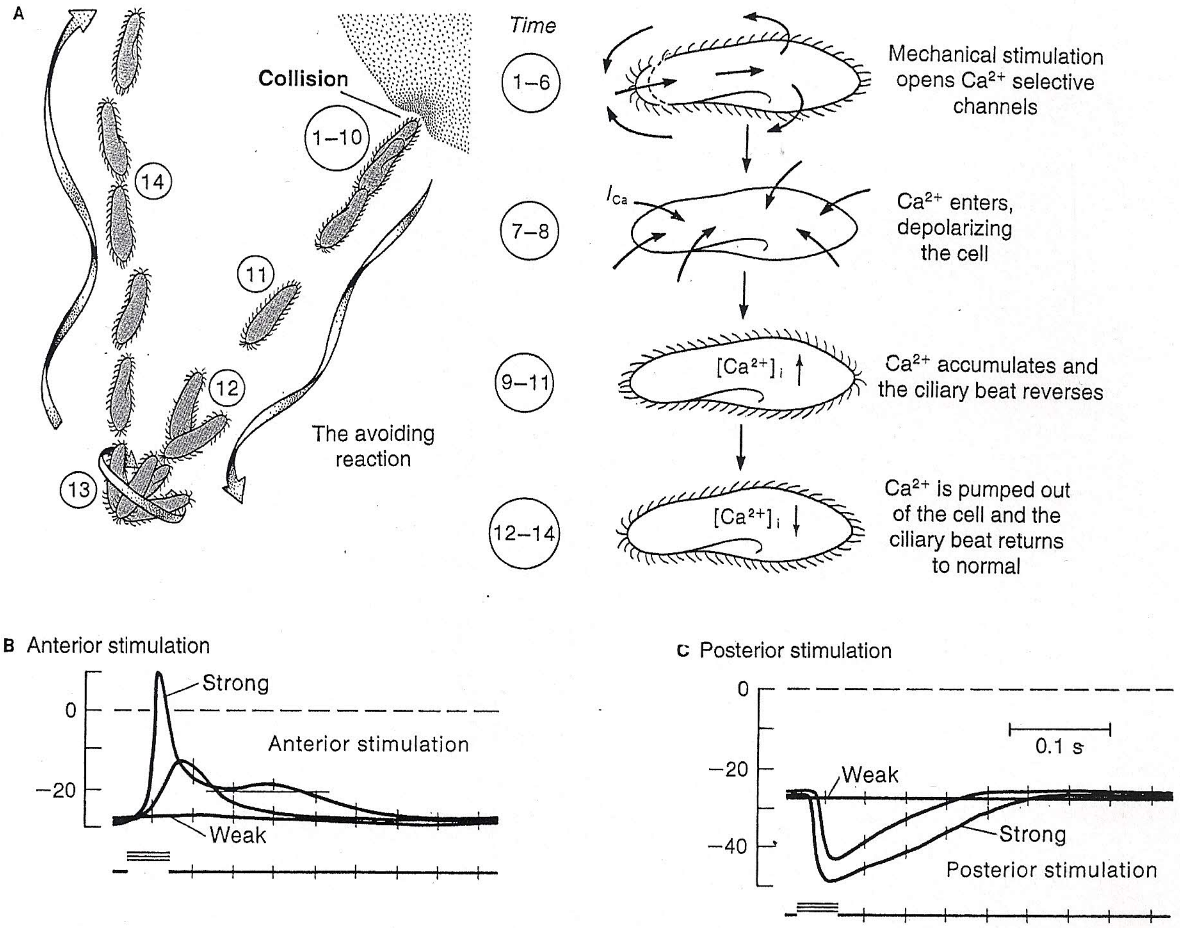


A *Paramecium* avoids objects with which it has collided by changing its direction and rate of swimming. **(A)** After it collides with an object, a *Paramecium* backs up, changes direction, and swims away in a new direction *(left)*. The passage of time is indicated by sequential numbers. Mechanical stimulation of the anterior end opens Ca^{2+}-selective channels *(right)*, increasing the internal free Ca^{2+} concentration, which in turn reverses the ciliary beat. **(B)** When the Ca^{2+} channels are opened by mechanical stimulation to the anterior end, the membrane depolarizes and produces a graded, but weakly regenerative, change in the membrane potential that is associated with reversal of the ciliary beat. **(C)** Mechanical stimulation of the posterior end opens K^+-selective channels, producing a graded hyperpolarization of the membrane that accelerates the ciliary beat by an unknown mechanism. [Part A adapted from Grell, 1973; parts B and C adapted from Eckert, 1972.]

NOTICE: V_{REST}

time scale

Orientation.

Ensemble of processes that organize behavior on the basis of environmental space features.

Functions:
- keeping preferred positions.
- orientation towards close (e.g., prey) or far (navigation) targets.
- stabilizing a body posture.

Non oriented movements (kinesis): e.g., fast in unfavorable environments
slow in favorable environments

Oriented movements (much more effective; -taxis or tropism)

E.g. *Dafnia*. In hypoxic water swims close to surface.
CO_2: triggering stimulus.
Light: orienting stimulus.

Nomenclature related to the stimulus nature: phototaxis, geotaxis, chemotaxis, galvanotaxis..

Nomenclatura related to other factors: phobotaxis, telotaxis….

Often **multiple mechanisms**.

E.g. butterfly (*Eumenis*). Phobotaxis towards the sun (eyesight-dependent).
The movement towards conspecific individuals does not depnd on eysight.

There is no rigid relation between stimulus and response.

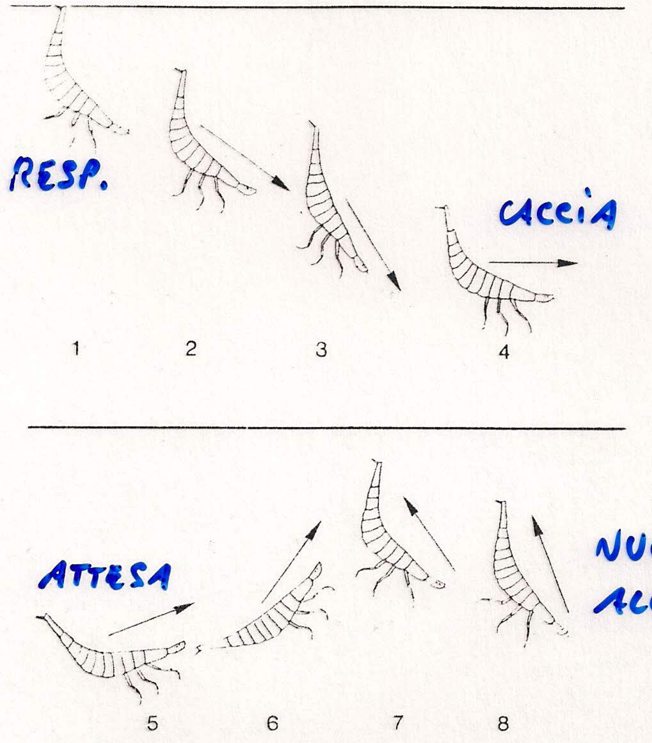
An animal's reaction depends on its physiological state and motivation (von Holst).

E.g. Fishes. Position in water depends on the balance between light and gravity (they have about equal influence).

(experimental manipulations: light direction and intensity, action on statolites, e.g. with a centrifuge, etc.)

In hungry animals, light prevails.

FLESSIBILITÀ (ENTRO CERTI LIMITI)



OCELLI → LUCE
STATOLITI
MOTIVAZIONE

Fig. 16.2. Otto posizioni caratteristiche nel comportamento della larva di *Acilius*, quando è illuminata dall'alto. Da H. Schöne (1962).

DITISCIDE

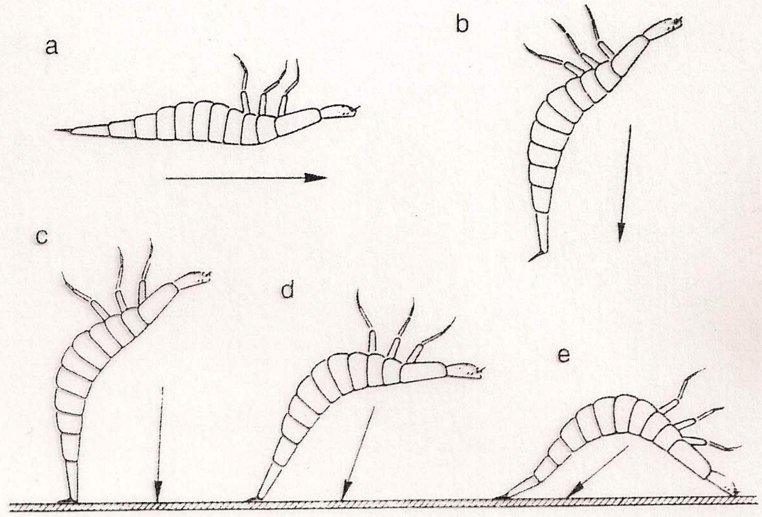


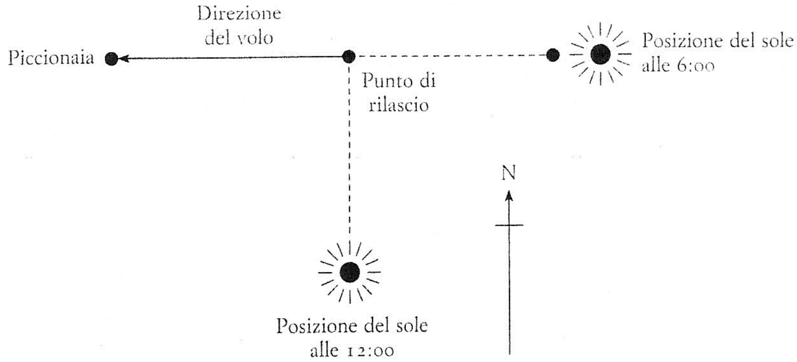
Fig. 16.1. Se illuminate dal basso, le larve di *Acilius* nuotano a dorso in giù. Nuoto orizzontale e tentativo di rifornirsi d'aria sul fondo. Da H. Schöne (1951).

Navigation strategies.

Possible mechanisms	Type of information
Orientation with a compass	Sun (internal clock necessary; possibly polarized light sometimes moon, at night); position of the stars; Earth's magnetic field. Many animal groups.
Following a trail or a learned route	Continuous environmental cues (e.g. smell) and landmarks.
Piloting	Discontinuous landmarks.
Trajectory integration (dead reckoning)	Integration of informations on direction and distance (compass needed) Estimation of distances necessary (e.g., optical flow, bees) Artropods, e.g., desert ants; also birds and mammals.

Often multiple mechanisms.

E.g. map + compass	Compass + landmarks or gradients (T, smell, etc.) Salmon: sun + water stream + smell of native river.



(*b*) Uccelli sperimentali con l'orologio interno spostato indietro di 6 ore

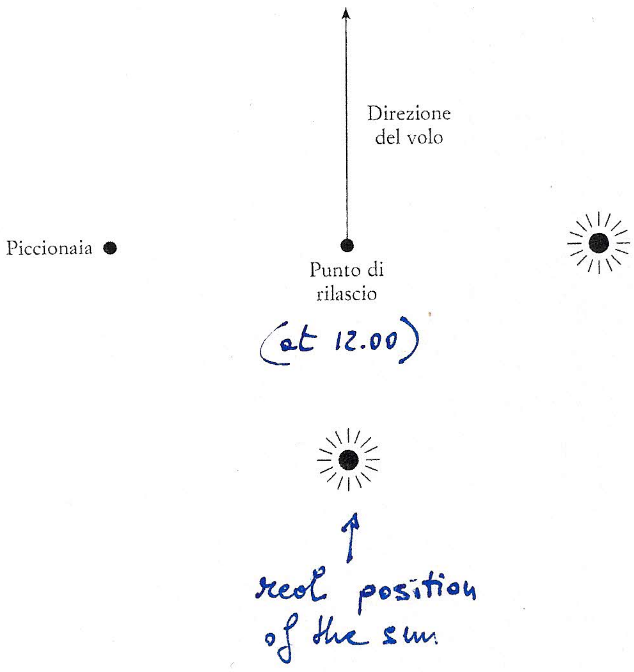
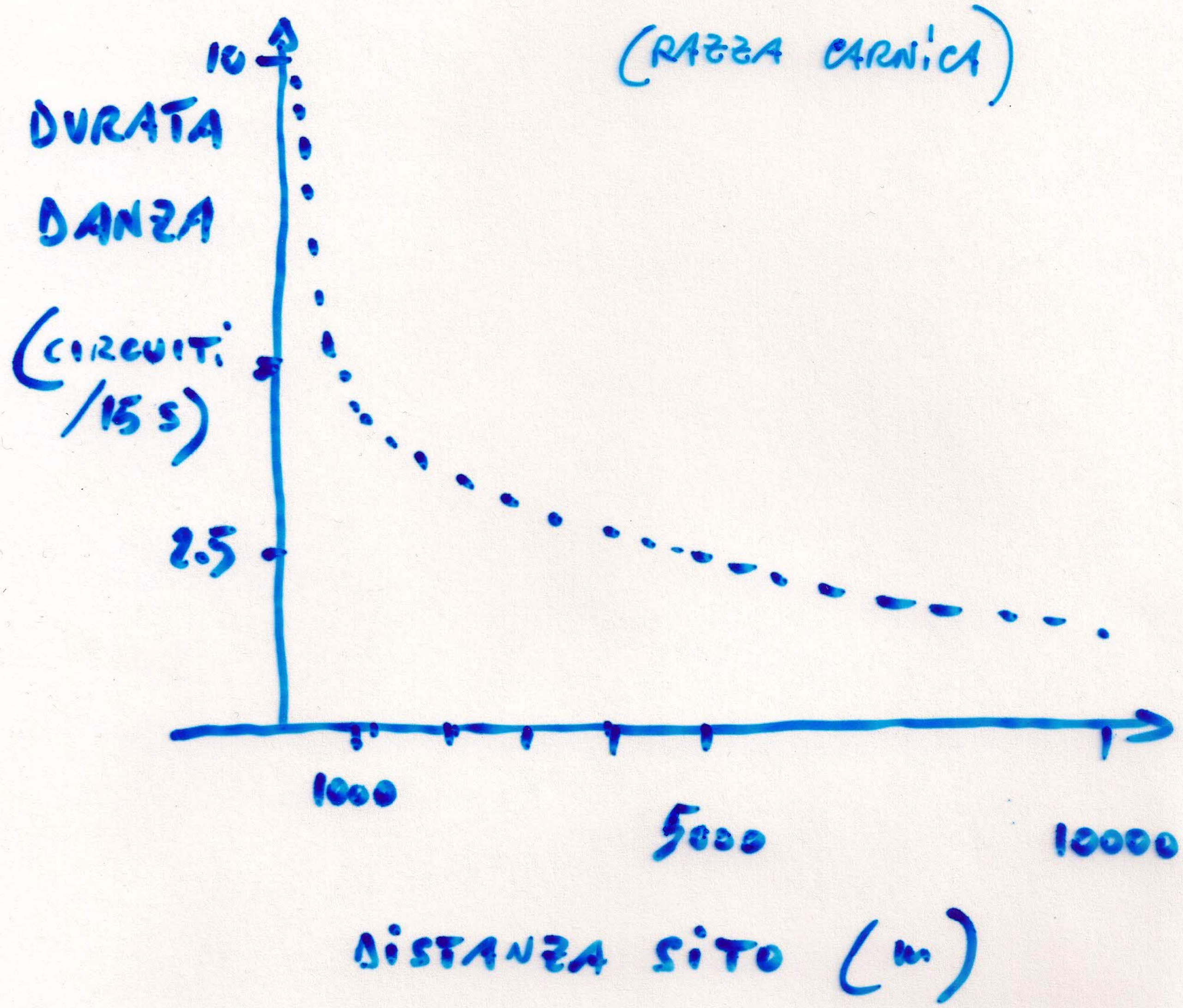


Figura 3.3
Diagramma che mostra l'effetto di uno «spostamento dell'orologio interno» sulla direzione presa dagli uccelli liberati a mezzogiorno in un punto localizzato a est della piccionaia. In (*a*) gli uccelli si orientano in modo da tenere il sole a 90° sulla sinistra. In (*b*) il loro orologio interno era stato spostato indietro di 6 ore e quindi, quando furono liberati a mezzogiorno, si comportarono come se fossero state le 6:00, tenendo il sole alle proprie spalle.

ODORE (CORPO + NETTARE)
DISTANZA
DIREZIONE



DANZA CIRCOLARE (VICINO)

" DELL'ADDOME (LONTANO)

KARL VON FRISCH

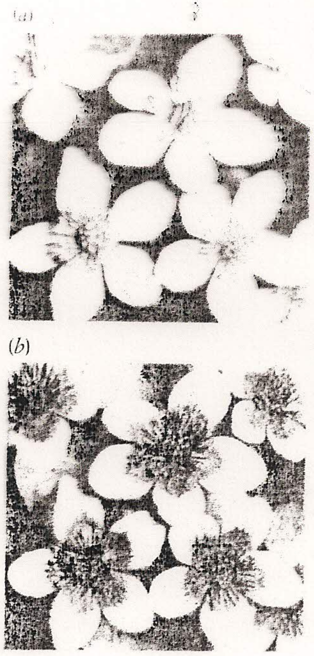
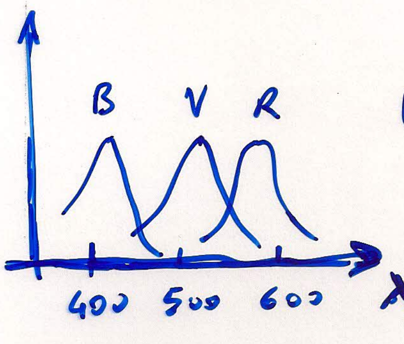
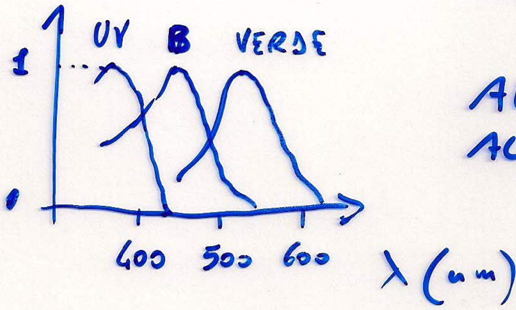


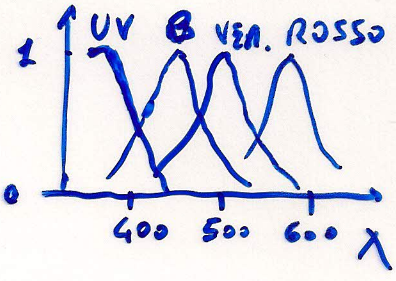
Figura 3.4
Fiori osservati con luce diversa. La fotografia (*a*) mostra ciò che è visibile per l'occhio umano: i fiori non sembrano avere alcuna «guida del nettare». La fotografia (*b*), ottenuta con un sistema sensibile all'ultravioletto, mostra all'incirca quel che vede un'ape, e rivela dunque un cospicuo disegno colorato. Fotografie di Thomas Eisner.



UOMO



API E MOLTI ALTRI INSETTI



PICCIONI E MOLTI ALTRI UCCELLI (E QUALCHE INSETTO)

(FORSE ANCHE 5, IN ALCUNE SPECIE, a 510)

'800 ——→ KARL VON FRISCH
(COMPORTAMENTO)

p. es. WEHNER
Le Scienze '76

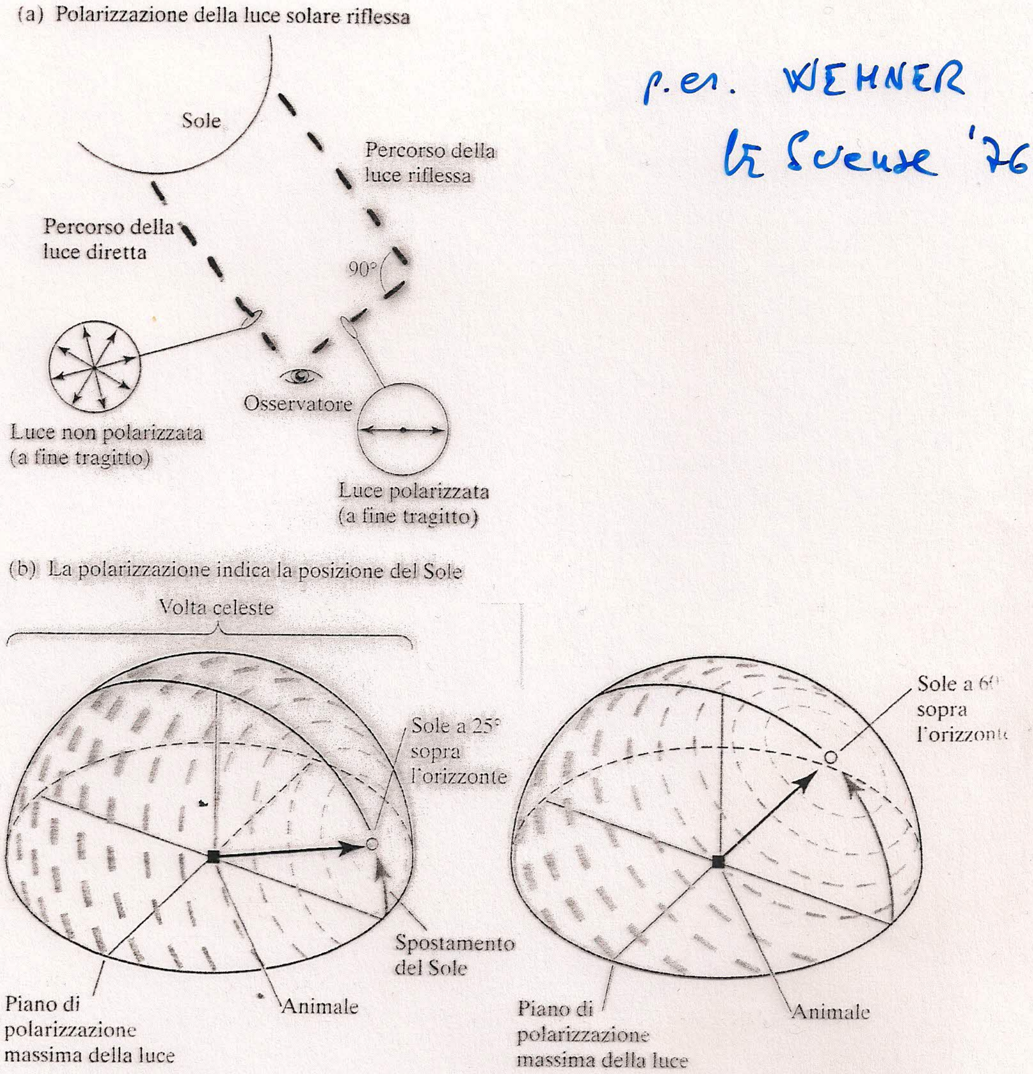


Figura 16.6 La polarizzazione della luce solare può servire a determinare la posizione del Sole. (a) Il blu del cielo deriva dalla dispersione della luce solare blu e violetta riflessa da particelle atmosferiche. La luce solare non è polarizzata; il suo vettore elettrico forma un angolo retto con la direzione di propagazione delle onde luminose, e può essere orientato in qualunque direzione. Gli inserti mostrano la vista alla fine del tragitto; nel caso della luce non polarizzata, le frecce mostrano i vettori elettrici in tutti gli orientamenti. La luce riflessa è invece polarizzata, con il vettore elettrico orientato secondo un'unica direzione (qui mostrata come orizzontale). (b) Lo schema di polarizzazione della luce con il Sole in due posizioni: 25° (a sinistra) e 60° (a destra) sopra l'orizzonte. Il piano di polarizzazione forma un angolo retto con il piano di dispersione e il grado di polarizzazione (la dimensione delle barrette) è maggiore a 90° rispetto al Sole. [*Fonte*: (b) Wehner, 1997.]

INSETTI
CROSTACEI
RAGNI
MOLLUSCHI

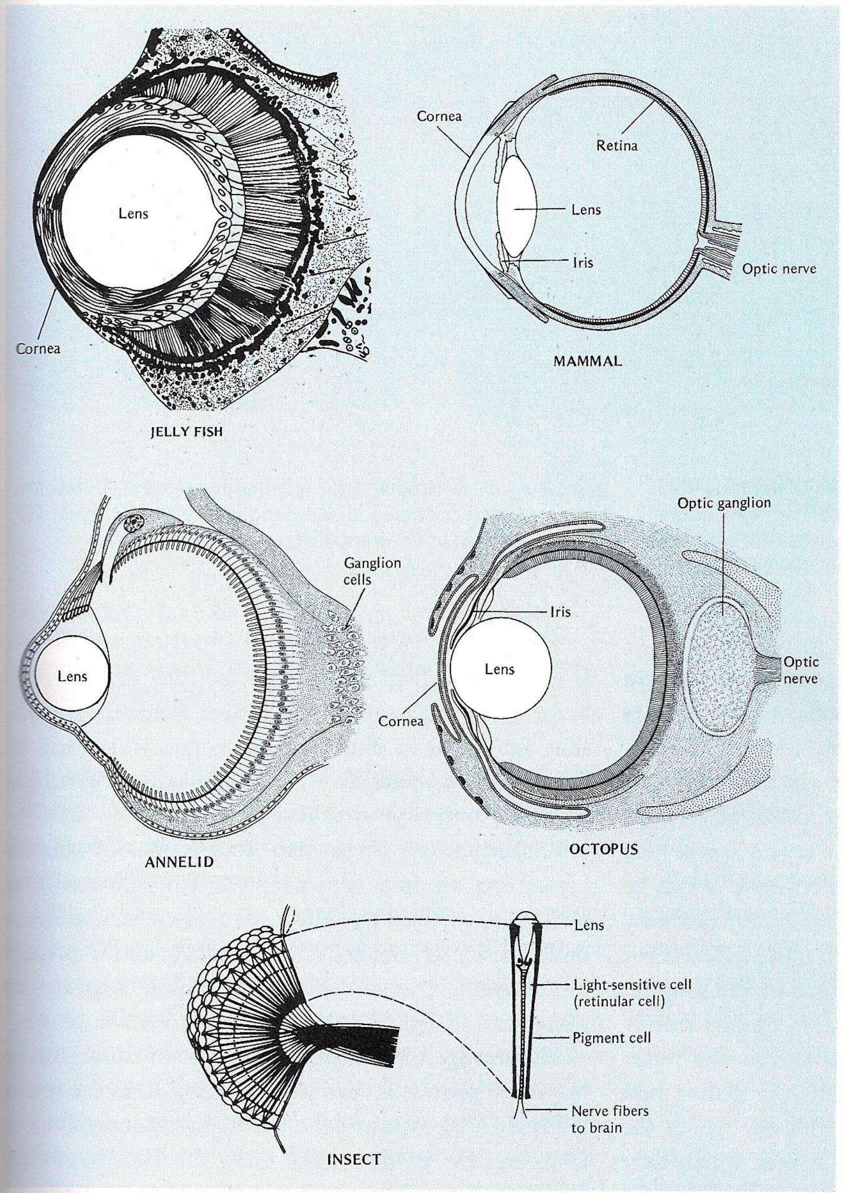
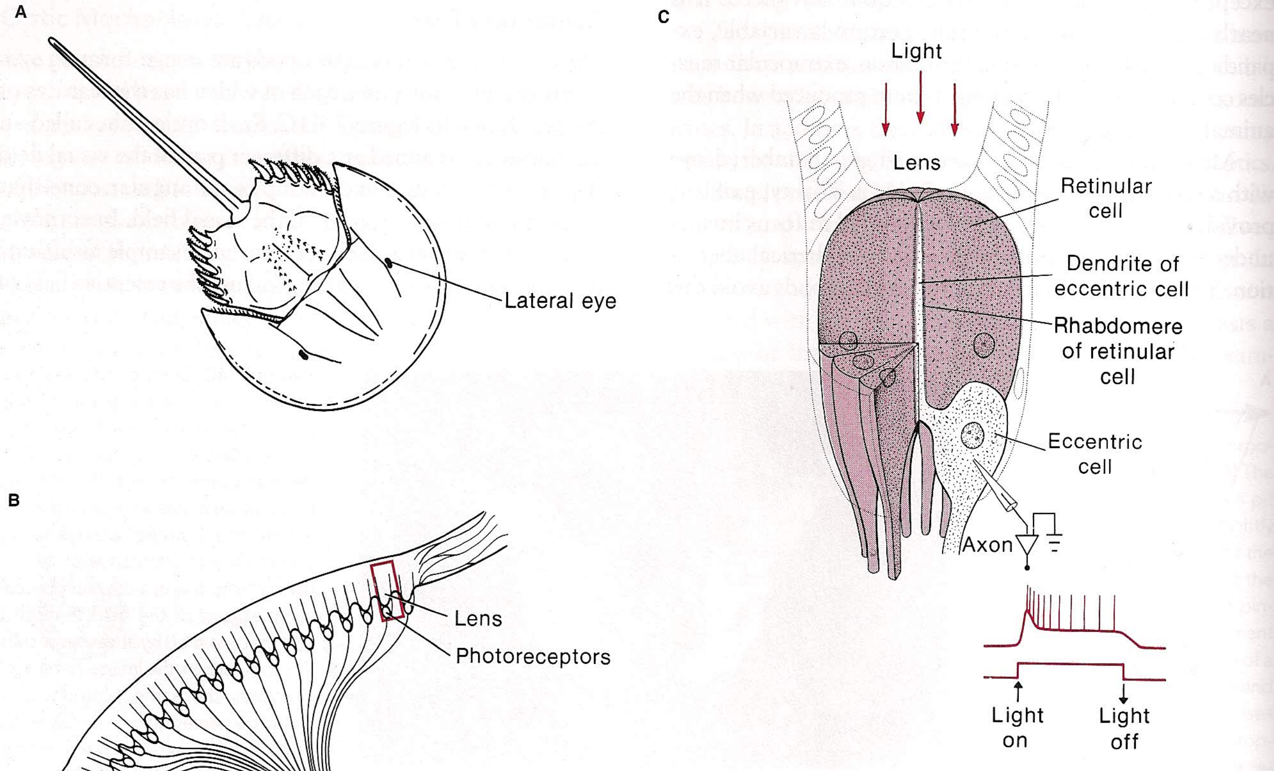


Figure 13.10 The eyes of vertebrates and some invertebrates have a lens and function on the same principle as a camera. Insects have compound eyes in which the single elements combine to form the image (a single ommatidium is shown in detail).

ultraviolet range, to slightly shorter wavelengths than the vertebrate eye. This is evident from the ability of honeybees to distinguish any spectral color between 313 and 650 nm from white light, an ability that is unrelated to

The mammalian retina is sensitive to ultraviolet light, but these wavelengths do not penetrate to the retina, primarily because of a slight yellowness of the lens, which acts as a filter. Persons whose lens has been surgicrab *Limulus polyphemus* (Figure 7-43). The two lateral eyes of *Limulus* are typical compound eyes, similar to those in Figure 7-42A, whereas the unpaired ventral eye is simpler in structure and more like the eyespot shown in Figure 7-41A. Most of the early electrical recordings made from single visual units were done with this lateral eye, because the eye was experimen-

into a dense profusion of **microvilli,** which are miniature tubular evaginations of the surface membrane (see Figure 7-43D). The microvilli greatly increase the surface area of the cell membrane in the rhabdomere. Light enters through the lens and is absorbed by molecules of the photopigment rhodopsin that are located in the receptor membrane within the rhabdomere. Transient, random depolarizations of the membrane po-



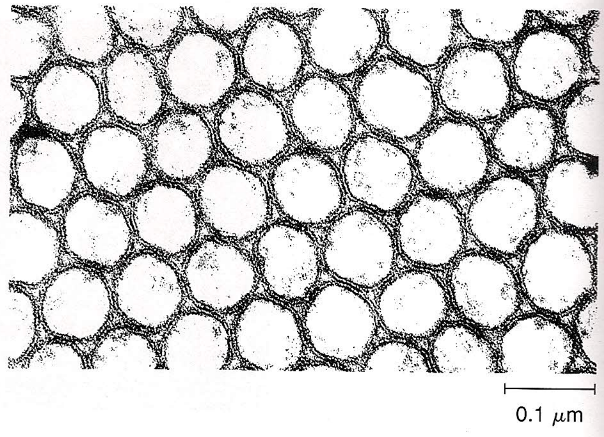


Figure 7-43 Early studies of the compound eyes of *Limulus polyphemus* provided insights into visual transduction. **(A)** The lateral eyes of the horseshoe crab *Limulus* are located on the dorsal carapace. **(B)** A cross section through a lateral eye, which is made up of ommatidia. **(C)** The structure of a single ommatidium (outlined in red in part B). Light enters through the lens and is intercepted by visual pigment in the rhabdomeres of the retinular cells. The cells are arranged like the segments of an orange around the dendrite of the eccentric cell. The eccentric cell depolarizes and generates APs when light shines on the rhabdomeres. **(D)** An electron micrograph of a cross section through the microvilli of a rhabdomere. [Part C from "How Cells Receive Stimuli," by W. H. Miller, F. Ratliff, and H. K. Hartline. Copyright © 1961 by Scientific American, Inc. All rights reserved. Part D courtesy of A. Lasansky.]

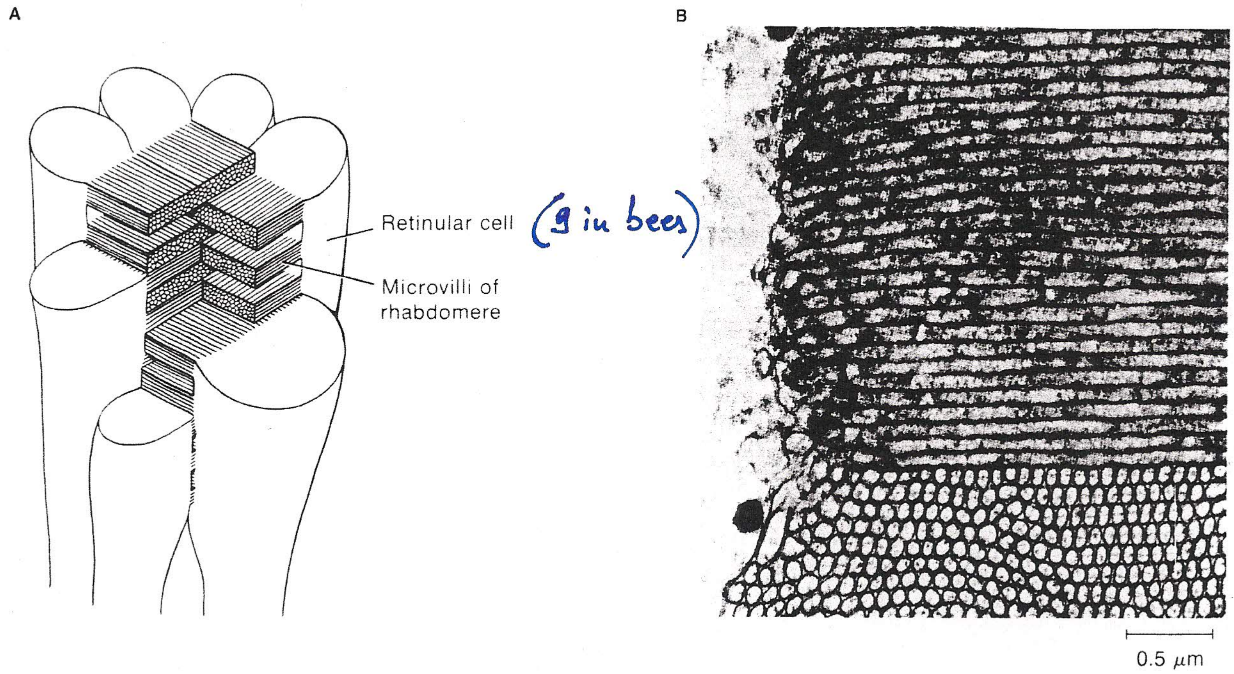


Figure 7-44 The structure of ommatidia allows some arthropods to perceive the plane of polarized light. **(A)** The interdigitating rhabdomeres of separate retinular cells produce two sets of mutually perpendicular microvilli. **(B)** Electron micrograph of a section through the rhabdome formed by two sets of microvilli. The upper microvilli were sectioned parallel to their longitudinal axis, and those in the lower set were sectioned perpendicular to their longitudinal axis. [Part A adapted from Horridge, 1968; part B courtesy of Waterman et al., 1969.]

PHOTORECEPTORS ARE ORIENTED SO THAT
MAX RESPONSE WHEN BEES ARE IN FRONT OF THE SUN

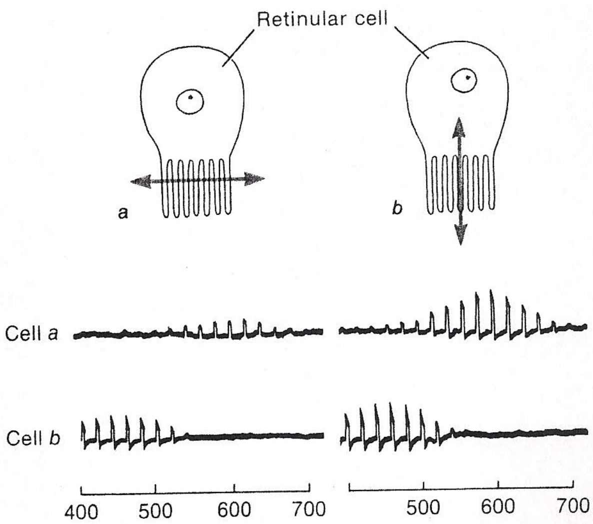


Figure 7-45 The response of crayfish photoreceptors to polarized light varies with the plane of polarization. Two cells, *a* and *b*, were presented with a series of equal-energy flashes of polarized light at various wavelengths. The color of light in each flash (indicated by its wavelength in nanometers) is indicated along the lower axis. Cell *a* responded maximally to light with a wavelength of about 600 nm; cell *b* responded maximally to light of 450 nm. When the plane of polarization (red arrow) was perpendicular to the microvilli, the responses in both cells were small *(left)*. Responses of both cells were enhanced when the plane of polarization (red arrow) was rotated so as to lie parallel to the microvilli *(right)*. [Adapted from Waterman and Fernandez, 1970.]

MEMORY OF TIME IN BEES.

Forel 1910.

Observed circadian return to a site.

Even in the absence of attracting food, smells, etc.

Beling & Wahl

Training to visit a feeding station at a given time. Bees can anticipate the food every day.

Bees could only be trained to a period close to 24 h (not for example 19 h or 48 h).

Internal clock:
- it works even at constant T, light, humidity.
- the effect of periodic air ionization was eliminated
- Deep at -180 m, to avoid cosmic radiations.
- Sensation of hunger.

Renner

Bees trained and tested in different geographical locations.

The endogenous and external signals reinforce each other.