

are completely uncorrelated "noise", Julesz's model is inapplicable. Further, Kaufman's brightness averaging hypothesis^{4,5} cannot be applied to our patterns (Figs. 1, 2 and 3) as "brightness averaging" could have resulted only in a uniform grey field in each eye.

It seems likely from our results that even the most "subjective" of subjective contours can yield depth effects in the absence of average brightness gradients and point to point correlation. Texture discrimination based on probability distributions (Fig. 1) and size of grain (Fig. 2) and the recognition of contours formed by changes in grating direction (Fig. 3) all occur "earlier" than stereopsis and considerably influence it. Any model that tries to "explain" stereopsis must take these facts into account. Our experiments also emphasize the importance of using random dot stereograms in perceptual research, for only by using Julesz patterns can one "skip" peripheral preprocessing (of the type seen in Figs. 1, 2 and 3) to obtain a truly cyclopean "counterpoint".

From our finding that a texture contour or a colour contour presented to one eye can produce stereopsis with an intensity contour presented to the other eye, we postulate a common contour processing centre for intensity, colour and texture contours where parallel inputs become confluent into a single channel. Sherrington postulated⁹ over 60 years ago "that during binocular regard . . . each monocular mechanism develops independently a sensual image of considerable completeness. The singleness of binocular perception results from union of these elaborated unocular sensations". Our results strongly support this important conclusion.

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Locomotion and Burrowing in Limbless Vertebrates

GAYMER¹ recently described "vermiform" movement as a fifth^{2,3} and "new" method of locomotion in limbless terrestrial vertebrates. On the basis of X-rays of limbless amphibians (caecilians) he stated that these animals can shorten their bodies by flexing the vertebral column into multiple curves of

short radius within the integumentary envelope. The shortened region is apparently fixed against the soil or tunnel walls and the head then moves forward from this stationary zone. The fixed region thus serves in force transmission to the soil, allowing the animal to pull up its posterior trunk, or send the anterior portion further along the path. Gaymer noted that the fixed zone thus formed may also serve as a base for ramming movements.

The shortening and thickening of the caecilian trunk by axial flexure have been known, if inadequately understood, for some decades⁴. Indeed, vermiform locomotion superficially resembles the movement of annelids, where part of the trunk is thickened and placed in static frictional contact with the walls of the tunnel. Forces transmitted here can move the body along a tunnel or let the animal push its way through the ground. These properties of vermiform motion are, however, those that characterize powered concertina movements, supposedly a distinct category^{2,3}. The difference between the usual concertina and vermiform forms of locomotion is that while the entire body flexes in the former, flexion is restricted to an axial mass in the latter so that the supervening soft tissues swell outwards. Thus vermiform locomotion is a variant of the concertina locomotion of limbless vertebrates; it is not a distinct method.

Gaymer's description of vermiform locomotion argues that such a pattern could not be developed in reptiles because their ribs extend into the body wall muscles close to the skin. However, this variant occurs in a number of limbless reptiles. Thus the slender and bilaterally compressed amphisbaenian *Agamodon compressum* uses it in tunnelling through packed sand. In the Uropeltidae, a relict family of snakes restricted to Central India and Sri Lanka (Ceylon)⁵, this method is most highly developed; it is used not only in progression and ramming but also in tunnel widening. The anterior part of the body can, by flexion of the vertebral column, be thickened to more than twice the normal diameter. In this case the basic concertina mechanism facilitates tunnel formation. The tiny head is driven in only to the level of the neck and thus serves primarily for the initial penetration. Widening of the tunnel to full diameter occurs by flexion between the anterior vertebrae, so that the penetrating and the widening functions are separated⁶.

Finally, Gaymer states that "the skin of reptiles is largely free from the underlying muscles for part or all of the body's circumference, being attached only by specially developed cutaneous muscles".

Amphisbaenians and such snakes as uropeltids do indeed have cutaneous muscles (that is, those cross-connecting different portions of the skin⁷), but these are not involved in the propulsion phase of rectilinear movement, which is enabled by slips of the axial musculature (Mm. costocutanei superiores and inferiores^{3,8}). In concertina, propulsive forces pass directly from the independently flexed vertebral column to the loosely connected skin. Behavioural evolution, coupled with only slight structural changes, accounts for repeated and varied development of concertina locomotion in reptiles.

Internal concertina is produced differently in squamates and caecilians. In uropeltids most bones, axial muscles, and viscera flex within an envelope consisting of the skin and cutaneous muscles. In caecilians the flexure is restricted to a central zone occupied by vertebrae, ribs, and spinal musculature (epaxial + hypaxial?)⁴; the remaining axial musculature has become attached to the body wall.

The slender slips of muscle may reposition the skin; they do not transmit the propulsive forces which pass in static contact from column to skin to tunnel wall. The reinforcement of the wall may protect the visceral contents in a short-ribbed, elongate burrower.

Gaymer argued that the caecilian morphology was shaped by the need for internal curvature. Actually the separation between axial and body wall muscles maintains the patency of the visceral cavity by muscular rather than by skeletal elements.

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Tropical Role of Bacteria in the Ecosystem of the Coral Reef

THE factors responsible for the high productivity of coral reefs in oligotrophic tropical waters are still not understood^{1,2}. The relative importance of the predatory and symbiotically herbivorous nutrition of corals is not clear³, and other feeding

microscopy on stained membrane filters. The rates of bacterial production and bacterial destruction and of photosyntheses of phytoplankton and phyto-benthos and a quantitative study of the feeding of aquatic animals with bacteria have been made using carbon-14⁸⁻¹¹. Some of my main results are summarized in Table 1 as quantitative estimates of the microflora in the water, bottom sediments and epibiotic layers covering dead corals.

The biomass and the production of bacteria are of the same range as those in a eutrophic or a mesotrophic lake¹², and several tens or even hundred times more than that in the pelagic regions of the ocean. The rate of destruction of organic matter usually exceeds the rate of primary production in the surface layers of water and sediments. The organic matter of microbial cells itself accounts for about 2–5% of the total organic matter of the reef sediments. The daily rate of bacterial production in sediments is usually around 30–60% of the photosynthetic production of phyto-benthos and results in a daily production of raw bacterial biomass in the reef sediments of about 5–15 g/m² of the bottom surface.

The high rate of bacterial production may provide a significant part of the food of the very rich fauna of the coral reefs, which includes the filtering and the sand and detritus-eating animals. The latter groups include a part of the coral fishes. The experiments with ¹⁴C-labelled bacteria as a food showed that most of the common reef filter feeders can feed on bacterial plankton at concentrations equal to those in the lagoon water (Fig. 1). The consumption of bacterioplankton by crude filter feeders such as tunicates, oysters, and crustaceans is facilitated

Table 1 Quantitative Estimates of Bacterial Biomass, and Daily Values of Production of Bacteria, Photosynthetic Production and Destruction* in Coral Communities

Sampling area	Type of samples	Bacteria		Photo-synthesis (ph)	Destruction (D)	P/B	D/ph
		Biomass (B)	Production (P)				
Open ocean, north trade wind current	Bottom sediment, red clay	1.0	0.032	—	0.08	0.03	—
	Surface water	1.7	2.6	0.51	6.9	1.6	13.6
Fanning Atoll, Line Island	Coral sand	91	22.6	38	56	0.25	1.5
Great Barrier Reef, close to Heron Island	Coral sand	42.5	27.6	61	69	0.61	0.85
	Water over the reef	41	20.2	67	53	0.49	0.79
Majura Atoll, Marshall Islands	Dusty fine sediment among dead corals	88	35.2	74	100	0.40	1.4
	Epibiotic layer on the dead corals	28	14.3	610	41	0.51	0.06
	Coral sand	21	7.2	20	20	0.34	1.0
	Water over the reef	19	7.5	4.1	21	0.39	5.1
Kaneoche Bay, Oahu Island, Hawaii	Coral sand	65	17.2	7.1	49	0.26	6.7
	Seston over the surface of dead corals	147	73.0	96	207	0.50	2.2
	Water over the reef	43	28.0	36.3	79	0.67	2.2
Butaritari Atoll, Gilbert Islands	Water near the shore	170	41.5	37	110	0.24	3.0
	Water in the centre of lagoon	79	24	17	64	0.30	3.7

* mg C l⁻¹ of raw sediment, or mg C m⁻³ of water.

Variation range between parallel duplicates: primary production 20%, microbial production in surface samples and shallow sediments 15%, deep sea samples 50%.

mechanisms, filtering and osmotic nutrition^{4,5}, have not been studied sufficiently. Furthermore, very little is known about the microbial population of the reef ecosystems. Di Salvo⁶ showed that reefs support an abundant and active microflora which participates in nutrient regeneration and serves as food for filter feeders including some corals⁷, but there are no quantitative data relating to the biomass and production of microflora on reefs.

I collected data at several atolls in the Pacific Ocean during 1968–1970. Microbial biomass has been determined by direct

by the presence of about 20–30% of the total bacterioplankton in aggregates larger than 5 μm¹¹. Sand and seston eaters also consume and assimilate labelled bacteria in the sediments (Fig. 2).

Several series of experiments with corals were also carried out. The common corals (*Porites*, *Pavona*, *Hydnophora*, *Montipora*, *Fungia*, *Porcillopora* sp.) were fed with the labelled natural bacterioplankton and seston, in which the bacterial population was labelled with ¹⁴C. The evolution of labelled metabolic CO₂ by corals previously fed with labelled bacterio-