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Photoperception and Photomovement [and Discussion]

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Photoperception and photomovement

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The photoperception systems in photomovement show a great diversity at several levels. (i) Different types of photomovement (namely photokinesis, photophobic response, phototaxis) make use of completely different perception systems even in the same organism. (ii) In different organisms a given type of photomovement is mediated by different and unrelated systems, as is shown in this paper particularly for phototaxis. (iii) In certain cases, a single response in one organism can be controlled by two separate and independent photoperception systems, which may even be located in different compartments.

This diversity sets photomovement apart from photosynthesis and vision, which are highly uniform and stable in evolution. Possible consequences for considering the evolution are discussed.

1. Introduction

For an autotrophic organism the most important environmental factor is light. Plants have therefore evolved what appear to be effective mechanisms to optimize the exploitation of the cosmic energy source, i.e. the sunlight. Among these mechanisms, different types of movement are known, which are controlled by light in different ways.

As a first example, unicellular or filamentous algae are mentioned, which move by gliding along solid surfaces in water. In these organisms the degrees of freedom of movement are restricted to two dimensions in space. Blue-green algae (Oscillatoriaceae, Nostocaceae) and diatoms have been well investigated in this respect, but some desmids and unicellular red algae also exhibit this type of movement.

A second example is given by flagellates, which are free-moving organisms: they can move in their aqueous medium in all dimensions of space.

In both of the above-mentioned types light can control or affect speed, continuity and direction of movement. The respective responses are termed photokinesis, photophobic response and phototaxis, as will be explained in the next section, and the general term is photomovement (Nultsch 1975; Häder 1979).

Under certain conditions these photomovements can lead to non-uniform distributions of the organisms in their environment, with patterns that are in some way related to the light. These results, macroscopically observed, are termed photoaccumulation, as long as no definite analysis has been made as to which of the photomovement types underlies the patterns (see Diehn 1979).

Besides the motility of whole organisms, the movement of chloroplasts in the cell can also be controlled by light. The resulting patterns of chloroplast distribution can be compared with photoaccumulation of motile organisms (see Britz 1979; Haupt 1982).

The following questions can be posed.

(i) If an organism exhibits different types of photomovement, is light perception identical in these different types?

(ii) If two organisms exhibit analogous photoresponses, do they use identical or at least comparable photoperception systems?

(iii) Are there organisms that make use of different photoperception systems for one response, independent from each other?

(iv) From the observations resulting from questions (i) to (iii), what are the conclusions about the evolution of photoperception?

2. Light perception in different types of photomovement in one organism

As an example, a well investigated genus of cyanobacteria (blue-green algae), *Phormidium*, will be described with its responses (see Häder 1979; Nultsch & Häder 1979). The organism consists of many cells in one-dimensional order, forming a trichome. The gliding movement requires contact with a solid surface and proceeds in the direction of the axis of the trichome. Since there is not an apico-basal polarity, both tips of the trichome are equivalent and can act as the advancing end or as the back end.

The different photoresponses are characterized as follows.

(i) Photokinesis: the steady-state velocity of movement depends on the intensity of constant light. It usually increases with increasing light, up to an optimum beyond which it decreases again.

(ii) Photophobic response: a sudden step down in light intensity evokes a transient response. The trichome ceases moving, and after a while it resumes movement in the opposite direction, soon reaching the steady-state velocity as dictated by photokinesis. Under certain conditions, a photophobic response can be induced also by a step up in light intensity. Thus the photophobic response interrupts the continuity of movement. However, even without a photophobic stimulus a reversal of movement can be found, but this autonomous reversal occurs with low frequency, i.e. every few minutes. Photophobic response, then, is a premature reversal.

(iii) Phototaxis: in unilateral light most of the organisms accumulate as far towards the light source as possible. Thus movement obviously has a relation to the light direction. This result is achieved by particular responses of the individual trichomes: if a trichome happens to glide in the 'wrong' direction (i.e. light coming from behind), it is induced to a premature reversal. If, however, movement proceeds in the 'right' direction (i.e. light coming from front), autonomous reversal is delayed. On average, therefore, movement towards the light prevails.

Thus the organism has to measure the steady-state light intensity for photokinesis, the constancy or change of intensity in time for photophobic response, and the light direction for phototaxis. In the next subsections, current knowledge about these photoperception processes in *Ph. uncinatum* will be described.

(*a*) *Photoperception in photokinesis*

In *Phormidium uncinatum* the action spectrum of photokinesis has maxima in the blue and red region, with peaks in the visible light around around 430 and 670 nm, and extending into the far red (figure 1*a*). This points to chlorophyll as the photoreceptor pigment.

Since absorption by the biliproteins contributes only slightly to the effect, photosystem I of photosynthesis is assumed to be important for photokinesis, and acceleration of movement with increasing intensity should simply be due to additional ATP from cyclic photophosphorylation.

Accordingly, uncouplers of photophosphorylation, e.g. desaspidin or carbonylcyanide *m*-chlorophenylhydrazone (CCCP), abolish the photokinetic effect. On the other hand, 3-(3,4-dichlorophenyl)-1,1-dimethylurea (DCMU), an inhibitor of the non-cyclic electron transport chain, has relatively little effect, corresponding to the ineffectiveness of the photosystem II pigments (Nultsch 1975; Häder 1979).

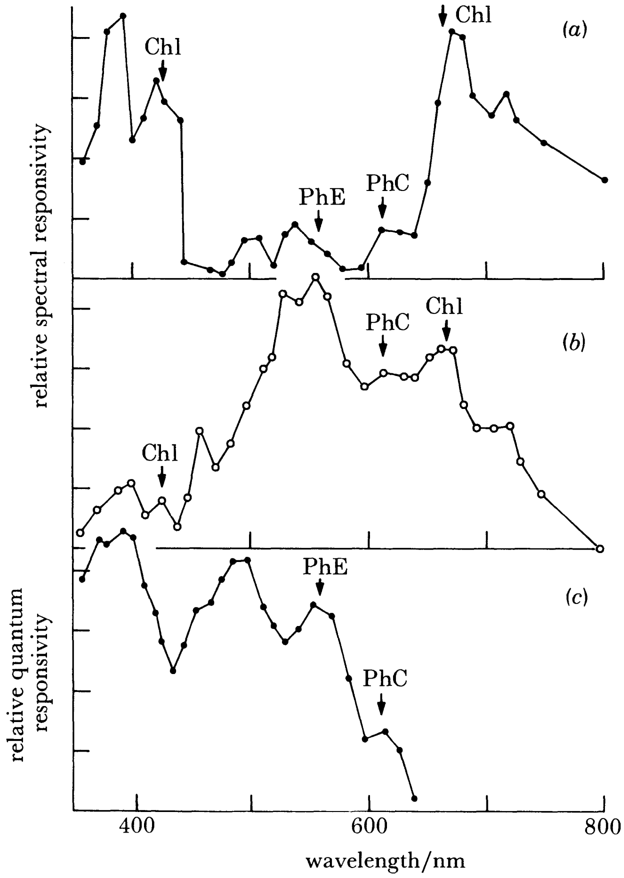


FIGURE 1. Action spectra for (*a*) photokinesis, (*b*) photophobic response and (*c*) phototaxis in ***Phormidium uncinatum***. The main absorption peaks of chlorophyll *a* (Chl), phycoerythrin (PhE), and phycocyanin (PhC) are indicated. (Modified after Nultsch (1962).)

In conclusion, in photokinesis light is used as an additional energy source for movement. Thus, strictly speaking, light does not act as a signal, in contrast to the responses in the following subsections, which are energetically independent of the light stimulus.

(*b*) *Photoperception in photophobic response*

The step-down photophobic response is most effectively induced by light between 530 and 680 nm, with peaks close to the absorption maxima of C-phycoerythrin, C-phycocyanin and chlorophyll, whereas absorption in carotenoids and in the blue peak of chlorophyll contributes little to the response (figure 1*b*). This action spectrum is taken as evidence for photosystem II as the most important photoperception system (Nultsch 1962; Häder 1979).

Indeed, inhibitors of photosynthetic electron flow inhibit the photophobic response specifically, whereas uncouplers of photophosphorylation have litte effect (Häder 1979). In such experiments, photokinesis can be used as a control, because there the effects are opposite.

From these results it has been assumed that a sudden decrease in light intensity transiently depletes an electron pool in the electron transport chain by reducing the input from photosystem II, while the outflow to photosystem I is less influenced. This hypothesis leads to an interesting consequence: the same effect should be obtained if the electron input is kept constant but the pool is drained by an increased photosystem I activity. And indeed, a step-up signal, too, can be followed by a photophobic response, provided that this light is predominantly absorbed by photosystem I. In fact the mixture of effects makes things rather complicated, but clear conclusions have been obtained by stimulation with step-up and step-down signals of monochromatic light on the background of constant light of different wavelengths (Nultsch, 1975; Häder, 1979). Finally, information about the localization of the pool has been obtained by the application of redox substances. Depending on their redox potential, they feed in or abstract electrons at different sites of the electron transport chain. From comparative inhibitions of photophobic response by these substances, plastoquinone has been decided on as the most promising candidate for the electron pool involved in photophobic response (Häder 1979).

Although we have no full understanding of the subsequent steps, bioelectric effects of the changed redox state of plastoquinone (Hader & Poff 1982) are assumed to be involved, and indeed changes in cell potential have been measured as an early result of photophobic stimulus (Häder 1978). Moreover, the final response, i.e. reversal of movement, can be inhibited by applying an external electrical field in the direction of movement (Häder 1979). In conclusion, the photoperception processes are completely different in photokinesis and photophobic response.

(*c*) *Photoperception in phototaxis*

The phototactic action spectrum extends from *ca.* 350 nm or below to *ca.* 600 nm (figure 1*c*). The peaks in the green and yellow region suggest that biliproteins act as photoreceptor pigments, but no firm conclusion is possible in the short-wavelength region, the peak near 490 nm suggesting carotenoids, but the near-ultraviolet peak pointing to a flavin (Nultsch 1962, 1975; Hader 1979).

Because chlorophyll is not involved, the perception system in phototaxis obviously has no relation to photosynthesis. This negative conclusion is almost the only knowledge we have about photoperception. In particular we do not yet understand the perception of directionality in *Phormidium*, i.e. the mechanism by which the organism can distinguish between light coming from the front or from the rear (see Haupt 1974).

As a result, the perception system of phototaxis in *Phormidium* is different from those of the two other photomovement responses. Particularly interesting is the comparison with the photophobic response: in both phototaxis and photophobic response the final effect is reversal of movement. But this reversal is induced in two completely different ways: in photophobic response by a temporal change in light intensity, via photosynthetic electron flow; in phototaxis by light coming continuously from the wrong direction, via an unknown chain of events. Thus the two photoperception systems differ fundamentally from each other, at least in their photoreceptor pigments and the parameters of the stimulus measured. Yet the two perception systems converge on a final response.

3. Uniformity or diversity in photoperception systems between different organisms?

Now the question can be asked whether the results in *Phormidium* can be generalized: that photokinesis and the photophobic response are mediated by photosynthesis, although via different mechanisms, but that phototaxis is mediated by a different system with blue light having the predominant effect. This question will be discussed for photokinesis and for phototaxis.

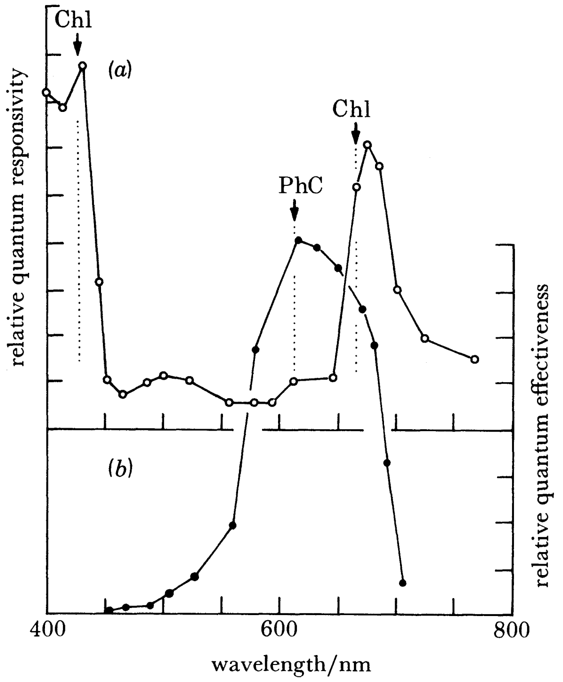


Figure 2. Action spectra for photokinesis in (*a*, ○) ***Phormidium autumnale*** and (*b*, ●) ***Anabaena variabilis***. The main absorption peaks of chlorophyll *a* (Chl) and phycocyanin (PhC) are indicated by the arrows and dotted lines. (Modified after Nultsch (1975).)

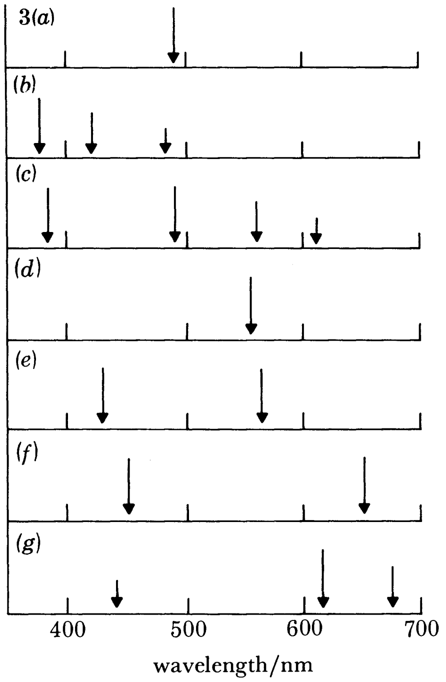
(*a*) *Photokinesis in different organisms*

The cyanobacterium (blue-green alga) *Anabaena variabilis* exhibits photokinesis similar to that in *Phormidium*, but the action spectrum points to C-phycocyanin as the main photoreceptor pigment (figure 2). It has therefore been concluded, and confirmed by inhibitor studies, that in *Anabaena* photosystem II is important and that pseudocyclic photophosphorylation is the checkpoint for the light action on motility. This organism thus differs from *Phormidium*, where mainly photosystem I and cyclic photophosphorylation are involved. Other blue-green algae appear to be mixed types’, making use of both photoperception systems (Nultsch 1975).

There are organisms, belonging to a diversity of groups, e.g. flagellates, diatoms and unicellular red algae, that exhibit photokinesis as well. In most of these cases, photosystem I or II, or both, of photosynthesis are involved, as in cyanobacteria, but in flagellates of the order Volvocales a pure blue-light effect is reported (Nultsch 1975; Häder 1979). It is unlikely that in that case light acts by providing additional energy for locomotion. Thus photokinesis can make use of different photoperception systems.

(*b*) *Phototaxis in different organisms*

An enormous diversity of perception systems in phototaxis becomes obvious if we compare phototactic action spectra of several organisms (figures 3 and 4). In a first group only blue light is effective. Several green flagellates like *Chlamydomonas*, *Platymonas* and *Volvox* (figure 3*a*) have their maximum near 500 nm, and this is usually interpreted as a carotenoid or carotenoprotein as photoreceptor pigment (see, for example, Ferrara 1975; Schletz 1976; Feinleib 1978; Nultsch & Hader 1979), but a rhodopsin-like pigment is also under discussion (Foster & Smyth 1980). More difficult to interpret is the compound action spectrum of the diatom *Nitzschia communis* (figures 3*b* and 4*b*). On the one hand, the strong peak in the near u.v. points to a flavin, but the blue peak is shifted to longer wavelengths, which appears more consistent with carotenoids; the latter view is supported by the observation that the colourless, carotenoid-free *Nitzschia alba* is non-phototactic (Nultsch & Hader 1979).



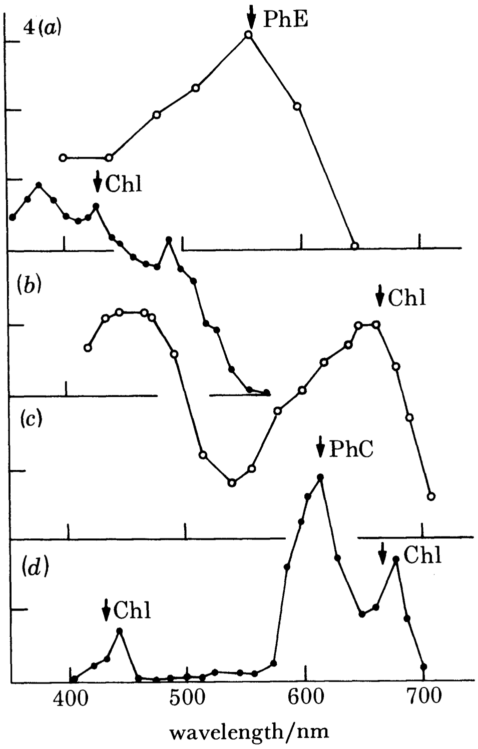


FIGURE 3. Spectral distribution of photoactic activity in different organisms: (*a*) *Volvox aureus*, (*b*) *Nitzschia communis*, (*c*) *Phormidium autumnale*, (*d*) *Cryptomonas* sp., (*e*) *Dictyostelium discoideum*, (*f*) *Micrasterias denticulata* and (*g*) *Anabaena variabilis*. The arrows indicate peaks in the respective action spectra, with their length being a qualitative measure of the peak height (for *d*, *b*, *f* and *g* compare the action spectra in figure 4). (After data of Neuscheler (1967), Nultsch (1975), Poff *et al.* (1973) and Watanabe & Furuya (1974).)

FIGURE 4. Action spectra for phototaxis: (*a*) *Cryptomonas* sp.; (*b*) *Nitzschia communis*; (*c*) *Micrasterias denticulata*; (*d*) *Anabaena variabilis*. The ordinate denotes quantum responsivity (*a*, *b*, *d*) or energy effectiveness (*c*). The main absorption peaks of chlorophyll *a* (Chl), phycoerythrin (PhE) and phycocyanin (PhC) are indicated. (Modified after Neuscheler (1967), Nultsch (1975) and Watanabe & Furuya (1974).)

In a second group of organisms, light between 500 and 600 nm, i.e. green and yellow light, is highly effective in phototaxis. As has been shown already, phycoerythrin and phycocyanin contribute to photoperception in *Phormidium*, besides the short-wavelength light (figure 3*c*; see also figure 1), and in the flagellate *Cryptomonas*, phycoerythrin appears to be the only photoreceptor pigment (figures 3*d* and 4*a*) (Watanabe & Furuya 1974). A similar spectral sensitivity for phototaxis in green light has been reported in the slime mould *Dictyostelium* (figure 3*e*), which, however, does not contain phycoerythrin; instead, a haem compound is proposed for photoreception (Poff *et al.* 1973; Poff & Butler 1974).

Finally, there are also examples with pronounced red-light effects, which point to an important role of the photosynthetic pigments in photoperception. In the desmid *Micrasterias*, the action spectrum peaks in the blue and in the red with almost equal effectiveness (figures 3*f* and 4*c*) (Neuscheler 1967), and in the cyanobacterium *Anabaena variabilis* the maximum coincides with the absorption of the accessory pigment of photosynthesis, phycocyanin, besides two less effective chlorophyll peaks in the blue and the red (figures 3*g* and 4*d*) (Nultsch 1975). Thus the photosynthetic pigments obviously act as photoreceptors for phototaxis in desmids and in *Anabaena* (see also Häder 1981), but in most of the other examples investigated no relation seems to exist between phototaxis and photosynthesis. Moreover, within this latter group a great variety of possibilities is suggested, as concluded from the action spectra (see figure 3*a–e*).

This diversity of photoreceptor pigments in phototaxis can be considered in the context of the diversity of orientation mechanisms. As has been stated above, in *Phormidium* the response simply consists of a modification of autonomous reversal of the gliding direction, induced by the direction of light. A similar mechanism has been found in some diatoms (see Nultsch 1975). Flagellates, on the other hand, orient by active steering, but it is not yet definitely known whether this steering is performed in the same way in all cases. Only in *Euglena* has the behaviour been analysed with some certainty. Here the cell rotates during movement; if it is not aligned with the light path, it receives a signal once each revolution, according to which it corrects its trail (Diehn 1979). Similarly the steering in *Volvox* is connected with the rotation of the colony, by which each individual cell experiences a temporal pattern of light absorption in unilateral illumination (Schletz 1976).

The trichomes of *Anabaena* steer towards the light as well, but in this case no rotation is involved and hence the directional signal has to be perceived continuously. Accordingly a continuous curving of the gliding trichome into the light path is observed as long as it moves (Nultsch 1975).

Finally, the gliding desmid *Micrasterias* steers continuously as well, but an additional peculiarity has been found in this organism (Neuscheler 1967). If a stationary cell is illuminated from a direction other than the direction of potential gliding, the cell rotates to the correct orientation, ready to glide straight towards the light as soon as movement is resumed.

As a result, much more diversity in photoperception systems exist in phototaxis than in photokinesis, and this diversity concerns both the input and the output of these systems, i.e. the photoreceptor pigments and the mechanisms of orientation, respectively. In detail, nearly all problems of the transduction processes are still open questions.

4. Responses mediated by more than one photoperception system

In the preceding sections some examples have been presented as evidence for different photoreceptor pigments underlying the same response in one organism: phototaxis in *Anabaena* uses chlorophyll *a* and C-phycocyanin (§3*b* and figure 4*d*). Likewise, for the photophobic response in *Phormidium*, light absorption in chlorophyll *a* as well as in phycoerythrin and phycocyanin is important (§2*b* and figure 1*b*). In these cases, however, the two or three pigments feed the light energy into photosynthesis, and thus only the very first step of photoperception is duplicated.

Less well understood is the example of phototaxis in *Phormidium* (§2*c* and figure 1*c*), where obviously light absorption by a yellow pigment and that by the biliproteins can start the photoperception process. We do not yet know where these two origins converge to a common chain of processes.

There is, however, one example that clearly demonstrates completely independent photoperception systems for the same response in one organism. This is light-oriented chloroplast displacement in the green alga *Hormidium*. The cylindrical cells of *Hormidium* contain one large chloroplast only, which covers about half the cell circumference (figure 5*a*). It can slide along the cell wall, thus orienting to light. In detail, this orientation depends not only on the light intensity but also on the surrounding medium: in low-intensity white light (less than 40 W m^{-2}), the chloroplast is preferentially found distal to the light source if the cell is surrounded by air, but proximal if paraffin oil is the surrounding medium. In the former case, the cell acts as a collecting lens, in the latter case as a diverging lens, due to the differences in the refractive indices (figure 5*b*). Thus the chloroplast always prefers the brightest region in the peripheral cytoplasm (Scholz 1976*a*).

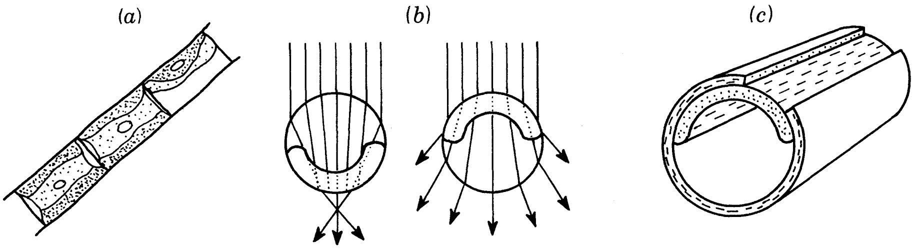


FIGURE 5. Chloroplast movement in *Hormidium flaccidum*. (*a*) Part of a trichome, showing the chloroplast facing the front or rear wall in two cells and facing the flank wall in one cell. (*b*) Cross sections of a cell in air (left) or in oil (right), showing refraction of parallel light rays. The resulting absorption gradient orients the chloroplast to the rear (left) or to the front (right). (*c*) Schematic drawing of a cell with part of the cytoplasm removed (cell wall omitted). The dashes represent the main transition moments of the photoreceptor molecules, with longitudinal orientation in the chloroplast and transverse orientation in the cytoplasm. (After Scholz 1976*b*), Haupt (1983) and Haupt & Wagner (1983).)

These responses are restricted to the blue-light region of the spectrum, and they exhibit an action dichroism, with polarized light being more effective if its electrical vector vibrates perpendicular rather than parallel to the cell axis. Potassium iodide, which is known as a quenching substance of the triplet excited state of flavins, inhibits the response; and a similar effect is found if the flavin content of the cell is reduced by a dark treatment for a couple of days. Finally, responsivity is resumed if iodide is washed out, or if the flavin-deficient cells are externally provided with flavin mononucleotide (FMN). There is therefore very good evidence for a flavin's being the photoreceptor pigment, and for its localization in the peripheral cytoplasm with a surface-parallel orientation of the transition moments, preferentially in a transverse direction (figure 5*c*).

So far, this description is a simplification, as detailed data show. In fact, the treatments with KI or with darkness do not abolish the response completely, but the chloroplast still orients.

However, under these conditions there is an increased tendency to approach the proximal region in all surrounding media, i.e. to orient towards the light source (figure 6). Obviously the lens effect becomes less important, and we have to assume another perception system that enables the cell to measure the light direction independently of light refraction. Information about the second photoperception system is obtained by additional observations: it operates at a broader range of fluence rates than the first system; the action spectrum has an accessory peak in red light, and this red-light effect is sensitive to DCMU; finally, the action dichroism is reversed, parallel-vibrating blue light being the most effective. These facts led to the assumption that this second system is localized in the chloroplast rather than in the cytoplasm (figure 5*c*), and that it has the photosynthetic pigments as photoreceptors. The light direction is sensed as a result of attenuation as light traverses the chloroplast, thus establishing a gradient of light intensity through the chloroplast (Scholz 1976*b*; see also Haupt 1983).

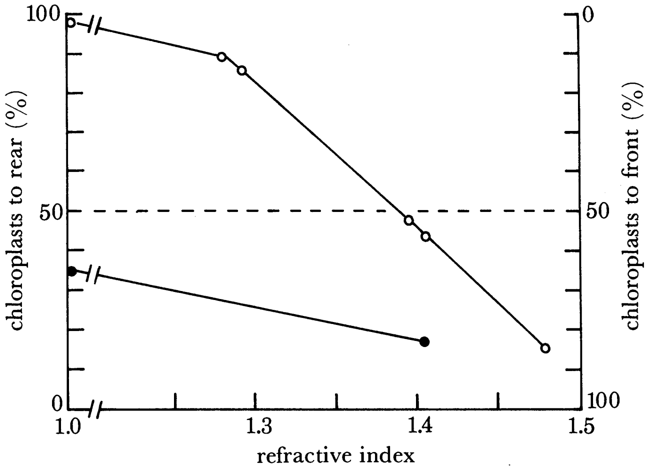


FIGURE 6. Chloroplast orientation in *Hormidium* to the front or the rear, respectively, as dependent on the refractive index of the environment (cf. figure 5*b*), and on the pretreatment (daily light-dark cycles (○) or 5 days of continuous darkness (●)). The broken line indicates a random distribution to front and rear positions. (After Haupt (1983), from data of Scholz (1976*b*).)

In conclusion, in *Hormidium* we have two clearly distinguishable photoreceptor pigments, located in two different compartments of the cell, and this also seems to be true in higher plants (Seitz 1979). Light absorption, then, starts two separate and independent perception processes, which finally have the same result: movement of the chloroplast in the direction of higher light absorption. Remarkably, this same result is found whether an absorption gradient is established in the moving organelle, i.e. in the chloroplast, or in its resting environment, i.e. in the cytoplasm at the membrane. It can be assumed that both perception processes start an elementary biochemical or biophysical process at some point, e.g. a change in active or passive ion fluxes across a membrane, as discovered in the alga *Vaucheria* (Blatt *et al.* 1981), and there is good evidence that those changes could activate the motor apparatus for chloroplast displacement, probably actin microfilaments in the cytoplasm (see Britz 1979; Haupt & Wagner 1983). This could be compared, then, with the activation of animal or human muscles by different types of stimulus, perceived by sensory systems that differ in structure, function and localization.

5. EVOLUTIONARY ASPECTS OF PHOTOMOVEMENT

(*a*) *Selection of photoperception systems in evolution*

It has been shown that in photomovement a great diversity exists concerning photoperception. This diversity is twofold: it concerns different types of response in one organism (§2), and it concerns one response among different organisms (§3). Thus photomovement differs fundamentally from photosynthesis, where a common photoperception system can be found throughout almost the whole plant kingdom. It also differs from vision in animals, where rhodopsin is found as the photoreceptor pigment throughout, irrespective of very different cytological structures of the sensory systems, and irrespective of differences in details of the secondary processes.

This suggests differences in the principle of evolution between the uniform and pluralistic systems, i.e. photosynthesis and vision on the one hand, and photomovement on the other hand. In the former cases, the pressure of selection must have been very heavy, allowing only one optimal system in each to survive. In the latter case, however, several trials of evolution have survived, which very probably are not completely equivalent to each other in their efficiency and in their economy.

This allows speculation that the photoreceptor pigments for photomovement responses have not evolved primarily for these responses. Instead, only an additional use of these already existing pigments had to be invented and to be established, together with completing the corresponding transduction chains (i.e. the perception processes in the sense of the present symposium).

Consistent with this speculation is especially the fact that two different perception chains for one response can sometimes be found in one organism, as has been reported for the chloroplast orientation in *Hormidium* (§4). Evolution of those cases is hard to understand solely on the basis of selection: as soon as one system has evolved, there are no reason and no means for a second system to be selected. Here the only reasonable explanation seems to be the pre-existence of parts of the perception systems, which must have been evolved for other reasons.

(*b*) *Ecology of photomovement*

If this speculation is correct, photomovement should prove to be advantageous for the organism, but not an absolute necessity for survival. I shall therefore try to come to a conclusion about the biological significance of photomovement.

The significance of *photokinesis* is not immediately obvious. Usually photokinesis is positive, i.e. the organism moves faster in light than in darkness. For an autotrophic organism one could speculate that this faster movement during periods of high photosynthesis would facilitate uptake of nutritional salts, which may be limiting: the organism could exploit a larger volume of the medium without exhausting it. However, such an interpretation, although plausible, does not take into consideration the density of organisms in the natural habitat, nor turbulences in the medium. Hence the interpretation is probably weak.

Much more obvious is the significance of the *photophobic response*, which is typically a step-down response. In an aqueous habitat that is partly shaded, e.g. by leaves, organisms live in a pattern of bright and dim regions. If an organism, during its movement, happens to cross a border from bright to dim, a photophobic response often brings it back to the bright region, thus avoiding an unfavourable reduction in photosynthesis. The bright regions, then, can act as light traps.

On the first view, *phototaxis* appears to be a very useful response: it brings organisms to the optimal light conditions by an active orientation. Indeed, this is true in the laboratory, where light intensity usually increases as the organism approaches the light source. In Nature, this situation can be found in partly shaded habitats: organisms (and non-living particles) in the lighted region are sources of effective scattering of light falling directly on them. Thus, organisms in the shaded region 'see' the scattered light, they respond phototactically, they orient to and they finally accumulate in the bright regions, where, by the way, they are trapped by their photophobic response. If, however, an organism were to move phototactically towards direct sunlight it would not experience any increase in light intensity; nor would the intensity decrease if the organism moved straight away from direct sunshine. Thus the usual interpretation has to be reconsidered, according to which negative phototaxis can be a means to protect the organism against damaging irradiation.

6. General conclusion

In research on photosynthesis and vision, much effort has been made to understanding the processes connecting light absorption with the final result. There is good reason to expect that many details of these findings can be generalized, at least within large groups of organisms. In photomovement, the situation is completely different. Even if, in a model organism, one perception system were analysed to the last detail, including all processes through to the final response, nothing could be concluded for other photomovement systems in that organism. The only generalization that can be made for photomovement is its diversity.

References

Blatt, M. R., Weisenseel, M. H. & Haupt, W. 1981 A light-dependent current associated with chloroplast aggregation in the alga *Vaucheria sessilis*. *Planta* **152**, 513–526.

Britz, S. J. 1979 Chloroplast and nuclear migration. In *Encyclopedia of plant physiology* (new series), vol. 7 (ed. W. Haupt & M. E. Feinleib), pp. 170–205. Berlin, Heidelberg and New York: Springer-Verlag.

Diehn, B. 1979 Photic responses and photosensory transduction in motile protists. In *Handbook of sensory physiology*, vol. VII/6A (ed. H. Autrum), pp. 24–78. Berlin, Heidelberg and New York: Springer-Verlag.

Feinleib, M. E. 1978 Photomovement of microorganisms. *Photochem. Photobiol.* **27**, 849–854.

Ferrara, R. 1975 General review on phototactic action spectra. In *Biophysics of photoreceptors and photobehaviour of microorganisms* (ed. G. Colombetti), pp. 121–145. Pisa: Lito Felici.

Foster, K. W. & Smyth, R. D. 1980 Light antennas in phototactic algae. *Microbiol. Rev.* **44**, 572–630.

Häder, D.-P. 1978 Extracellular and intracellular determination of light-induced potential changes during photophobic reactions in blue-green algae. *Arch. Microbiol.* **119**, 75–79.

Häder, D.-P. 1979 Photomovement. In *Encyclopedia of plant physiology* (new series), vol. 7 (ed. W. Haupt & M. E. Feinleib), pp. 268–309. Berlin, Heidelberg and New York: Springer-Verlag.

Häder, D.-P. 1981 Effects of inhibitors on photomovement in desmids. *Arch. Microbiol.* **129**, 168–172.

Häder, D.-P. & Poff, K. L. 1982 Spectrophotometric measurement of plastoquinone photoreduction in the blue-green alga, *Phormidium uncinatum*. *Arch. Microbiol.* **131**, 347–350.

Haupt, W. 1974 Phototactic movements in plants. In *Progress in photobiology* (*Proc. VI Int. Congr. Photobiol.*) (ed. G. O. Schenk), p. 26. Frankfurt: Deutsche Gesellschaft für Lichtforschung.

Haupt, W. 1982 Light-mediated movement of chloroplasts. *A. Rev. Pl. Physiol.* **33**, 205–233.

Haupt, W. 1983 Movement of chloroplasts under the control of light. In *Progress in phycological research 2* (ed. F. E. Round & D. J. Chapman), pp. 227–281. Amsterdam: Elsevier Science Publishers.

Haupt, W. & Wagner, G. 1983 Chloroplast movement. In *Membranes and sensory transduction* (ed. G. Colombetti & F. Lenci). London: Plenum Press. (In the press.)

Neuscheler, W. 1967 Bewegung und Orientierung bei *Micrasterias denticulata* Bréb. im Licht. *Z. PflPhysiol.* **57**, 151–172.

Nultsch, W. 1962 Phototaktische Aktionsspektren von Cyanophyceen. *Ber. dt. Bot. Ges.* **75**, 443–453.

Nultsch, W. 1975 Phototaxis and photokinesis. In *Primitive sensory and communication systems* (ed. M. J. Carlile), pp. 29–90. London, New York and San Francisco: Academic Press.

Nultsch, W. & Häder, D.-P. 1979 Photomovement of motile microorganisms. *Photochem. Photobiol.* **29**, 423–437.

Poff, K. L. & Butler, W. L. 1974 Spectral characteristics of the photoreceptor pigment of phototaxis in *Dictyostelium discoideum. Photochem. Photobiol.* **20**, 241–244.

Poff, K. L., Butler, W. L. & Loomis, W. F. Jr 1973 Light-induced absorbance changes associated with phototaxis in *Dictyostelium. Proc. natn. Acad. Sci. U.S.A.* **70**, 813–816.

Schletz, K. 1976 Phototaxis bei *Volvox*-Pigmentsysteme der Lichtrichtungsperzeption. *Z. PflPhysiol.* **77**, 189–211.

Scholz, A. 1976*a* Lichtorientierte Chloroplastenbewegung bei *Hormidium flaccidum*: Perception der Lichtrichtung mittels Sammellinseneffekt. *Z. PflPhysiol.* **77**, 406–421.

Scholz, A. 1976*b* Lichtorientierte Chloroplastenbewegung bei *Hormidium flaccidum*: Verschiedene Methoden der Lichtrichtungsperception und die wirksamen Pigmente. *Z. PflPhysiol.* **77**, 422–436.

Seitz, K. 1979 Cytoplasmic streaming and cyclosis of chloroplasts. In *Encyclopedia of plant physiology* (new series), vol. 7 (ed. W. Haupt & M. E. Feinleib), pp. 150–169. Berlin, Heidelberg and New York: Springer-Verlag.

Watanabe, M. & Furuya, M. 1974 Action spectrum of phototaxis in a cryptomonad alga, *Cryptomonas* sp. *Pl. Cell Physiol.* **15**, 413–420.

Discussion

A. W. Galston (*Plant Breeding Institute, Cambridge, U.K.*). (1) Professor Haupt showed a slide on which a filament of *Anabaena* had made a right-angled turn in the direction of a unilateral light source. Is anything known about the physical basis for such a movement? (2) What is known about the mechanism of the gliding movements of *Phormidium*?

W. Haupt. (1) Nothing is known about the mechanism of gliding in *Anabaena*, even if it moves straight forward. Hence it is premature to ask for the mechanism of steering. Theoretically, for an orientation to take place it must be assumed that a gradient of light absorption in a cell results in different light effects on the motor apparatus at the lighted and shaded sides.

(2) In *Phormidium* the trichome moves while rotating around its axis. Phenomenologically this is identical with the gliding in *Oscillatoria*, and hence extrapolation from this organism may be justified. Here, undulations of an outer layer of the cell wall appear to be the cause of gliding, including rotation, and the undulations are supposed to be brought about by the activity of fibrillar structures found beneath this layer. These structures are probably different from actin microfilaments, because we are dealing with prokaryotic organisms, which do not possess actin.

J. Bennett (*Department of Biological Sciences, University of Warwick, U.K.*). Which phytochrome-mediated responses seem to involve the fewest steps between photoreception and action?

G. Wagner (*Botanishces Institut der Justus-Liebigs-Universität, Giessen, F.R.G.*). So far there is no case where the complete series of steps between photoreception and action has been analysed. Those cases in photomorphogenesis where regulation of gene expression is involved, probably contain many steps. On the other hand, relatively few steps are assumed for phytochrome-mediated chloroplast orientation in *Mougeotia*. In this regard, I refer to the posters [exhibited outside the lecture hall during the meeting] by Haupt *et al.* and in particular by Wagner *et al.* entitled 'Calcium vesicles and calmodulin from *Mougeotia*'. The main topics of this poster are: isolation and characterization of calcium vesicles from *Mougeotia*; isolation and identification of calmodulin from *Mougeotia*; location of actin within *Mougeotia* by fluorescent phallotoxin. These data, taken together with earlier findings [shown in the poster by Haupt *et al.*], indicate a phytochrome action in *Mougeotia* via calcium–calmodulin–actomyosin to perform light-induced chloroplast reorientation in *Mougeotia*.