Wave produced changes in underwater light and their relations to vision

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Synopsis

Maximal visual sensitivity of most vertebrates and invertebrates coincides with the dominant wave-induced flicker frequencies associated with underwater light. Waves also produce patterns off reflective objects that resemble many of the body markings found on fishes. The close relationship that exists between the physiological properties of spatial and temporal vision thus suggests an ancient adaptation to the wave-induced fluctuations and spatial patterns associated with underwater light.

Introduction

Visual perception requires the analyses of both the temporal and spatial properties of light. Temporal perceptions of space, as in movement detection, are superimposed against a fixed spatial background. To persist, the perception of fixed objects requires periodic changes in the images presented to the eye. In humans any scene that is optically stabilized on the retina rapidly fades from view, leaving only a sense of luminance (Alpern 1972). If the luminance of the stabilized image is changed, or if the eye moves ever so slightly, the scene does not fade. Pattern discrimination is therefore closely interwoven with the time-dependent mechanisms of vision, i.e. temporality (Robson 1966, Kelly 1972a, b).

Given that temporality is central to visual function, how then is it inserted into the visual process and, why is it so dominant a part of the visual equation? We examine these questions here and conclude that the temporal and spatial characteristics of vision may find explanation in the optical properties of waves and represent an ancient adaptation that enhanced the visibility of targets underwater then as now.

Modes of temporal change in light

At least three events impart temporal change in the visual process: 1) actions that move the image of the outside world on the retina: such as locomotion, head movements, and eye movements; 2) motion of objects across the visual field; 3) variation in the light cast on the photoreceptor array, i.e., the light flickers.

The first two mechanisms shift the image from one area of the retina to another, and produce temporal change by successively exciting different photoreceptors and receptive fields. The destabilization of fixed images in humans is accomplished by small involuntary movements of the eyes known as saccades (Alpern 1972), which also occur in

mammals (Carpenter 1977), pigeon (Nye 1969), fishes (Easter 1971), and crustaceans (Burrows & Horridge 1968). Although the precise relation between saccades and vision remains controversial (Barlow 1969), it is clear that saccades improve visual acuity in humans (Barlow 1963, Yarbus 1967).

Flicker may be produced by three mechanisms, two biological and the other physical. One type of biological process, e.g. eye blinking, modulates light entering the eye by chopping it into pulses. A second biological process does not actually modulate light entering the eye. Instead the photoreceptor cells are periodically turned on-and-off via inhibitory neural feedback loops, as postulated for *Limulus* (Fuortes & Hodgkin 1964, Fuortes & O'Bryan 1972) and for dipterans (Loew 1974). The physical mechanism modulates light before it irradiates a target and its background. Natural mechanisms by which physical modulations of light are produced are scarce: e.g. surface water waves and ripple, action of wind on leaves, convective heating of air (mirages), and cloud movement. Only the flicker produced underwater via the optical action of waves and surface ripple, in our opinion, has been fundamental in the evolution of vision. What exactly is the temporal character of wave induced flicker?

Light fluctuations in aquatic habitats

Temporal considerations – wave induced flicker

The fluctuations in light observed when viewing the water surface or when looking at the patterns that dance across a reflective sand bottom, are produced by the action of waves as complex lenses. In general, the focal plane depth increases as a wave's period increases (Schenk 1957). Thus short, steep waves focus light closer to the surface than shallower waves. For mixed-waves the focus to collimated light, as approximated by sunlight, is extended over a range of depths. Because of these lensatic properties, light from flicker can achieve several times the average illumination at any focal depth, but fluctuations are usually greatest near the surface (Dera

& Gordon 1968, Snyder & Dera 1970). Here we refer to conditions of high water clarity. With increased turbidity and/or more diffuse skylight conditions (e.g. during night or cloudy conditions) extreme scattering and, therefore, increased defocusing occurs.

Little attention has been directed at the biological implications of wave-induced flicker (e.g. in primary production of algae, Dera & Gordon 1968; in vision of fishes, McFarland & Munz 1975b, Munz & McFarland 1977). Light fluctuations measured to 5 m depth in the Florida current, revealed flicker frequencies below 8 Hz, with a dominant at slightly less than 1 Hz (Gordon et al. 1971). Unfortunately, the frequency response of their instrument cut-off at 3.7 Hz, underestimating the contribution of any higher frequencies. In addition, the instrument measured irradiance, i.e. the detector was sensitive to light over a wide angle. This would tend to average the higher frequency components. To measure the flicker frequencies important to a visual
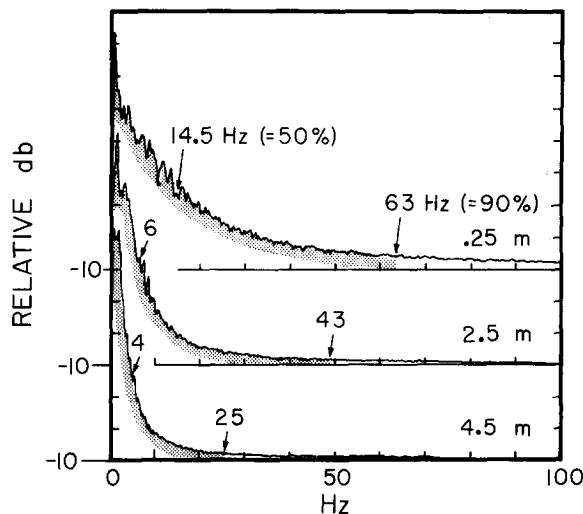

Fig. 1. Power spectra of wave-induced light fluctuations at different subsurface depths in a typical shallow tropical sea. The data depicted are for a clear sunny sky within a coral reef area at St. Croix, U.S.V.I. Note the offset of each curve along the ordinate; divisions equal −1 db and frequency (Hz). Depths below the water surface are indicated to the right of each curve. The two values indicated on each curve are the boundary frequencies in Hz for 50 and 90 percent of the total power spectrum (i.e. the partitioning of a complex waveform on the basis of frequency). Note the reduction of the higher frequencies with increased depth.

174

Table 1. Critical fusion frequency (CFF) for various animals in bright light (photopic) and in dim light (scotopic) conditions. The flicker frequency for maximal contrast sensitivity is estimated as equal to 15% of the photopic CFF, with the exception of flies (see reference 7).

Type animal	Photopic CFF	Scotopic CFF	Maximal contrast sensitivity	References
Octopus	70	—	11	1
Arachnids				
Limulus	15	—	2	2
Wolf spider	50–100	—	11	3
Crustacea				
Cambarus & Pagurus	50–56	—	8	4
Ligia	120	—	18	5
Insects				
Bees, wasps, flies & dragonflies	300–400	50	16	6, 7
Butterflies, moths & beetles	80	—	12	6
Cricket & cockroach	—	5–15	—	8
Dytiscus	70	50	11	9
Fishes				
Ray	30	6	5	10, 11
Shark	10	7	2	10
Holosteans	38	—	6	12
Teleosteans	38–87	15	5–13	10, 13, 14
Amphibia				
Frog	40	25	6	15
Reptile				
Turtle	53	27	8	15
Lizard	26–60	17	4–9	15, 16, 17, 18
Birds	34–150	22	5–23	6, 19, 20
Mammals	50–60	25–35	8	24, 25, 26
Range	(15–400)	(5–35)	(2–23)	

References: 1) Hamasaki 1968, 2) Ratliff et al., 1967, 3) DeVoe 1966, 4) Waterman 1961, 5) Ruck & Jahn 1954, 6) Autrum 1958, 7) Laughlin 1980, 8) Loew unpublished, 9) Jahn & Wolff 1941, 10) Kobayashi 1962, 11) Green & Siegel 1975, 12) Gramoni & Ali 1970, 13) Tamura & Hanyu 1959, 14) Ali & Kobayashi 1968, 15) Crozier & Wolf 1941a, 16) Crozier & Wolf 1939, 17) Hamasaki & Peregrin 1970, 18) Jenssen & Swenson 1974, 19) Crozier & Wolf 1941b, 20) Dodt & Worth 1953, 21) Svaetichin 1956, 22) Granit 1963, 23) Hamasaki 1967, 24) Kelly 1972a, 25) Smith et al. 1976, 26) Witzel & Smith 1976 (from 24).

system a radiance photometer (5° angular field) with a frequency responses flat beyond the highest response reported for any animal (~ 300 Hz, Table 1) was built.

Flicker from downwelling light was characterized in a clear tropical sea within a coral reef area at various intervals from 0.25 to 5 m depth by establishing the power spectrum from a two-minute measurement fed into a Nicolet Fast Fourier Transform Spectrum Analyzer. The power spectra extend further towards higher frequencies the closer recordings were made to the surface (Fig. 1). The power at higher frequencies represent a transition from the lower frequency surface gravity waves to the much higher frequencies associated with surface ripple, or capillary waves (>10 Hz, van Dorn 1974). However, at all depths the power spectrum was dominated (i.e., $>50\%$) by frequencies below 15 Hz (Fig. 1). Nevertheless, some power was present above 50 Hz at all depths over which we recorded.

Visual responses to temporal properties of light

A common technique for indexing the temporal response of a visual system is electrophysiological

and/or behavioral measurement of the frequency at which a flickering light appears to have constant brightness, i.e., when the repeated stimuli fuse. This is termed the critical fusion frequency (CFF). A compilation of CFF values from a variety of animals (Table 1) reveals: 1) photopic CFF is usually higher than scotopic CFF, and 2) eco-behavioral correlates exist, e.g., diurnal fliers have higher CFF values than non-fliers, or nocturnal fliers. High CFF values are associated with the resolution of fast moving objects (Walls 1967) and implies that retinal after images fade rapidly. This is requisite for resolution, as otherwise blurring would occur. In a few instances CFF values show species specific correlations with the photic nature of the habitat (diurnal vs. crepuscular activity in lizards, Crozier & Wolf 1939; and sun vs. shade seeking species of *Anolis*, Jenssen & Swenson 1974), or with

rapidity of motion and presumed predator-prey interactions (insects, Autrum 1950; some fishes, Protasov 1968).

CFF values are dependent on factors such as stimulus intensity and size, background illumination, etc. For comparison we have included only the highest CFF values in Table 1. Care should be exercised in interpreting the comparisons because it is difficult to correct for the different methods employed. Furthermore, the CFF probably has only limited real behavioral or ecological significance. A plot of photopic sensitivity versus flicker frequency for humans (Fig. 2) reveals that maximal response occurs between 5 and 10 Hz, remains high to frequencies below 1 Hz, but falls off toward higher frequencies (DeLange 1958, Kelly 1959), the cut-off of which is the CFF. The relevant temporal response therefore may be the broad peak in visual sensitivity to flicker, and not the CFF. Although these measurements are not available for a wide variety of animals, where they are the peak usually falls within 10 to 20 percent of the CFF values. In most diurnal animals the maximal response occurs at flicker ranges between 3 to 10 Hz (Table 1). Why is this frequency range common to so many animals?
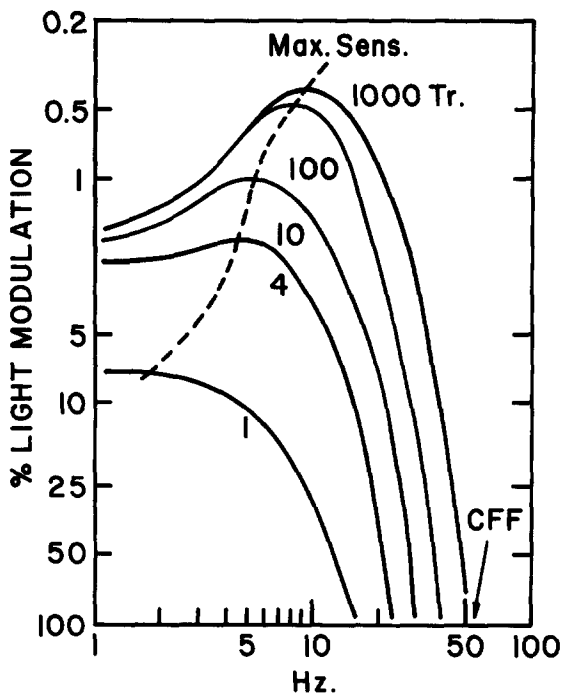

Fig. 2. Flicker threshold sensitivities in a human at different levels of illumination for different frequencies (Hz) (modified after Kelly 1972a). Percent light modulation is the threshold amplitude change in the light intensity of a small test spot presented against a steady background; a value of 100 refers to complete extinction (darkness) of the test spot with each oscillation. Numbers on each curve are retinal illumination levels in Trolands.

Correlations between flicker and vision

A correlation exists between the dominant frequencies of wave-induced flicker (<15 Hz) and the frequencies of maximal response of most animals, especially the aquatic species (Table 1). In addition, the highest CFF values for fishes coincide with surface living diurnal species, such as atherinids and anchovies (Protasov 1968) where wave-induced flicker rates are highest (Fig. 1), or with predatory fishes like trout (Gramoni & Ali 1970) where detection of prey against or near the water surface is routine. Similarities also exist between frequencies of involuntary eye movements, which are important in sustaining image perception (Alpern 1972), and frequencies of wave-induced flicker. Both are irregular but range from <1 Hz to values above 20 Hz, with 1 to 5 Hz most typical.

To use flicker effectively, a match between flicker frequencies underwater and the frequencies for

maximal sensitivity would be expected and, certainly, the available data fit. Only in diurnal flying insects (Autrum 1950), the pigeon (Dodt & Worth 1953) and a crustacean (Ruck & Jahn 1954) do measured CFF values exceed 100 Hz; in most animals the CFF's are below 50 Hz (Table 1). This discrepancy makes sense in rapid flyers, where speed and manoeuvers require a rapid sequential analysis of the outside world.

Spatial considerations – wave produced patterns

Waves create an ever changing series of light and dark spatial patterns underwater. These patterns are not visible, however, unless a reflective object(s) is present. Simple periodic waves, as from a spreading ripple, produce very organized patterns. In oceans and large lakes, however, simple wave patterns mix to produce complex patterns.

For given sea conditions observed patterns from a reflective surface are a function of: 1) solar angle, 2) depth, and 3) the orientation of the reflective object relative to sun and surface (Fig. 3). Three-dimensional objects will reflect more complex patterns than flat surfaces, but for simplicity we used a flat surface. First, pattern detail and spatial frequency decrease with depth. The high flicker frequencies associated with focused ripple (Fig. 1) are clearly associated with the high spatial frequencies and details of pattern just beneath the surface (Fig. 3).

Second, changes in orientation of the reflective surface to sun and water surface produced two primary patterns. With the sun overhead and the reflective surface oriented vertically a series of vertical light and dark bands that resembled a vertical linear-grating was seen (Fig. 3A). When the reflective surface was angled upward this linear pattern changed into a reticulated mosaic, the cells of which were smaller and their details finer close to the surface (Fig. 3B). When the sun's altitude was lower the pattern on the vertical reflector appeared again as a reticulated mosaic (Fig. 3C). The relationship of reflector angle to solar path seems clear. Reflective surfaces perpendicular to the sun have mosaics with elliptically shaped cells. As the angle between sun and reflector becomes acute the cells

elongate. At very acute angles the cells elongate sufficiently that their sides create light and dark bands similar to those depicted in Fig. 3A.

A related sequence of patterns is created (if the sun is not overhead) when a vertical surface is rotated about its axis (Fig. 3D). Near the surface a band of finely detailed cells grade into a linear-grating whose bands deviate from the vertical in proportion to the suns altitude. We have yet to examine the effects of a variety of angles and orientations between sea surface, sun and reflector, and particularly, under different sea conditions. Certainly additional subtleties of pattern will be revealed. But this initial analysis indicates how complex waveforms can produce organized and recognizable patterns with identifiable spatial frequencies.

These very patterns are surprisingly similar to the markings observed on a variety of fishes – e.g. on mackerel, tuna, barracuda, etc. – a circumstance that we suspect is more than coincidence.

Visual responses to the spatial properties of light

A general procedure used to evaluate the ability of animals to resolve detail is measurement of their responses to linear gratings (Campbell & Maffei 1974, Maffei 1978). Grating properties are defined in terms of spatial frequency (i.e. the number of cycles per degree as determined from the number of bands per unit length of grating, and the gratings distance from the viewer) and modulation depth (i.e. contrast). In general, resolution of high spatial frequencies by an animal correlates with 'good' visual acuity.

Further insight into how animals 'see' spatial detail is obtained by varying the spatial frequency and the contrast of the bands and/or the illumination of a grating. In this manner the relationship(s) between visual contrast sensitivity and an object's detail can be established.

This approach has been exhaustively applied in humans, where response from the subject is easily obtained (Fig. 4). The shapes of the spatial frequency curves for humans at high luminance show a striking parallel to the temporal frequency response curves (Fig. 2). As for temporal frequencies there is a range of spatial frequencies to which the
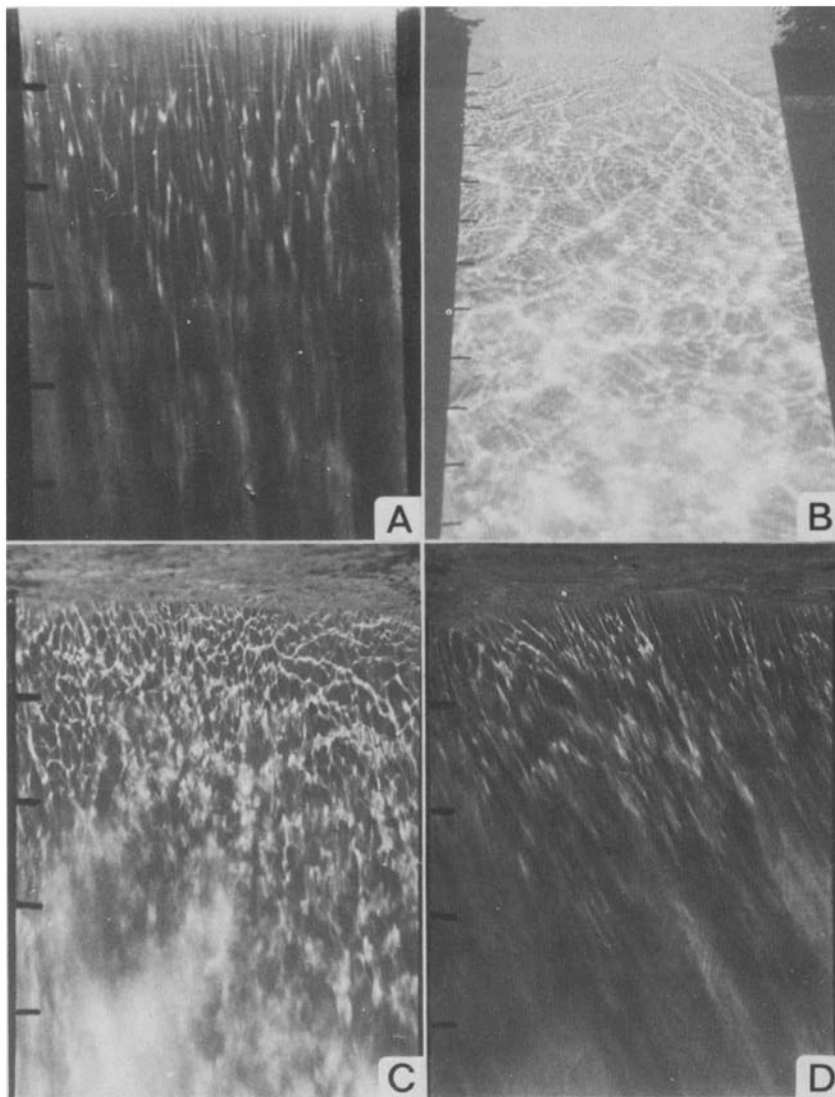
Fig. 3. Wave-induced spatial patterns on a flat reflector just beneath the water surface. Distance between markings is 10 cm (in A and C only where the reflector was perpendicular to camera axis). A – vertical orientation of reflector with sun almost directly overhead; B – orientation of reflector 30° from vertical, sun almost overhead; C – vertical orientation of reflector, normal to solar azimuth, sun altitude 45°; D – vertical orientation of reflector, 45° from solar azimuth, sun altitude 45°. Note that two basic patterns occur: reticulated mosaics and linear-bands.

human is maximally sensitive. Stated in eco-behavioral terms resolution of highly detailed patterns (high spatial frequencies) requires intense illumination and maximal contrast in the pattern. Patterns with less detail (intermediate spatial frequencies) are more easily resolved (Fig. 4), while coarse patterns again must have a higher contrast and illumination.

Although shifted along the abscissa, the few comparable curves that are available for other vertebrates have similar shapes (Fig. 4). These spatial frequency shifts are not unexpected, since the goldfish and cat have lower visual acuity than a human (Johns & Easter 1978).
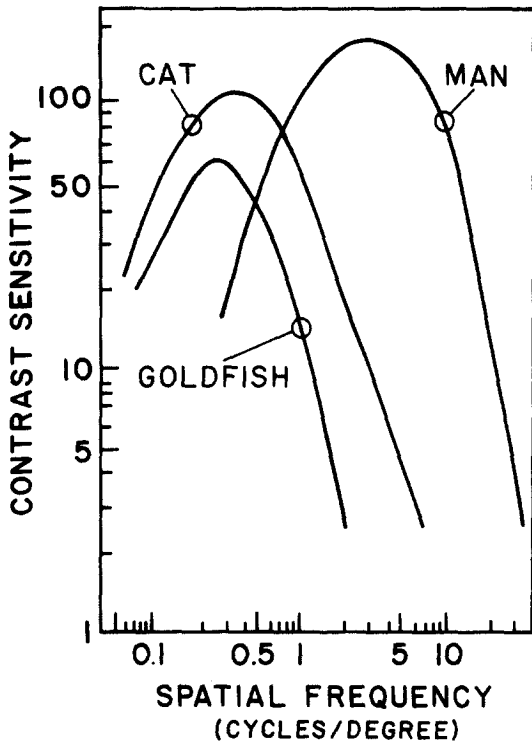
Fig. 4. Contrast sensitivity to linear-gratings of different spatial frequencies in the human, cat and goldfish (after Northmore et al. 1978). Illuminance levels varied for the different species tested. Note the similarity in the shape of each curve and their general likeness to the temporal frequency curves shown in Figure 2.

Spatio-temporal interactions in vision

It is possible to combine temporal and spatial frequency analysis by presenting gratings of different spatial frequencies at different temporal frequencies, or by moving gratings at different velocities. Simultaneous spatio-temporal experiments are most relevant because they more closely approximate how visual stimuli are received in nature and, especially, underwater. This analysis has only been performed with humans (Robson 1966, Kelly 1972b, Burr & Ross 1982). Maximum sensitivity is achieved over a limited temporal and spatial frequency range (Fig. 5). Because the discrete spatial and temporal frequency response curves for those animals that have been examined are similar to humans (see Table 1, Figs. 1, 4), we believe it is reasonable to assume that the combined

spatio-temporal sensitivity of most vertebrates will approximate the shape for humans (Fig. 5).

Wave induced flicker, spatial patterns and fish behavior

Environmental illumination comes in two forms; usually as fluctuating pulses in aquatic habitats and a steady flux in terrestrial systems. Light does not fluctuate underwater during calm periods, nor does it do so at great depths where only a sense of light directionality remains (Jerlov 1968). But mostly light flickers near the surface and thus has the potential to produce patterns underwater.

In general, targets underwater are more difficult to detect than in air (Duntley 1951, Lythgoe 1966, 1979, Munz & McFarland 1977). If fishes are qualitatively similar in visual performance to humans, then fishes must have minimum contrast thresholds to objects whose radiance fluctuates between 1 and 10 Hz (Figs. 2, 5). Near surface
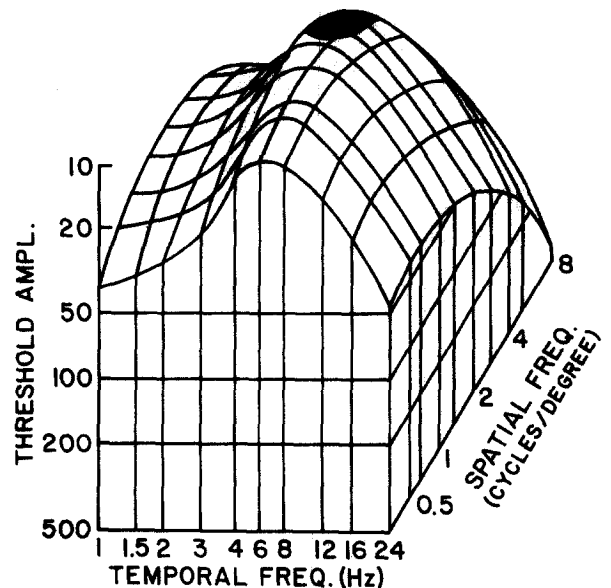

Fig. 5. Threshold amplitudes in humans to the simultaneous presentation of temporal and spatial information (after Kelly 1972b). The results clearly show that linear-gratings of intermediate frequencies (2–4 cyc per degree) are most easily seen when they flicker at intermediate frequencies (4–6 Hz); blackened area indicates region of maximum sensitivity.

objects therefore should be more visible to a fish when illuminated by wave induced flicker than during periods of calm. The acutal visibility of flickering objects underwater, however, depends on several additional factors.

Object size and location

In general, large flickering targets are more obvious than small ones not only because they are bigger, but also because fluctuating patterns are reflected from them (Fig. 3). Very small objects, such as zooplankton, are observed most easily in the upper meter of the water column, where they flash on and off at a noticeable rate. This can be attributed to: 1) the increase of flicker rates in the maximal temporal sensitivity range of humans (Figs. 1, 2, 5); 2) the higher levels of irradiance close to the surface (Jerlov 1968, McFarland & Munz 1975a); and 3) the greater modulation contrast of an object that should result from the greater amplitude shifts of flickering light that occur in the upper meter (Dera & Gordon 1968, Snyder & Dera 1970). Thus, object size and depth beneath the surface determine whether it will reflect a fluctuating pattern or merely 'flash'. The line-of-sight significantly affects the visibility of flickering objects. Viewed from below they merge into the flickering glare of Snell's window. But viewed from the side or from above they 'flash' against a non-flickering background (McFarland & Munz 1975b, Lythgoe 1979).

Countershading

Pelagic fishes readily merge with the water background when viewed from most directions (Denton & Nicol 1966). Dark dorsally and silvery on the flanks and belly, these countershaded patterns also reduce flicker, especially when viewed against the homochromatic light typical in the pelagic habitat (McFarland & Munz 1975b).

For inshore habitats the bottom is often reflective and photic conditions along different lines-of-sight are more variable than in the pelagic zones (McFarland & Munz 1975a, Munz & McFarland 1977). Interestingly inshore semi-pelagic fishes are countershaded less heavily than pelagic fishes. Several

factors explain this difference. Darkly counter-shaded pelagic fishes viewed from above would form silhouettes against a reflective background like sand. Inshore waters are less clear than offshore water masses, for they contain bottom particles and more plankton. As a result inshore water tends to have higher veiling-brightness (Lythgoe 1966, 1979). In these circumstances diminished counter-shading decreases silhouette contrast as 'seen' from above, and because less heavily countershaded fishes reflect some light off their backs they better match the 'brighter' horizontal spacelight of inshore waters.

Many semi-pelagic inshore fishes have little countershading and some species can modify their countershading (ballyhoo, many anchovies and atherinids, carangids, needlefish, and barracuda, personal observations). Often these fishes feed and remain close to the surface throughout the day. Viewed from above, as by a predatory bird or fish, they merge with the bottom because their silvery backs flicker in synchrony with the wave-induced light fluctuations displayed on the sand. When viewed from the side, however, they are obvious because spatial pattern (Fig. 3) flick along their backs against the non-flickering background. Seen from below these non-countershaded fishes may or may not flicker against the oscillating surface, dependent on sun angle and depth. When threatened these fishes employ a specific evasive behavior consisting of movement to the surface. By so doing they literally merge with the flickering surface and are extremely difficult to fixate, let alone see. Only their darker eyes offer an obvious target. A counter-shaded fish employing the same tactic would not flicker but appear as a silhouette against the bright flickering surface. Thus, diminished countershading in many inshore fishes may serve to decrease their visibility when viewed against fluctuating light backgrounds.

Wave induced spatial patterns and body markings in fishes

Numerous marine and fresh-water fishes possess recurrent types of body markings. Common are spots, vermiculations and vertical bars (examples

inshore: sergeant majors, many butterfly fishes, cichlids and centrarchids; offshore: many carangids, wahoo, tunas, marlins). Suggested functions for vertical bars are: 1) advertisement-improved visibility, 2) camouflage, e.g. a barred fish in emergent vertical vegetation (Lythgoe 1979). No single hypothesis explains barring in fishes, for they are present in many demersal fishes as well as in free swimming fishes. But we are impressed that lineargratings represent one of the two types of spatial patterns that we could define in wave induced flicker (Fig. 3).

Do vertical bars mimic these wave-induced patterns? And, do bars diminish or increase visibility? Perhaps they do both. For example, the five vertical bars in the sergeant major *Abudefduf saxatilis*, make it highly visible to humans (Lythgoe 1979, p. 204). Vertical gratings improve object visibility underwater because image boundaries are rapidly degraded by light scattering along the optical path. Spatial frequency detectors, which are characteristic of vertebrates, respond to the internal dimensions of a display rather than the sharpness of its edges (Lythgoe 1979). But, seen against the flickering water surface, where they often feed during the day, individual sergeant majors are extremely difficult to fixate. As they wheel at the surface the spatial frequency presented by their vertical bars quickly changes and, at least for humans, their visibility changes rapidly – now you see one, now you don't. This 'confusing' visual task is even more difficult at dusk when light levels decline. Similar sized unbarred Horse-eye jacks, *Caranx latus*, swimming with the sergeant majors, were always more visible. Without experimentation it is difficult to dissect the basic cause of these visual differences, for the body shapes and swimming behaviors of each species were different. Nevertheless, our impressions introduce the possibility that vertical bars act not only to improve visibility, but also that sudden changes in the spatial frequency of a fish's bars might confuse potential predators. This idea runs parallel to the confusion-effect hypothesis widely used to explain how schooling functions as an antipredator device (Hobson 1968, 1979). Vertical bars serve as camouflage, as attention getters and, perhaps, to confuse predators by interrupting fixation.

Another body pattern common on fishes, and particularly on pelagic species, is disrupted vermiculations on the back. These markings are similar to the flickering reticulations reflected from surfaces that are not parallel to the solar beam (Fig. 3B, 3C). In fact, the presence of these dorsal vermiculations that grade into linear bars on the flanks, and sometimes even on the bellies of the pelagic fishes (bonita), if not a mimicry of wave-induced spatial patterns are, certainly, at the anatomical locations that one would predict from the observations. A vivid example of this phenomenon is illustrated in the photograph of a great white shark taken by David Doubilet (Clark 1981, see pp. 186–187). The dorsal vermiculations and vertical barrings reflected off the body flanks and head of the shark are graphic replicas of those shown in Fig. 3. But more precise field observations and experimentation are required to establish or to reject these suggestions.

Evolution of temporal and spatial vision

Are the close relationships between spatial and temporal vision evidence of an ancient time reference within which the physiological properties of the eyes of both invertebrates and vertebrates evolved? We think so. For example, the first vertebrates evolved in shallow tropical Cambrian seas (McFarland et al. 1979) and co-existent with them were ancient crustaceans, arachnids, and molluscs. All must have experienced flickering light with frequencies not unlike those of tropical seas today.

Waves provide the only consistent and geographically widespread source of fluctuating light with a time frame that matches the temporality of both invertebrate and vertebrate vision. We conclude that the neural architecture and physiology of the image forming eyes of early invertebrates and vertebrates evolved to function in the fluctuating light of shallow seas, and that remnants of this ancient photic adaptation persist in living species.

Summary and conclusions

1) The spatial and temporal frequency responses of animals with image forming eyes are qualitatively similar to humans. For most animals flickering stimuli fuse (CFF) below 100 Hz, but maximal contrast sensitivity occurs at lower frequencies (2–23 Hz).

2) Contrast sensitivity is maximal at intermediate levels of detail (spatial frequencies).

3) The spatio-temporal frequencies at which contrast sensitivity is maximal vary in different species and, probably, represent adaptations to detect objects relevant to each species life-style. These broad similarities in spatio-temporal perception suggest that the evolution of image forming vision in both invertebrates and vertebrates was influenced by the same selective force.

4) Surface waves acting as lenses focus sunlight at various depths beneath the surface. Flicker rates from this process match the frequency responses of animals with image forming eyes. We suggest that the similar temporal characteristics of the visual systems of both invertebrates and vertebrates evolved to function in the time-frame set by wave-induced flicker in shallow seas.

5) Waves can produce fluctuating patterns of different spatial frequencies underwater. For given wave conditions spatial frequency (detail) and pattern structure are a function of sun altitude, depth, and the orientation of a reflective object to the solar beam and to the water surface. Two major patterns occur – reticulations and linear-gratings. The vermiculated dorsal patterns and vertical bars observed on many fishes probably relate to these wave-induced patterns. These body markings function in several ways, with camouflage, advertisement, and interruption of fixation, or visual 'confusion' representative of specific examples.

Acknowledgements

References cited

Ali, M.A. & H. Kobayashi. 1968. Electroretinogram – FFF in albino trout. Experientia 24: 454–455.

Alpern, M. 1972. Eye movements. pp. 303–330. In: D. Jameson & L.M. Hurrich (ed.) Handbook of Sensory Physiology, Springer-Verlag, Heidelberg.

Autrum, H. 1950. Die Belichtungs-potentiale und das Sehen der Insecten. Z. Vergl. Physiol. 32; 176–227.

Autrum, H. 1958. Electrophysiological analysis of the visual systems in insects. Exp. Cell. Res. Suppl. 5: 426–439.

Barlow, H.B. 1963. Slippage of contact lenses and other artifacts in relation to fading and regeneration of supposedly stable retinal images. Quart. J. Exp. Psychol. 15: 36–51.

Barlow, H.B. 1969. Stabilized retinal images. pp. 431–439. In: W. Reichardt (ed.) International School of Physics Enrico Fermi, Academic Press, New York.

Burr, D.C. & J. Ross. 1982. Contrast sensitivities at high velocities. Vision Res. 22: 479–484.

Burrows, M. & G.D. Horridge. 1968. The action of the eyecup muscles of the crab, Carcinus, during optokinetic movement. J. Exp. Biol. 49: 223–250.

Campbell, F.W. & L. Maffei. 1974. Contrast and spatial frequency. Sci. Amer. 231: 106–114.

Carpenter, R.H.S. 1977. Movements of the Eyes. Pion Ltd., London. 420 pp.

Clark, E. 1981. Sharks magnificent and misunderstood. Nat. Geog. 160: 137–187.

Crozier, W.J. & E. Wolf. 1939. The flicker response contour for the gecko (rod retina). J. Gen. Physiol. 22: 555–566.

Crozier, W.J. & E. Wolf. 1941a. The flicker response contour for Phrynosoma (horned lizard; cone retina). J. Gen. Physiol. 24: 317–324.

Crozier, W.J. & E. Wolf. 1941b. The simplex flicker threshold contour for the Zebra finch. J. Gen. Physiol 24: 625–633.

DeLange, H. 1958. Research into the dynamic nature of the human fovea-cortex systems with intermittent and modulated light. I. Alternation characteristics with white and colored light. J. Opt. Soc. Amer. 48: 777–784.

Denton, E.J. & J.A.C. Nicol. 1966. A survey of reflectivity in silvery teleosts. J. Mar. Biol. Assoc. (U.K.) 46: 685–722.

Dera, J. & H.R. Gordon. 1968. Light field fluctuations in the photic zone. Limnol. & Oceanogr. 13: 697–699.

DeVoe, R. 1966. A non-linear model of sensory adaptation in the eye of the wolf spider. pp. 309–328. In: C.G. Bernard (ed.) The Functional Organization of the Compound Eye, Per-

gammon Press, Oxford.

Dodt, E. & A. Worth. 1953. Differentiation between rods and cones by flicker electroretinography in pigeon or guinea pig. Acta. Physiol. Scand. 30: 80–89.

Duntley, S.Q. 1951. The visibility of submerged objects II. Proc. Armed Forces, Nat. Res. Coun. Vision Comm. 28: 60.

Easter, S.S., Jr. 1971. Spontaneous eye movements in restrained goldfish. Vision Res. 11: 333–342.

Fourtes, M.G.F. & A.L. Hodgkin. 1964. Changes in time scale and sensitivity in the ommatidia of *Limulus*. J. Physiol. (London) 172: 239–263.

Fuortes, M.G. & P.M. O'Bryan. 1972. Generator potentials in invertebrate photoreceptors. pp. 279–320. *In*: M.G. Fuortes (ed.) Handbook of Sensory Physiology, Springer-Verlag, Heidelberg.

Gordon, H.R., J.M. Smith & O.B. Brown. 1971. Spectra of underwater light-field fluctuations in the photic zone. Bull Mar. Sci. 21: 466–470.

Gramoni, R. & M.A. Ali. 1970. L'Electroretinogramme et la frequence de fusion chez *Amia calva* (Linne). Rev. Can. Biol. 76: 37–58.

Granit, R. 1963. Sensory Mechanisms of the Retina. Hafner Publishing Co., New York. 412 pp.

Green, D.G. & I.M. Siegel. 1975. Double branched flicker fusion curves from the all-rod skate retina. Science 188: 1120–1122.

Hamasaki, D.I. 1967. An anatomical and electrophysiological study of the retina of the owl monkey, *Aotes trivirgatus*. J. Comp. Neurol. 130: 163–174.

Hamasaki, D.I. 1968. The electroretinogram of the intact anesthetized octopus. Vision Res. 8: 247–258.

Hamasaki, D.I. & J. Peregrin. 1970. A blue-sensitive system in the lateral eye of the green iguana. Vision Res. 10: 121–127.

Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. Bur. Sport Fish. Wildl. Res. Rep. 73: 1–92.

Hobson, E.S. 1979. Interactions between piscivorous fishes and their prey. pp. 231–242. *In*: H. Clepper (ed.) Predator-prey Systems in Fisheries Management, Sport Fishing Inst., Washington.

Jahn, T. & V. Wolff. 1941. Influence of a visual diurnal rhythm on flicker response contours of *Dytiscus*. Proc. Soc. Exp. Biol. Med. 48: 660–665.

Jenssen, T.A. & B. Swenson. 1974. An ecological correlate of critical flicker-fusion frequencies for some *Anolis* lizards. Vision Res. 10: 965–970.

Jerlov, N.G. 1968. Optical Oceanography. Elsevier, London. 194 pp.

Johns, P.R. & S.S. Easter, Jr. 1978. Growth of the adult goldfish eye. II. Increase in retinal cell number. J. Comp. Neurol. 176: 331–342.

Kelly, D.H. 1959. Effects of sharp edges in a flickering field. J. Opt. Soc. Amer. 49: 730–732.

Kelly, D.H. 1972a. Flicker. pp. 273–302. *In*: D. Jameson & L.M. Hurvich (ed.) Handbook of Sensory Physiology, Springer-Verlag, Heidelberg.

Kelly, D.H. 1972b. Adaptation effects on spatio-temporal sine-wave thresholds. Vision Res. 12: 89–102.

Kobayashi, H. 1962. A comparative study on electroretinogram in fish with special reference to ecological aspects. J. Shimonoseki Coll. Fish. 11: 17–148.

Laughlin, S.B. 1980. Neural principles in the visual system. pp. 133–280. *In*: H. Autrum (ed.) Handbook of Sensory Physiology, Springer-Verlag, Heidelberg.

Loew, E.R. 1974. CO_2-induced changes in the critical fusion frequency of the fly, *Sarcophaga bullata*. J. Insect Physiol. 20: 1737–1748.

Lythgoe, J.N. 1966. Visual pigments and underwater vision. pp. 375–391. *In*: R. Bainbridge, G.C. Evans & O. Rackham (ed.) Light as an Ecological Factor, Blackwell, Oxford.

Lythgoe, J.N. 1979. The Ecology of Vision. Clarendon Press, Oxford. 244 pp.

Maffei, L. 1978. Spatial frequency channels, neuronal mechanisms. pp. 39–66. *In*: R. Held, H. Leibowitz & H.L. Teuber (ed.) Handbook of Sensory Physiology, Springer-Verlag, Heidelberg.

McFarland, W.N. & F.W. Munz. 1975a. Part II: The photic environment of clear tropical seas during the day. Vision Res. 15: 1063–1070.

McFarland, W.N. & F.W. Munz. 1975b. Part III: The evolution of photopic visual pigments in fishes. Vision Res. 15: 1071–1080.

McFarland, W.N., F.H. Pough, T.J. Cade & J.B. Heiser. 1979. Vertebrate Life. Macmillan, New York. 875 pp.

Munz, F.W. & W.N. McFarland. 1977. Evolutionary adaptations of fishes to the photic environment. pp. 193–274. *In*: F. Crescitelli (ed.) Handbook of Sensory Physiology, Springer-Verlag, Heidelberg.

Northmore, D., F.C. Volkmann & D. Yager. 1978. Vision in fishes: color and pattern. pp. 79–136. *In*: D.I. Mostofsky (ed.) The Behavior of Fish and Other Aquatic animals, Academic Press, New York.

Nye, P.W. 1969. The monocular eye movement of the pigeon. Vision Res. 9: 133–144.

Protasov, V.R. 1968. Vision and Near Orientation of Fish. Israel Prog. for Sci. Translations, 1970, Transl. by M. Raveh. U.S. Dept of Commerce, Washington, D.C. 175 pp.

Ratliff, F., B.W. Knight, J. Toyoda & H.K. Hartline. 1967. Enhancement of flicker by lateral inhibition. Science 158: 392–393.

Robson, J.G. 1966. Spatial and temporal contrast-sensitivity functions of the visual system. J. Opt. Soc. Am. 56: 1141–1142.

Ruck, P. & T.L. Jahn. 1954. Electrical studies on the compound eye of *Ligia occidentalis dana* (Crustacea: Isopoda). J. Gen. Physiol. 37: 825–849.

Schenck, H. 1957. On the focusing of sunlight by ocean waves. J. Op. Soc. Amer. 47: 653–657.

Smith, E.L. III, D.A. Witzel & D.G. Pitts. 1976. The waveform and scotopic CFF of the sheep electroretinogram. Vision Res. 16: 1241–1245.

Snyder, R.L. & J. Dera. 1970. Wave-induced light-field fluctuations in the sea. J. Op. Soc. Amer. 60: 1072–1079.

Svaetichin, G. 1956. Receptor mechanisms for flicker and fusion. Acta. Physiol. Scand. 39, Suppl. 134: 47–54.

Tamura, T. & I. Hanyu. 1959. The flicker electroretinogram of the carp eye. Bull. Jap. Soc. Sci. Fish. 25: 624–631.

van Dorn, W.G. 1974. Oceanography and Seamanship. Dodd, Mead & Co., New York. 481 pp.

Walls, G.L. 1967. The Vertebrate Eye and Its Adaptive Radiation. Hafner, New York. 785 pp.

Waterman, T.H. 1961. Light sensitivity and vision. pp. 1–64. *In*: T.H. Waterman (ed.) The Physiology of Crustacea, Academic Press, New York.

Witzel, D.A. & E.L. Smith, III. 1976. Unpublished pilot data mentioned *In*: The waveform and scotopic CFF of the sheep electroretinogram, E.L. Smith III, D.A. Witzel & D.G. Pitts. 1976. Vision Res. 16: 1241–1245.

Yarbus, A.L. 1967. Eye Movements and Vision. Plenum Press, New York. 222 pp.