

**Table 1** Principal calcareous encrusting organisms

Excavation depth	Substrate upper surface	Substrate under surface
0–20 cm	Calcareous red algae (up to 8 mm-thick crusts) <i>Porolithon</i> sp., <i>Lithophyllum</i> sp., <i>Neogoniolithon</i> sp.	Calcareous red algae (crusts <2 mm) <i>Mesophyllum</i> sp., <i>Neogoniolithon</i> sp. Encrusting foraminiferans <i>G. plana</i> , <i>H. rubrum</i>
20–40 cm	Platy corals (~10 cm diameter) ( <i>Agaricia agaricites</i> , <i>Porites astreoides</i> ), calcareous red algae (crusts <2 mm), <i>Porolithon</i> sp., <i>Lithophyllum</i> sp., <i>Neogoniolithon</i> sp., <i>Mesophyllum</i> sp. Delicate branching <i>Stylaster</i> sp. corals occur in concave downward-facing bends or joints of <i>A. palmata</i> branches	<i>Neogoniolithon</i> sp., <i>Mesophyllum</i> sp., <i>G. plana</i> , <i>H. rubrum</i> , <i>Carpentaria utricularis</i> , cheilostome ectoprocts, serpulids (? <i>Hydroides</i> sp. ? <i>Filagrana</i> sp.), thectidioid brachiopods
40–60 cm	<i>Lithophyllum</i> sp. <i>Mesophyllum</i> sp. <i>Neogoniolithon</i> sp. <i>Gypsina plana</i> <i>Homotrema rubrum</i> Cheilostome ectoprocts <i>Agaricia agaricites</i>	<i>Mesophyllum</i> sp. <i>Neogoniolithon</i> sp. <i>H. rubrum</i> Cheilostome ectoprocts <i>G. plana</i> Serpulids <i>C. utricularis</i>
60–80 cm	<i>Mesophyllum</i> sp. Serpulids <i>H. rubrum</i>	Cheilostome ectoprocts Serpulids Thectidioid brachiopods
80–100 cm	Nestling sponges ? <i>Orina calcinea</i> <i>H. rubrum</i> Cheilostome ectoprocts Serpulids <i>C. nicholsoni</i> (2 per 100 cm <sup>2</sup> ) Solitary coral (? <i>Astrangia</i> sp.) Nestling sponges ? <i>Orina calcinea</i> ?Rhizamminid foraminifera	<i>C. nicholsoni</i> (7 per 100 cm <sup>2</sup> ) Cheilostome ectoprocts Serpulids <i>C. nicholsoni</i> (20 per 100 cm <sup>2</sup> ) <i>H. rubrum</i> Thectidioid brachiopods
100–120 cm	Cheilostome ectoprocts <i>H. rubrum</i> Serpulids <i>C. nicholsoni</i> (4 per 100 cm <sup>2</sup> ) Solitary corals (? <i>Astrangia</i> sp.) ?Rhizamminid foraminifera	Cheilostome ectoprocts Serpulids <i>C. nicholsoni</i> (30 per 100 cm <sup>2</sup> ) <i>H. rubrum</i> Thectidioid brachiopods
120–140 cm	Serpulids Cheilostome ectoprocts <i>C. nicholsoni</i> (20 per 100 cm <sup>2</sup> ) Thectidioid brachiopods	<i>C. nicholsoni</i> (50 per 100 cm <sup>2</sup> ) Thectidioid brachiopods Solitary corals (? <i>Astrangia</i> sp.) <i>H. rubrum</i> Serpulids
140–160 cm	Serpulids <i>C. nicholsoni</i> (20 per 100 cm <sup>2</sup> ) Cheilostome ectoprocts	Cheilostome ectoprocts <i>C. nicholsoni</i> (50 per 100 cm <sup>2</sup> ) Cheilostome ectoprocts
160–180 cm	<i>C. nicholsoni</i> (5 per 100 cm <sup>2</sup> ) Serpulids	<i>C. nicholsoni</i> (20 per 100 cm <sup>2</sup> ) Serpulids
180–200 cm	Thin cover of sand-sized sediment Encrustations of platy corals, <i>A. agaricites</i> (dead)	<i>C. nicholsoni</i> (10 per 100 cm <sup>2</sup> ) Serpulids

pile of rubble accumulated at one depositional event, otherwise a progressive sequence from photophilic to sciaphilic encrusters, would be expected on each coral fragment.

Presently, in sheltered hollows at the surface of the rubble, 10-cm diameter platy corals (*Agaricia agaricites* and *Porites astreoides*) are attached to, and to an extent binding, the *A. palmata* fragments. Unless broken by another major storm, these platy corals, with time, should be preserved as a crudely horizontal platy encrustation on the top of the storm rubble but beneath further 'calm weather' deposits of *A. palmata*, which, no doubt, will soon cover the reef crest. The occurrence of dead encrustations of platy *A. agaricites* at the base of the excavation suggests that we had reached the top of the previous increment of rubble.

Clearly, the depositional histories of cliff or core sections of coral rubble cannot be completely unravelled by studies of the fragments' texture and disposition alone; the nature and sequence of assemblages of encrusting organisms, however, can help to elucidate the rate of supply of coral branches.

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## Real and apparent movement nulled

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**It is a controversial issue whether 'real' movement, seen from the successive stimulation of retinal receptors by a moving image, and 'apparent' ( $\phi$ ) movement, which is produced by stimuli separated in space and time, are transmitted by the same or different neural channels. With this question in mind, we have devised ways to oppose real against opposite-direction apparent movement, to see whether they cancel. Cancelling, especially in a variety of conditions, would be expected for a single but not for separate neural movement channels. As we report here, we find that opposed-direction real and apparent movements will cancel, allowing null measurements to be made.**

The simplest method is to rotate a sector disk at constant speed, in, say, a clockwise direction, and illuminate it with two sources—flashes of light at a constant rate, and a continuous light. An electronic stroboscope provides short (1  $\mu$ s) flashes which are set at a repetition rate to make the sector disk rotate apparently backwards (anticlockwise). The continuous light signals the disk's true (clockwise) rotation as for normal viewing. As the stroboscope flashes are short, the retinal images of the

sectors are essentially stationary for each flash, and so only apparent movement is signalled (anticlockwise) while the continuous light signals clockwise real movement. The question is: is there an intensity ratio of the intermittent and continuous lights at which the opposed real and apparent movements cancel? We find that there is a critical balance of intensities at which systematic movement ceases. At this cancelling null point, all that remains is rapid flicker, or a random jiggle. This is phenomenally similar to what happens when two oppositely moving gratings are viewed superimposed, to cancel two real movements. The finding that opposed real and apparent movements can cancel suggests that they are carried by the same neural channel.

At a lower relative intensity of the continuous light, the apparent movement from the stroboscope dominates and the disk rotates anticlockwise; at higher intensities, it rotates clockwise by real movement. The mean luminance, which is not critical, was in the lower photopic range.

As the disk can have any number of equally spaced sectors, and as the apparent movement occurs at several flash rates, there are many independently controllable parameters, which is exceedingly useful. The real edge velocity of the sectors, given by the rotational velocity of the disk, may be varied independently of the apparent movement, as for any rotational velocity this is given by the number of sectors and the flash rate which are independently variable. For some uses, a band of bars is better than a sector disk, which may have its centre blanked off to restrict the range of velocities along the radii of the sectors. The disks were rotated between 10 and 100 r.p.m., as selected with a stepped ratio gear box driven by a synchronous motor.

It is interesting that with large jumps of the flashed sectors, although apparent movement is maintained cancelling does not occur. The appearance is of two oppositely rotating disks passing through each other, both movements being seen, rather than cancelling. Thus, it seems that only 'short-range' movement<sup>1</sup> will cancel for nulling, and that 'long-range' movement<sup>2</sup>, which does not cancel, is signalled by different neural channels. This occurs, for example, in the following conditions: six equally spaced white and six black sectors on an 18-cm disk, rotating at 50 r.p.m., viewed from 2 m. Illumination is: flashes of  $1 \mu\text{s}$  at 8 flashes per s, with a peak luminance of about  $10 \text{ Cd m}^{-2}$ . This flash rate gives the highest attainable apparent velocity in this situation. The displacements of the signalled sector positions exceed the short-range limit for most of their radii. The added constant light is adjusted for of  $2 \text{ Cd m}^{-2}$ . These rather critical conditions give simultaneous counter-rotations when the apparent and real movements are balanced instead of nulling. When this is viewed with a fourfold reduction of size at the eye, to bring the flash image jumps within short-range movement, it is seen as nulled rather than as opposed movements.

In the more generally holding conditions for nulling, when colour filters are added, to make, say, the stroboscope flashes blue and the continuous light red, nulling still occurs in spite of colour contrast between the opposed real and apparent movements. Following prolonged fixation of this double-colour nulled movement, no significant after-effect appears, either for white light or when the stationary test pattern is viewed with blue or with red light. These observations provide further evidence that the real and apparent movements are being transmitted by the same neural channel, and that the movement channel is independent of the colour systems. This is confirmed by the observation that, following several minutes' fixation of the rotating disk set up with nulled movement, there is no significant movement after-effect. As would be expected, after-effects are seen in the opposite directions to the adapting real or apparent movements following stimulation either side of the null point.

If the nulled movement is viewed through a defocusing lens to blur the edges of the moving sectors, the null point remains essentially unchanged. However, when viewed through a neutral density filter (or a pin hole), placed before the eyes so that both illuminations are reduced equally, the null point changes. The real movement from the continuous source is now less effective

than the apparent movement from the stroboscope—as now it rotates anticlockwise. This occurs dramatically with a filter of less than half a log unit, and the shift of the null point is greater with higher filter factors. The null can be restored by resetting the luminance ratio, so this effect can readily be measured. It is evidently associated with the eye's adaptation level, and so may indicate its integration time, which increases with dark adaptation; for when a bright light is shone into the eyes, producing light adaptation, the null point shifts in the opposite direction to the shift with the dark filter. This effect is greater for low illuminations of the sector disk, while the dark filter is more effective at higher illuminations, which is to be expected for an adaptation effect. The impairment of real movement may be explained in these terms, for increased integration time must impair temporal resolution of the receptors, which will affect the sequential signalling of real movement as the image runs continuously along the receptors, but can hardly affect the signalling of flashes separated beyond the eye's longest integration time, of a few milliseconds.

Nulling can be achieved without a continuous light—by lengthening the stroboscope flashes. This is done with an electromechanical shutter driven by variable-frequency and duration pulses, and arranged to interrupt a projector illuminating the disk. The real and apparent movements can now be cancelled and nulled with no continuous light, by setting the flash duration so that the real movement which is signalled during each flash equals the opposed apparent movement, given by the repetition rate. Nulling is obtained in this way by adjusting the flash duration around 5–10 ms. The dark filter changes this null point, less than for the short flash plus continuous light. In both cases increase in the eye's integration time with dark adaption impairs continuous movement without impairing the apparent movement, at least for these low flash rates of under 10 Hz.

Repeated texture patterns, in place of the sectors, should allow pattern-signalled movement to be compared with edge signalled movement. It has been shown that apparent movement is lost with isoluminant colour contrast for alternating texture patterns, though not for clearly separate features or objects<sup>3</sup>. The movement nulling technique will be used with isoluminant colour contrast displays, both with repeated texture patterns and with clearly separated sectors or dots, to explore these effects of luminance and colour contrast for textures and individual features, both with the short-range movement, which allows cancelling and nulling, and with long-range movement which, as it does not cancel, seems to work by different neural mechanisms from those of short-range apparent and real movement.

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## Induction of the ipsilateral retinothalamic projection in *Xenopus laevis* by thyroxine

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**Hormones are important in the development of behaviour and there is now abundant evidence that they also affect the morphological development of the nervous system<sup>1–6</sup>. In principle, hormones could act by inducing new patterns of connectivity between widely separated structures in the nervous system or by influencing local connectivity. Most available work documents effects of the latter sort. We present here evidence for**

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