meiosis. This dissociation is also suggested by the possibility of mitosis at the hexaploid level, as indicated by the tissue cultures.

The hexaploid oogonium that enters pachytene must therefore provide for two-by-two synapsis from sets of six homologous chromosomes. If a trio of homologs were represented by $I^AI^BI^C$, then the sister replicates added by endomitosis would be $I_r^AI_r^BI_r^C$. Random formation of bivalents from the homologous sextet $I^AI^BI^CI_r^AI_r^BI_r^C$ would result in combinations such as $I^AI_r^A$, I^AI^B, I^AI^C, and so forth. However, the gynogenetic inheritance pattern of triploid *Poeciliopsis* indicates that it is sister replicates that pair as bivalents. If univalents, trivalents, or higher associations occurred, or if bivalent pairing were random among homologs, then segregation would also be random, and the ovum would contain recombinations of chromosomes. I observed only bivalents (Fig. 1C), and 23 laboratory generations of triploids have shown no genetic evidence of random segregation (*4*). Thus, sister-replicate pairing ($I^AI_r^A$, $I^BI_r^B$, $I^CI_r^C$) conserves the genotype of the clone.

Endomitosis also occurs prior to the meiosis of the triploid ($3n = 69$) parthenogenetic lizard *Cnemidophorus uniparens*, which contains 69 bivalents during metaphase I (*13*).

Russian populations of triploid gynogenetic goldfish (*Carassius auratus gibelio*) possess a tripolar spindle during oogenesis (*1*). One chromosome set collects at each pole. The spindle aborts, and all three sets collect in the oocyte nucleus, a mechanism that is similar to that of the triploid parthenogenetic vegetable weevil, *Listroderes costirostris* (*14*). On the other hand, diploid gynogenetic goldfish from eastern Europe, studied by Lieder (*3*), apparently undergo both maturation divisions. Lieder concluded that diploidy is restored by suppression of the first cleavage division. However, this mechanism would lead to homozygosity of all alleles, including recessive lethals, and therefore must be viewed with some suspicion.

The first unisexual vertebrate discovered was the gynogenetic diploid poeciliid, *Poecilia formosa* (*2*). Although this species was known for almost 40 years, the mechanism by which it produces its eggs is still unknown. The techniques I used, if applied to *Poecilia*, might provide the answer. It is plausible that an endomitosis like that in triploid *Poeciliopsis* produces in *Poecilia* a tetraploid oogonium, which enters meiosis and is reduced to a diploid ovum. Three precedents for such a mechanism in vertebrates now exist.

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7. Midbody regions were fixed in freshly prepared methyl-Carnoy (absolute methanol : glacial acetic acid, 3 : 1). After infiltration with amyl acetate [D. H. Barron, *Anat. Rec.* **59**, 1 (1934)], serial paraffin sections were cut at 15 μm, stained with Feulgen, and counterstained with fast green [A. K. Sharma and A. Sharma, *Chromosome Techniques* (Butterworth, London, 1965)]. Techniques are fully described in M. C. Cimino, thesis, University of Connecticut (1971).
8. Chromosome complements reconstructed from optical sections were often somewhat hypoploid, due to one or more of the following: (i) small chromosomes overlooked in the reconstruction, (ii) chromosomes so close to one another that they were not distinguishable as separate, and (iii) chromosomes already synapsed and so closely appressed that they appeared as a single chromosome. The last possibility is most likely, since synapsis begins during zygotene.
9. Air-dried preparations (*10*) were used for karyotype studies, to be reported elsewhere. Pachytene chromosomes were easily distinguishable from the chromosomes used for karyotyping, in that the latter are short, densely staining, and obviously composed of two chromatids connected by a centromere, whereas the former are thin, long, faintly staining, and apparently single.
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A Visual Pigment with Two Physiologically Active Stable States

Abstract. *Red illumination of a* Balanus amphitrite *photoreceptor that has been adapted to blue light leads to prolonged depolarization in the late receptor potential. This depolarization can be switched off by further exposure to a blue stimulus. The early receptor potential in this cell is purely depolarizing or largely hyperpolarizing; the former is true if the cell has been adapted to red light, and the latter, if blue light has been used. The color-adaptation "memories" for both early and late receptor potentials appear to be permanent. The existence of two stable states for the early receptor potential directly implies a pigment with two stable states, and these apparently contribute antagonistically to the late receptor potential.*

Correlation of the origin of photoreceptors' physiological response—the late receptor potential (LRP)—with the changes undergone by the visual pigment molecule after absorbing the photon has been hindered by the impossibility of substantially manipulating the pigment process in conditions where the LRP remains intact. We have now found a pigment that has two thermally stable and physiologically active states. These states have different absorption spectra and are interconvertible by light, so stimulation by different colors activates the two states to different degrees and leaves them in different relative proportions.

Figure 1 shows intracellular recordings in photoreceptors of the lateral ocellus of the barnacle *Balanus amphitrite* (*1*). The response to strong light (traces A and B) appears to be made up of two parts—a small, fast component, which is positive (depolarizing) in A and negative in B, and which we identify as the early receptor potential (ERP); followed by a large, slow, positive LRP. The slow response sometimes conveniently disappeared spontaneously, leaving the fast responses of traces D and E. The identification of these fast responses as ERP's (*2*) was confirmed by their short latency (less than 0.3 msec), their roughly linear dependence on intensity, their relative independence of ionic medium (for example, high concentration of K^+), and their survival after glutaraldehyde fixation, which destroyed the LRP (*3*).

Responses to strong white light of cells previously adapted to red light (about 600 nm) are shown in Fig. 1, traces A and D; and responses of cells adapted to blue light (about 450 nm) are given in traces B and E. The ERP is of reversed sign in the two cases; it is positive (depolarizing) in a cell adapted to red light and negative in a cell adapted to blue (or white) light. After an initial brief recovery period (*3*) that follows the adaptation, the responses are independent of the time (up to at least 60 minutes after adaptation) that cells spend in the dark before they are tested (*4*).

The action spectra for the ERP responses (reciprocal of intensity for criterion response) are shown in Fig. 2. For the red-adapted cell, a positive response of criterion shape and size could be matched at all wavelengths of stimulation within the range of sensitivity. A Dartnall nomogram (*5*), with a peak at 495 nm, is shown for comparison. In the blue-adapted cell, the response shape varied when stimulus wavelengths were less than 600 nm; this was true especially at low temperatures, where the response shape was biphasic, with variable positive/negative ratio. The points in this region therefore are for matched negative amplitudes but not shapes, and so do not represent a true action spectrum. Nevertheless, a Dartnall nomogram, with a peak 535 nm, is shown for comparison.

The simplest hypothesis consistent with the ERP observations is that there is a single pigment with two thermally stable states that are interconvertible by light. According to this hypothesis, one of these states (P) gives a purely positive ERP, and the other (N), with an absorption spectrum extending further into the red than that of P but overlapping it elsewhere, gives a purely negative ERP (*6*). Adaptation to a red light then produces a nearly pure P state, and adaptation to any other light produces a mixed state. The ERP responses of the mixed state vary with stimulus wavelength. The ERP action spectrum of the red-adapted cell then represents the absorption spectrum of the P state, while the ERP action spectrum of the blue-adapted cell corre-

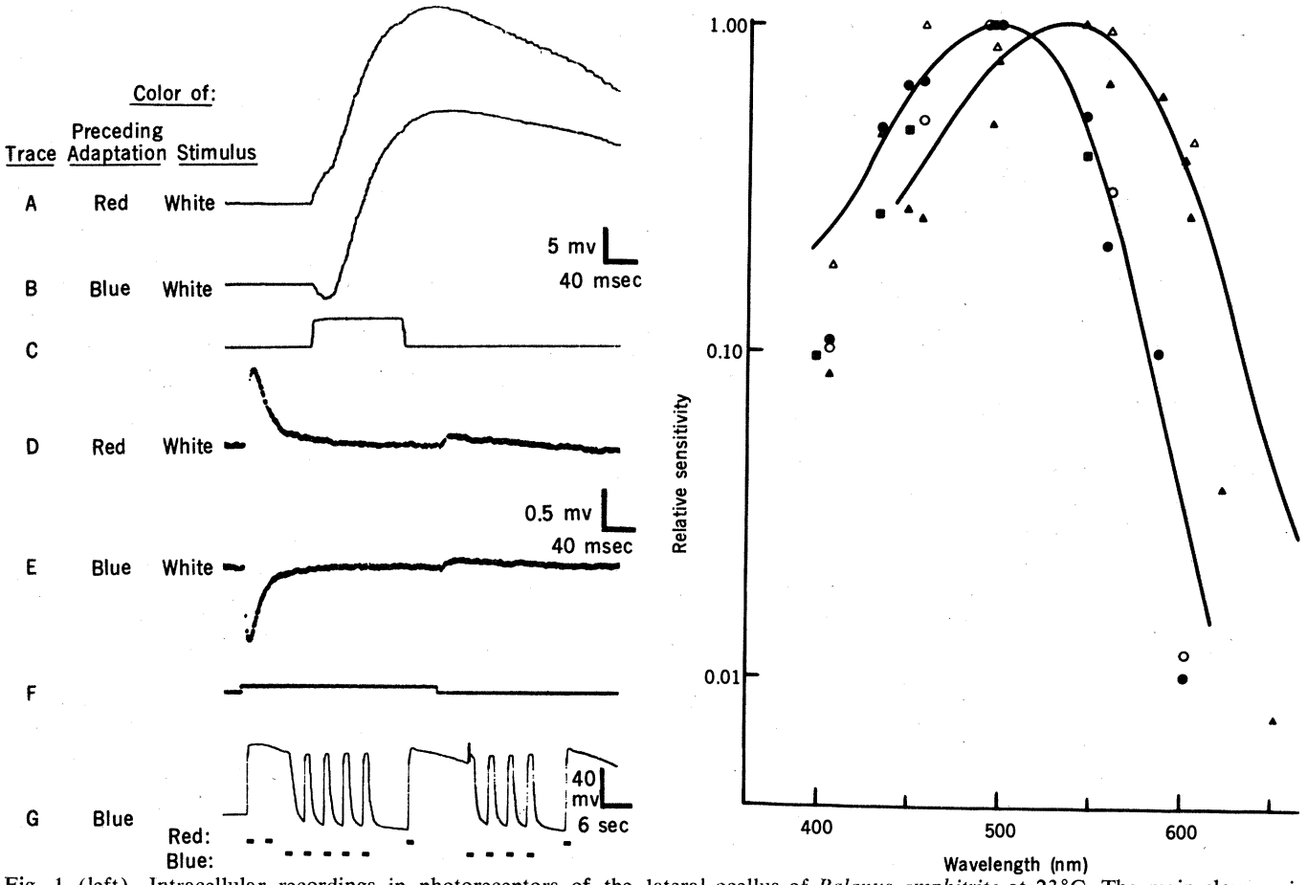

Fig. 1 (left). Intracellular recordings in photoreceptors of the lateral ocellus of *Balanus amphitrite* at 23°C. The main slow positive (depolarizing) response in A and B is identified as the late receptor potential (LRP); and the small initial part, positive in A and negative in B, as the early receptor potential (ERP). Traces D and E show the ERP in a cell in which the LRP had disappeared spontaneously. Trace G is the LRP of another cell; with these weaker, colored lights the ERP is invisible on this scale. The red light here induces, and the blue light cuts off, an extended LRP depolarization that otherwise lasted for about 5 minutes in this cell. Since a blue light that is sufficient to suppress the tail is also sufficient to adapt the cell to blue light, the third and fourth red stimuli again induce tails. The light trace C and the calibration axes above it apply to traces A and B; light trace F and the calibration axes between traces D and E apply to traces D and E; and the axes within trace G and the black bars below it (representing light durations) apply to trace G. Fig. 2 (right). Action spectra for ERP and LRP. The ordinate is the reciprocal of the relative number of photons needed to match a fixed criterion: a criterion amplitude and shape positive ERP response from a red-adapted cell at 8°C (solid circles) and 22°C (open circles); a criterion amplitude negative ERP response from a blue-adapted cell at 8°C (solid triangles) and 22°C (open triangles) (it was possible to match a criterion shape only above 600 nm, so the points represent a true action spectrum only in this region); and a criterion suppression of the extended LRP depolarization (as in trace G of Fig. 1) at 22°C (squares). Dartnall nomograms (*5*), with peaks at 495 and 535 nm, are shown for comparison with the ERP action spectra. All five sets of points and the nomograms are normalized to 1 at their highest points.

sponds to the N-state absorption spectrum only at wavelengths greater than 600 nm (*7*).

At lower light intensities, the LRP responses in these cells show little or no dependence on wavelength of stimulation or of preceding adaptation, except for a small increase in sensitivity in red-adapted cells. Ogden and Stratten (*8*) showed that the LRP action spectrum in such cells, when white-adapted, shows a peak at 535 nm; and we have found the same peak in red- and blue-adapted cells. The absorption spectrum of the N state of the ERP pigment probably has a peak somewhere near 535 nm (Fig. 2). This coincidence of action-spectrum peaks suggests that the same pigment, and in particular its N state, may be responsible for the LRP. However, the increase in sensitivity of the red-adapted cell (which has a reduced proportion of pigment in the N state) apparently also requires some role for the P state.

Clearer evidence for the identity of the ERP and LRP pigments and for the role of the N state in the LRP comes from the observation that strong red illumination (*9*) of a blue-adapted cell (and no other combination) induces an extended depolarization, which can take from seconds up to 30 minutes in the dark to decay back to baseline but can be suppressed by further strong blue illumination (Fig. 1, trace G) (*10*). As with the ERP reversal, the state of color adaptation of the cell—with respect to the presence or absence of a tail in the response to red light—was fully preserved in the dark for at least 60 minutes. Furthermore, the absolute amounts of light necessary to bring about the various LRP and ERP changes are approximately equal. For example, the amount of red light needed to induce a saturated LRP tail in a blue-adapted cell is about that which reverses the ERP response from negative to positive in the same cell (*11*).

Now, according to our hypothesis, red illumination of a blue-adapted cell (the tail-producing combination) activates mainly the N state of the ERP pigment, while all other combinations either activate both states to comparable degrees or activate mainly the P state. The action spectrum for the induction of this tail also follows the N-state absorption spectrum in the narrow region —above 600 nm (Fig. 2)—in which the N-state spectrum is determined.

The action spectrum of the suppression of the tail (Fig. 2), on the other hand, closely follows the absorption spectrum of the P state (that is, the ERP action spectrum of the red-adapted cell).

This suggests that strong activation of the N state of the ERP pigment induces the LRP tail, which can be suppressed or prevented from appearing by strong P-state activation.

Finally, that the tail induction by N-state activation and the tail suppression by P-state activation act on the same membrane process is suggested by bridge measurements. These measurements show decreases in cell resistance roughly in parallel with the courses of the depolarizations during and after the various stimuli, including during the decay or suppression of the tail (*12*).

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7. The pigment process also involves a number of thermally unstable states and thermal and light pathways; these observations will be discussed (B. Minke, S. Hochstein, P. Hillman, in preparation).
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Response Decrements in the Cochlear Nucleus of Decerebrate Cats during Repeated Acoustic Stimulation

Abstract. *In the cochlear nucleus of decerebrate, paralyzed cats, multiple-unit responses to an acoustic stimulus showed significant decrements when the stimulus was repeatedly presented once every 5 seconds. These decrements developed in the absence of peripheral receptor adaptation. The responses recovered to the level prior to stimulation when stimulation was withheld for 5 to 10 minutes. Dishabituation by somatic stimulation of the forepaw, however, was less effective than in the intact cat. The continued development of response decrements after strychnine blockade of peripheral olivocochlear influences and central postsynaptic inhibition suggests a mechanism of decreased synaptic effectiveness, which has previously been postulated for neuronal habituation in brainstem and spinal cord.*

The extent to which response decrements develop in the auditory relay nuclei during acoustic habituation has long remained unclear. Particularly in the more peripheral nuclei of the acoustic pathway, for example, the cochlear nucleus, evoked potential studies over the past 10 years have provided both positive (*1*) and negative (*2*) support for such response plasticity. These contradictory data may largely reflect confounding and important variables of acoustic habituation experiments that have only gradually become recognized; for example, the sound-field alterations that accompany movements of the un-