EDITORS' PREFACE

Light and time are usually considered to be the playground of the physicist. However, the work presented in this volume clearly places them as central to the living world. The link between light and time is also striking, even to the point where, at the molecular level, the perception of light and the mechanism of the biological clock are inseparable (Macino *et al.* and Dunlap *et al.*, this volume).

Life as we know it is impossible to envisage without the sun as our primary source of energy, and photosynthetic organisms to harvest this. In parallel with the evolution of the photosynthetic machinery, a range of intriguing responses to light have developed, allowing organisms to respond in subtle and even pre-emptive ways to changes in the light. The diurnal rhythm has also been adopted as a central component to many organisms which cannot harvest light energy, light being a source of information relating to many other aspects of the environment as well as a key agent responsible for damaging macromolecules. Not surprisingly therefore, light is directly involved in setting of the circadian clock which, in turn, affects a wide range of biological phenomena in organisms as diverse as cyanobacteria and human beings.

In the opening chapter, John Allen has presented an overview lucidly demonstrating the breadth of the field, which extends over a time scale ranging from femtoseconds to gigayears (see also Lloyd and Gilbert, this volume). The physics of light absorption, its concomitant dangers and benefits, the transfer of the energy, and its final demands and consequences on the cell's physiology and development are all addressed. The predictive nature of the circadian clock and questions relating to evolution, and the horizontal transfer of some of these key biological systems are also considered.

Light is an exploitable energy source with the consequence that, in the most common form of photosynthesis, oxygen is generated. However, oxygen and light are a lethal combination. The biological response has been to evolve a variety of behavioural and regulatory strategies. The principal behavioural response is phototaxis, with positive phototaxis towards light of a usable wavelength and negative phototaxis from wavelengths that are harmful. The regulatory approach includes the synthesis of photoprotective molecules such as carotenoids when appropriate (Hodgson and Berry, this volume) and the synthesis of photoharvesting assemblies only in the absence of oxygen, as in the purple bacteria (Cogdell *et al.* and Phillips-Jones, this volume) and halobacteria (Spudich, this volume). In addition to this regulatory response, both these bacteria also employ the behavioural option.

In the photosynthetic bacteria, described by Judith Armitage, it appears that behaviour and photosynthesis are linked via the photosynthetic/respiratory electron transfer chains of these organisms, or possibly a protometer (Δp), both of which are also influenced by other factors such as redox, and which therefore also influence behaviour. The ability of the organism to sense, signal and respond to several components within its environment simultaneously demands co-ordination and this, in turn, seems to have produced mechanical links to integrate the various systems involved.

However, simple strategies are also available such as the self-regulating buoyancy mechanism employed by some cyanobacteria involving gas vesicles (Walsby, this volume). In the case of some micro-organisms there is an apparent ability to determine the direction of a light source, such as in the flagellated alga *Chlamydomonas* (Hegemann and Harz, this volume). The eye, which is only 1 μm across, is able to detect the intensity of the light, and its variation with respect to the rotational movement of the organism also allows orientation. The life cycle and development of moss is dependent on light as a cue at various stages (Cove and Lamparter, this volume). One of the most intriguing aspects of this plant's responses to light is seen in the regeneration of protoplasts, which requires high levels of light; most interestingly, they display polarity of growth, which is principally determined by blue light.

The evolutionary link between the proteins responsible for harvesting light for energy transduction and those involved in signalling has been explored at the molecular level in *Halobacterium* by John Spudich. The four principal proteins are structurally related but have diverged, depending on their role in energy or signal transduction. A detailed structural analysis of the light harvesting centres from several organisms (the antenna complexes) reveals a diverse array of structures (Cogdell *et al.*, this volume). The available molecular detail, rather than defining a clear model, demonstrates variety which almost certainly reflects the ecological niches of the respective organisms, where the system has to be adapted to the appropriate wavelengths and intensities of light to maximally convert the available energy without damage. This careful balancing act requires precise regulation of the light harvesting machinery, which is considered in detail for both the pigment proteins in *Rhodobacter* (Phillips-Jones, this volume) and carotenoid synthesis in *Myxococcus xanthus* (Hodgson and Berry, this volume). Parallels can be drawn between these prokaryotic signalling pathways and those of the eukaryotes. The filamentous fungus *Neurospora crassa* is sensitive to blue light, which acts as a signal for developmental processes, including carotenoid biosynthesis, and the circadian clock (Macino *et al.*, this volume). The molecular characterization of the signal transduction pathway has recently led to the identification of two transcription factors. Interestingly, these have motifs common to bacterial proteins involved in redox sensing (the PAS domains) and DNA binding domains shared with the principal erythroid transcription factors of vertebrates. This suggests a convoluted evolutionary history as well as an intriguing correlation of light and oxygen.

The remaining five chapters are all concerned with time, and with the way in which light and other environmental components are crucial in setting the biological clock. Susan Golden and co-workers (this volume) have demonstrated that, in at least some prokaryotes (the cyanobacteria), the features that define the clock share properties common to eukaryotic organisms. The cyanobacteria are presented with the problem that the oxygen produced by photosynthesis is not compatible with the key enzyme in nitrogen fixation, nitrogenase. Thus the processes of photosynthesis and nitrogen fixation have to be separated temporally as well as spatially. This temporal requirement is achieved with a molecular clock which can be entrained by both light and oxygen.

Perhaps the most striking combination of circadian phenomena described in this volume is that of the marine dinoflagellate *Gonyaulax polyedra* (Roenneberg and Rehman). The circadian rhythm defines a periodic rise and fall of the organism within its marine environment of up to 30 metres, the timing of mitosis, photosynthesis and two distinct forms of bioluminescence. The signals involved in altering the clock are equally complex, with both red and blue light acting separately, combined with a role for nitrogen sources. Mitosis and the cell cycle, as aspects of biological time, are explored further in the review by Lloyd and Gilbert (this volume), who catalogue the wide range of time domains observed within living systems.

Perhaps the most interesting work relating to the molecular basis of the biological clock has come from the dissection of the molecular basis of the circadian clock in *Neurospora crassa* (Dunlap *et al.*, this volume). From this work we have our first detailed overview of the clock mechanism. One of the central components, the gene frequency, having been cloned and characterized, has been shown to integrate the known components of the circadian clock, the light response, a temperature compensation, and a periodic rise and fall in the level of the active protein product within the cell, which appears to define the circadian rhythm. This involves regulation at the level of transcription, translation and post-translation. When extending studies from microbial systems to insects, vertebrates (Kyriacou, Piccin and Rosato, this volume) and plants, it would appear that the basic components and organization of biological clocks are similar, with light as a principal signal, temperature compensation built in, and a variety of clock responsive genes integral to a wide range of processes from basic metabolism to development. Whether these parallels continue to be strengthened with the rapidly accruing molecular detail remains to be seen. The recent finding that the microbial PAS dimerization domain is involved, even in animal systems, suggests that microbial clocks are excellent models with broad relevance. The rapid pace of research in this field will mean that many of the remaining fundamental questions will not be unanswered for long.

The authors have presented an excellent range of current reviews and include a number of different scientific approaches, extending from the ecological to the biophysical, to describe and dissect a variety of phenomena which are pertinent to most, if not all, biological systems. We thank all the contributors for their considerable efforts, which have resulted in this wide-ranging and comprehensive account, and our hope as editors is that they prove both illuminating and timely.

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and M. K. Phillips-Jones, December 1997