**LETTERS TO NATURE**

**Rapid adaptive camouflage in tropical flounders**

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**DESPITE the commonly held view that flatfish can change their surface markings to match their background pattern**, there have been few systematic studies\(^1\) and it has recently been claimed\(^2\) that their capacity for such adaptive changes is minimal. **Here we show that the tropical flatfish *Bothus ocellatus* can achieve pattern-matching with surprising fidelity. By adjusting the contrast of different sets of ‘splotches’ of different grain size (or spatial frequency) on the skin, the fish can blend into a wide range of background textures in just 2–8 seconds.**

Summer\(^3\) placed flatfish of the genus *Paralichthys* on checkerboard patterns and noticed that after a few days the fish seemed to develop large splotches as if to mimic the checks. These experiments were recently repeated in two genera\(^4,5\), giving rise to claims that their ability to change had been grossly exaggerated and that for the most part the flatfish simply had a ‘universal texture’ that allowed it to blend into any environment. It was also suggested that many of the photographs of flounders showing apparent camouflage (including those in refs 2 and 3) contained artefacts produced by film nonlinearities that tended to enhance the apparent resemblance between the fish and its background.

Even without any dynamic change, the flatfish can blend surprisingly well with a wide range of variegated backgrounds\(^6\). But we wondered whether it was also capable of dynamic changes in pattern. Five specimens of the Caribbean shallow-water flatfish *Bothus ocellatus* were used in the experiment. They were initially housed in a tropical salt-water aquarium at 30 °C and transferred to four small 25 × 20 × 30 cm rectangular plastic tanks for testing. Their eyes are mounted on short stalks and move independently (like a chameleon’s eyes) through 180°, and the fish could track and pounce on a thin vertical bar moving horizontally.

The following patterns covered the bottoms of the test tanks: a coarse gravel; printed checkerboards, either 1-cm or 2-mm checks; a homogeneous grey sheet, the luminance of which was identical to the mean luminance of the checks; or fine, yellow beach sand. While in the home tank, all fish appeared almost identical in colour and pattern to the yellowish beige gravel on the floor (similar to that in Fig. 1a). When we transferred the fish (one per tank) each changed its surface markings within 2–8 s to resemble closely its new background. Each fish was then moved to a different, randomly selected, tank and once again exhibited a strong change in pattern to match the new background. As long as the fish were healthy and active, such changes could be brought about several times (Fig. 1).

We were concerned that the resemblance between the fish and the various backgrounds might be an optical illusion: that the effect seen in Fig. 1 might be in the eye of the beholder and the fish might not have changed significantly. We therefore took colour photos of the same fish on different backgrounds and then simply cut them out and displayed them on a plain background. It was clear that the pattern on the fish was changing physically. We also took black and white half-tone pictures (Fig. 1b–d) and asked 20 naive subjects to choose the background pattern that most closely matched each of the three cut-out fish. They did this correctly in 58 of 60 trials, providing unequivocal evidence that the fish were changing physically in the appropriate direction. The reason that Saito’s results\(^6\) were not as clear may be that he used cold-water rather than tropical flatfishes and that the latter may have evolved a greater ability to engage in pattern matching. Indeed, our own

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initial results with cold-water genera (for example, *Paralichthys*) were very similar to those obtained by Saidel.

A convenient way to characterize visual texture is by means of the Fourier transform of the flounder pattern. From photographs of the fish that had had time to adapt to a variety of different background patterns, we obtained the radial power spectrum of the back of the fish, and a corresponding region of the background pattern, averaged over orientation and phase. A principal components analysis of these spectra showed that there were three predominant channels of independent information about the background texture being expressed in the flounder camouflage patterns (Fig. 2). These may be most easily described as a low-frequency/high-frequency opponent channel, a predominantly mid-frequency channel, and a channel with a narrow peak at 8 cycles per fish and a suggestion of higher harmonic structure. The important result from this analysis was that (like human colour vision) flounder patterns have three dimensions of useful control

FIG. 1 Photographs of the same fish on 4 different backgrounds. The adaptive change took 2–8 s in each case. We ruled out the possibility that these effects were simply a consequence of the fish being transparent. This was a problem mainly with smaller specimens (<4 cm), but transparency in the specimens studied was also ruled out on the following grounds. First, analysis of the videotapes showed that there was a delay before the fish resembled the background. Second, the blotches on the fish had no spatial coherence with the background squares. Third, after the fish had changed its pattern, we placed an oval piece of grey opaque cardboard between it and the pattern and this did not eliminate the camouflage (photographs were also taken for subsequent analysis). And fourth, when the fish was displaced passively with a ruler, the pattern moved with the fish. The texture changes were unequivocal but emphasis should not be placed on the colour changes as these were not measured objectively (the exact tints seen in these reproductions could be artefacts produced by lighting). We also noted that as the fish were cycled through the tanks repeatedly they seemed to learn to respond faster to the background pattern. It remains to be seen whether this curious form of perceptual learning is specific to the particular pattern to which the fish is exposed.

FIG. 2 Correlation analysis of the background texture information mimicked by the flounder patterns. To condense the information, we took a radial average of the 2-D power spectra around successive annular bands with widths of 1/4 octave. This provides a 1-D graph of the spatial-frequency content of the pattern of the fish or the background, averaged over orientation and phase. From photographs of the fish on 23 different background patterns to which they had had time to adapt, we obtained the radial power spectrum of the back of the fish (excluding the motile fringe and tail regions, which were semi-transparent), and an oval region of the background matching the shape of the fish. The degree of adaptive matching of the fish to the background was obtained by means of a cross-correlation matrix of the spectral power at each background frequency with that at each frequency in the flounder pattern. A principal components analysis (singular value decomposition of the cross-correlation matrix of 33 x 33 spatial frequencies) showed that there were three predominant channels of independent information about the background texture being expressed in the flounder camouflage patterns, as depicted by the six curves. (The eigen values of the first six components were 5.68, 5.02, 3.03, 0.94, 0.87 and 0.75.) The three significant components (full curves) may be most easily described as a low-frequency/high-frequency opponent channel, a predominantly mid-frequency channel, and a channel with a narrow peak at 8 cycles per fish and a suggestion of higher harmonic structure. Further components (dashed curves) are of low amplitude and do not appear to contain much structured information. The flounder patterns have three dimensions of useful control by the environmental information. The particular spectral form of the underlying mechanisms may consist of any linear combination of the depicted functions, which correspond to a vector space of the control parameters between the background texture and the fish patterns.
FIG. 3 Different surface markings on Bothus ocellatus. The fish seemed to have some degree of independent control over the different types of markings. These markings were: A, large 'H'-shaped splotches lining the margins of the fish; B, small dark rings within each 'H' and elsewhere on the surface, and similar light rings scattered over the surface; C, small central black spots, one in the middle of each ring; D, stippling over the surface of the fish; E, a central 'eye spot' in the middle of the fish which was made up of an 'H' splotch with a ring and central spot in the middle; and F, a 'spectacle frame' around the eyes. Additionally, in between each ring and the central black spot was a pale area that was lighter than the yellow-brown colour of the rest of the fish. Each set of markings was essentially a cluster of specific size and shape composed of melanocytes. The luminance gradient seen across the whole photograph is artefactual.

FIG. 4 Response of specimens to sparse black polka dots (a, b) and a homogeneous light grey (c). These adaptive changes took several minutes rather than seconds. In a and b, the fish increased the contrast of the central 'eye spot' and the dark spectacles around the eyes while the rest of the fish became pale. A grey background (c), the mean luminance of which was equal to this pattern, did not produce this effect. Similarly, when the fish was placed on a photonegative of a (sparse white polka dots on black) the fish became much darker and developed prominent white spots near its margins, an effect that was not seen on a homogeneous black background. Again, it is difficult to avoid the conclusion that these white spots were made more prominent to mimic the sparse white polka dots in the surround.
Vasoactive effects of fibrinogen on saphenous vein

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NORMAL plasma fibrinogen concentrations are critical to haemostasis. Higher fibrinogen concentrations are associated with increasing risk of atherothrombotic disease and with graft stenosis and occlusion after saphenous vein bypass surgery. Vein graft stenosis is characterized by the localized proliferation of intimal smooth muscle cells, causing narrowing of the graft with increased risk of thrombotic occlusion. In rabbit arteries, fibrinopeptide B is reported to have both vasoconstrictor and mitogenic properties. We report here that fibrinopeptides had no vasoactive effects on saphenous vein rings; however, fibrinogen (0–2 μM) affected an endothelium-dependent relaxation, followed by recontraction at higher concentrations. The fibrinogen-mediated relaxation was inhibited by K+ channel blockers and antibodies to ICAM-1. Coupled signalling pathways for the synthesis of vasoactive mediators and mitogens could underlie the association between fibrinogen and the development of vein graft pathology.

We studied the changes in isometric tension of saphenous vein rings in response to thrombin, fibrinogen and fibrinopeptides. Vein rings exhibited endothelium-dependent relaxation to increasing doses of thrombin, maximum relaxation 42 ± 4% at 1 U ml–1 which increased to 63 ± 5% in the presence of 0.25 μM fibrinogen, but no response to fibrinopeptides (A + B) alone, at concentrations of up to 5 μM. Unexpectedly, vein rings showed a concentration-dependent relaxation in response to fibrinogen (0–2 μM), this relaxation being reversed at higher concentrations of fibrinogen (Fig. 1). The response to fibrinogen was not observed when vein rings were denuded of endothelium (Fig. 1). However, when intact vein rings were incubated with fibrinogen and the supernatant transferred to a vein ring denuded of endothelium, progressive relaxation occurred (Fig. 1). Other plasma proteins, albumin and transferrin, in concentrations of up to 12 μM, did not cause relaxation of vein rings or attenuate the response to fibrinogen. Addition of the fibrinogen 1dG,1eG fragment complex (0–15 μM) did not effect relaxation of precontracted vein rings but preincubation of vein rings with the 1dG,1eG complex (10 μM) abolished the relaxation in response to fibrinogen (Fig. 2). These experiments suggest that specific fibrinogen receptors on saphenous vein endothelium mediate vasomotor responses.

Nitric oxide and prostacyclin are the two best characterized vasodilators synthesized by endothelium, with nitric oxide stimulating the synthesis of cGMP in the underlying smooth muscle. However, preincubation of vein rings with indomethacin (10 μM), the nitric oxide synthase inhibitor L-NAME (0.1 mM) or the nitric oxide trap haemoglobin (100 μM ml–1) only effected a small reduction of the fibrinogen-mediated relaxation (data for L-NAME and indomethacin in Fig. 1 and for haemoglobin in Fig. 2). The lipoxigenase inhibitor nordihydroguaiaretic acid (10 μM) did not alter the fibrinogen-mediated relaxation, but inhibited the vasoconstriction observed at higher fibrinogen concentrations (Fig. 1). Preincubation of vein rings with both indomethacin and L-NAME reduced the maximum relaxation in response to fibrinogen from 63 ± 3% to 40 ± 3%, P = 0.03 (Fig. 1). The concentration of cGMP extracted from the vein rings of five patients was measured by radioimmunoassay, at baseline, after treatment with 2 μM fibrinogen or 0.5 μM A23187 (which evokes the synthesis of endothelial nitric oxide): the concentrations of cGMP were 28.9 ± 4.8, 39.0 ± 6.4 and 116.5 ± 31.6 fmol mg–1 protein, respectively. The modest increase in cGMP concentration in response to fibrinogen contrasts with the fourfold increase in cGMP concen-