TREE vol. 7, no. 5, May 1992

Visual Textures, Machine Vision and Animal Camouflage

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The psychophysics of visual texture perception and texture discrimination have been investigated extensively during the past 30 years. Humans have been the main study subjects, but some research on texture perception has involved other species, and there is good reason to think that the most general results from humans apply to other vertebrates as well. Psychophysicists have suggested that some of their findings on human vision reflect adaptive 'tricks' for countering prey camouflage, but this possibility has not been widely communicated to evolutionary biologists. We review the psychophysicists' main conclusions on texture discrimination, and list additional questions that their results raise when animal coats are considered as visual textures. We also suggest ways in which advances in computer vision can be combined with psychophysics to provide new perspectives on the function of animal coat patterns.

Most people probably associate the word 'texture' with tactile features of woven materials or surfaces. However, researchers in visual perception have come to use 'texture' to describe any repetitive luminance pattern in a portion of visual space. Such patterns can result from tangible features on surfaces of objects when they are viewed closely, but collections of objects can also produce a visual texture. For example, views of meadows produce different visual textures from views of beaches or forests because the pattern of light reflectance for grass blades differs from that for sand or trees. Gibson[1] was the first to speak of visual textures in this way. He emphasized the value of texture gradients for depth perception because surface textures appear finer (shifted to higher spatial frequencies) with increasing distance from the viewer.

Patterns on animal coats can also be considered as visual textures. In species for whom concealment is adaptive, natural selection should favor the evolution of coat textures that are difficult to discriminate from background textures[2]. Among species for whom visual detection of other animals is adaptive, natural selection should favor visual systems that can discriminate coat textures from background textures. What limits or promotes the visual system's ability to make such discriminations? This question has been the subject of much research in perceptual psychology and psychophysics over the past 30 years. Much of the work has been on humans and other primates, but some behavioral studies with comparable results have been done on cats[3], falcons[4] and pigeons[5]. Furthermore, the fact that many animal species not hunted by humans look cryptic to us suggests that our visual perceptions are similar to those of many other vertebrate species[6].

Stereopsis as a 'camouflage-breaking' system

Using pairs of computer-generated textures ('random-dot stereograms'), Julesz[7] showed that stereopsis (binocular perception of depth) is possible without monocular depth cues such as texture gradients or movement parallax (Fig. 1). This ability depends in part on neurons tuned to binocular disparity in the input stage of the visual cortex[8,9]. In the biological literature, the evolution of stereopsis has

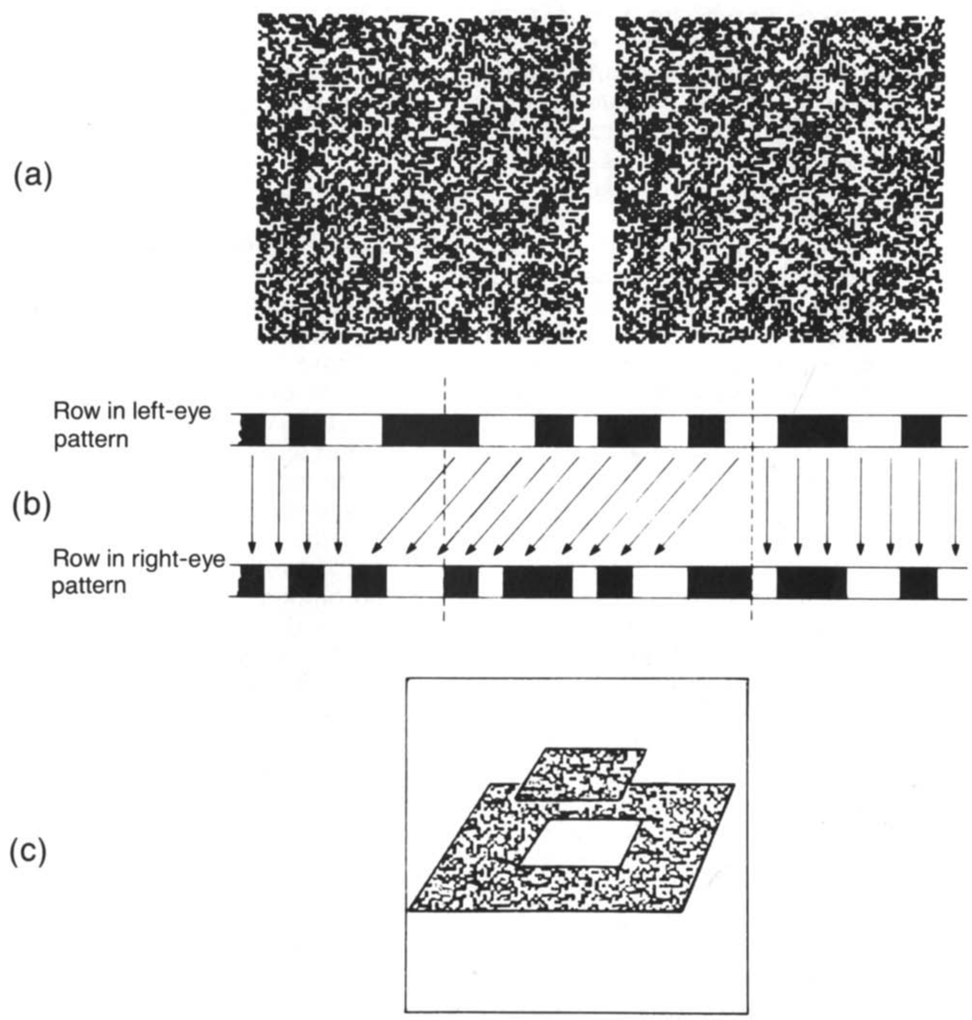

Fig. 1. (a) A pair of random-dot stereo textures. (b) To generate a row in the right-eye pattern, the sequence in the central portion is shifted a constant number of positions to the left. Outside the central portion, both textures consist of random dots in identical sequence. (c) When viewed stereoscopically, the central region appears to stand out from the background. *Reproduced with permission from Ref. 37.*

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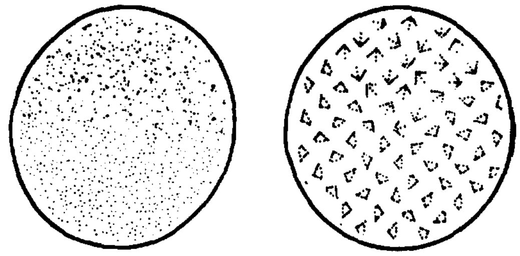


Fig. 2. Two pairs of preattentively discriminable textures. (a) Upper and lower halves differ in second-order statistics. (b) Upper quadrant has the same second-order statistics as the rest of the image, but it is still preattentively discriminable. *Reproduced with permission from Ref. 38.*

typically been attributed to the need for predators to judge distances accurately when pouncing on prey or when reaching for food items. But Julesz and others[10–12] have argued that another (perhaps primary) benefit of stereopsis is to facilitate detection of camouflaged prey: 'Even if binocular disparity [is] a weak depth cue, it is a powerful asset. Since time immemorial animals [have] developed camouflage and easily blended with the environmental background. It is possible to hide rather successfully this way when the predator has only monocular vision. ... However, ... even under ideal monocular camouflage, the hidden objects jump out in depth when stereoscopically fused. What is more, this object separation does not necessitate any familiarity with the stimulus and therefore could evolve at a relatively early stage in the processing chain of vision' (Ref. 7, pp. 145–146).

The 'camouflage-breaking' effect of stereopsis suggests a number of questions for further research. Does the vulnerability of prey hunted by predators with stereopsis increase with the dimension of the prey's body perpendicular to the background? Have prey that are hunted by predators with stereopsis been selected to minimize their three-dimensional aspect more than prey hunted by predators without stereopsis? If stereopsis is more highly developed in predators than in prey, are coat textures of prey better three-dimensional matches to backgrounds than those of predators? Are countershaded pigmentation patterns, which at best can only counteract monocular depth cues[13], less common among species needing to avoid detection by stereoscopic animals than among those avoiding animals without stereopsis?

Apparently the only existing application of Julesz' idea in a comparative context is Pettigrew's observation[12] that among birds stereoscopic vision is present only in species that search for prey against the ground; Pettigrew suggests that stereopsis would not help break camouflage for aerial predators whose prey are silhouetted against the sky.

Although stereoscopic vision may help some animals to differentiate coats of other animals from background textures, it apparently does not completely negate an advantage to monocular texture-matching because many prey species of stereoscopic mammals and birds have coats that look cryptic to us in two dimensions. It may thus be informative to consider the specific mechanisms by which two-dimensional textures are visually discriminated and the ways in which animal coat patterns might counteract or promote these mechanisms.

Discrimination of static two-dimensional textures

Julesz[6] used pairs of two-dimensional random-dot patterns to investigate features that allow people to discriminate them 'preattentively' (very rapidly and without effort or search). At first, Julesz thought that textures could be differentiated preattentively only when they differed in first- or second-order statistics (those based on luminances of individual pixels or on luminances of pixel pairs). This would require the visual system to perform a spatially extensive ('global') analysis of the information in an image. However, counterexamples were discovered that disproved this conjecture (Fig. 2). Julesz[14] then suggested that preattentive texture discrimination was a 'quasi-local' process, based on perception of differences in conspicuous features across portions of an image-space. These features collectively were called 'textons'. The definition and identification of textons have become controversial[15], but this controversy has not prevented computer-vision researchers from producing systems that replicate some aspects of human performance in texture-discrimination tasks.

A variety of computational approaches for segmenting two-dimensional visual textures have been suggested[16]. Current emphasis is on methods that filter information with respect to orientation and spatial frequency (resolution) in local portions of images before determining texture boundaries[17–23]. Such approaches have dovetailed with neuroanatomical demonstrations of cells in the visual cortex that respond to orientations and spatial frequencies of localized image features[24] and with studies suggesting that this arrangement provides an efficient way of dealing with natural scenes, which tend to be fractal[25–27].

In a zoological context, the process of preattentive texture discrimination is probably most relevant to actively searching, generalist predators who must distinguish coat textures of potential prey from background textures without carefully scrutinizing every surface in their visual space. It is also relevant to foraging prey who periodically scan for predators. Work of psychophysicists and computer-vision researchers thus raises or reformulates[2] a number of questions for comparative studies of animal coat patterning: Do various texture elements (stripes, spots, rosettes) found, for example, on coats of forest-dwelling cats provide equally effective camouflage when the coats are viewed at resolution levels appropriate for the circumstances under which it is adaptive for these animals to be cryptic? When coat textures function in display, do they differ from backgrounds in spatial frequencies or in orientations to which the intended viewers are most sensitive? If predators generally have higher-resolution vision than their prey, does it follow that prey coat textures should be better high-resolution matches to backgrounds and that predator coats should be better low-resolution matches? If nocturnal life is associated with lower-resolution vision than diurnal life, are cryptic species active at night better low-resolution texture matches and diurnal species better high-resolution matches? Are coat textures fractal?

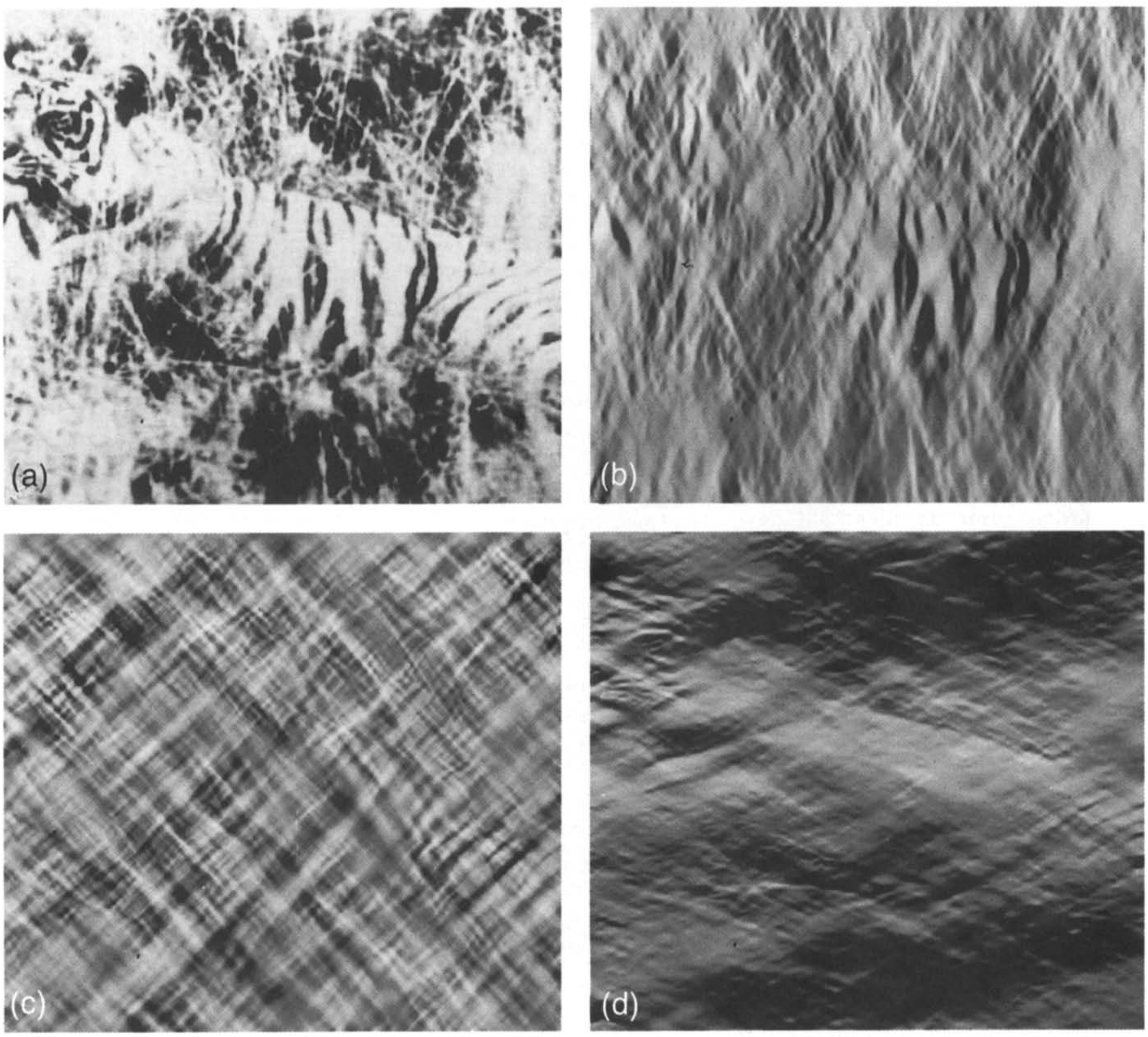
Box 1. Orientation-specific reconstructions of images by wavelet analysis

Wavelet methods have applications in many areas of signal analysis[21]. The wavelet transform decomposes a one-dimensional signal into a weighted sum of certain elementary functions which are dilations and translations of a unique function called a 'mother wavelet'. In effect, the signal is viewed through a set of windows varying in width. Wide windows capture slowly varying (low-frequency) features, while narrow windows track sharp (high-frequency) details. After decomposition, the signal can be reconstructed on the basis of specific space-frequency parameters.

Techniques for wavelet-based decomposition and reconstruction can also be applied to two-dimensional signals such as images. The elementary functions derived from a mother wavelet then correspond to windows that vary not only in size (frequency), but also in direction (orientation). The existence of cells in the mammalian visual cortex that respond to stimuli of specific orientations or spatial frequencies[24] suggests that some visual systems in animals use a similar approach.

As an example of how wavelet methods can provide new perspectives on coat-pattern function, consider the photograph of a tiger (image a, *reproduced with permission from Ref. 28*). Orientation-specific reconstructions (all frequencies included) show that the animal is generally a good match to its background in the vertical channel (image b) and in the diagonal channel (image c). On the other hand, the tiger's dorsal edge and facial features are quite apparent in the horizontal channel (image d).

It has been suggested that mammals develop greater visual sensitivity to features conforming to the dominant orientations of their visual environments[39]. If the prey of tigers are visually most sensitive to vertical features, as seems possible in the tigers' reed-dominated habitats, then tigers are well camouflaged. Their horizontal facial features might provide a 'private channel' for intraspecific communication. If their prey are also highly sensitive to horizontal features, then tigers might do well to avoid looking directly at them until it is too late for the prey to escape.



An interesting start in addressing such questions with machine-vision techniques was made by Godfrey *et al.*[28], who applied Fourier analyses to images of a tiger and a zebra with their natural backgrounds. These authors extracted specific spatial-frequency bands from the Fourier transforms and then inspected the reverse transforms of each band independently. The reconstructed images were interpreted as showing that both tiger and zebra were moderately cryptic at lower spatial frequencies; on the other hand, the zebra was conspicuous at higher frequencies and the tiger was not. A possible objection to Godfrey *et al.*'s technique arises from the fact that Fourier analysis is global, so that the reconstructions are based on amplitude spectra for the entire image. This can complicate comparisons of camouflage effectiveness if the original images differ in the proportions constituted by the animal and by its background. Newer approaches such as 'wavelet' analysis[21,23] may be more informative because, like the visual system, they treat local brightness variation at varying orientations and resolutions (Box 1).

Discrimination of moving textures

Of course, most animals need to move occasionally at least. A texture that is statically cryptic may not conceal an animal when it is moving because movement of one object's surface past another generates powerful visual cues. Motion processing seems to be a universal feature of animal visual systems[29]. Even house flies can discriminate movement of a two-dimensional random-dot texture over an identically textured background[30]. In mammals, neuroanatomical pathways similar to those used for stereopsis handle perception of object motion[9]; however, there are important differences between depth- and motion-perception systems[31]. For detecting moving objects, the visual system makes greater use of low-frequency information and less use of fine texture details[9,31].

Computer-based methods for motion perception are more complicated than those for analysing static images because movement requires that a sequence of images be compared rapidly. Still, machine-vision systems have been developed that can replicate important features of human motion-perception, including illusions of movement[32,33]. Such approaches may make it possible to assess quantitatively effects of coat features, such as bands and stripes, that have been suggested to cause inaccurate perception of animal speed or direction[34,35].

Concluding caveats

Because of their emphasis on human perception, computer-vision methods based on psychophysical studies must be used with caution[36]. Applications to zoological questions should invoke properties of human systems that are likely to be shared with other species, or the methods should be adapted for specific visual characteristics of animal species. Purely comparative questions about animal camouflage can be addressed with machine-vision systems designed to mimic human vision as long as discrepancies between such systems and animal vision do not bias the outcome of the comparison. For testing adaptive effects of coat textures, machine-vision approaches based on psychophysics will never replace conditioning experiments with live animals. But at a cost of somewhat reduced certainty, they can vastly increase the types and functions of coat textures that are investigated.

Acknowledgements

We thank Jian Fan for assistance with the illustrations and reviewers for helpful suggestions.

References

1 Gibson, J.J. (1950) *The Perception of the Visual World*, Houghton Mifflin
2 Endler, J.A. (1978) *Evol. Biol.* 11, 319–364
3 Wilkinson, F. (1986) *Behav. Brain Res.* 19, 71–82
4 Fox, R. (1978) in *Frontiers in Visual Science* (Cool, S.J., Smith III, E.L. and MacAdam, D.L., eds), pp. 316–327, Springer-Verlag
5 Blough, D.S. (1985) *J. Exp. Psychol.* 11, 261–280
6 Julesz, B. (1975) *Sci. Am.* 232 (4), 34–43
7 Julesz, B. (1971) *Foundations of Cyclopean Perception*, University of Chicago Press
8 DeAngelis, G.C., Ohzawa, I. and Freeman, R.D. (1991) *Nature* 352, 156–159
9 Livingstone, M. and Hubel, D. (1988) *Science* 240, 740–749
10 Ramachandran, V.S. (1985) *Perception* 14, 97–103
11 Nakayama, K., Shinsukek, S. and Silverman, G.H. (1989) *Perception* 18, 55–68
12 Pettigrew, J.D. (1986) in *Visual Neuroscience* (Pettigrew, J.D., Sanderson, K.J. and Levick, W.R., eds), pp. 208–222, Cambridge University Press
13 Kiltie, R.A. (1988) *Trends Ecol. Evol.* 3, 21–23
14 Julesz, B. (1981) *Nature* 290, 91–97
15 Julesz, B. (1989) *Proc. Soc. Photo-Opt. Instrum. Eng. (SPIE)* 1077, 246–268
16 Haralick, R.M. (1986) in *Handbook of Pattern Recognition and Image Processing* (Young, T.Y. and Fu, K-S., eds), pp. 247–281, Academic Press
17 Rubenstein, B.S. and Sagi, D. (1990) *J. Opt. Soc. Am.* A7, 1632–1643
18 Bergen, J.R. and Landy, M.S. (1991) in *Computational Models of Visual Processing* (Landy, M.S. and Movshon, J.A., eds), pp. 253–271, MIT Press
19 Porat, M. and Zeevi, Y.Y. (1989) *IEEE Trans. Biomed. Eng.* 36, 115–129
20 Daugman, J.G. (1989) *IEEE Trans. Acoust. Speech, Signal Process.* 36, 1169–1179
21 Mallat, S.G. (1989) *IEEE Trans. Pattern Anal. Mach. Intell.* 11, 674–693
22 Unser, M. and Eden, M. (1989) *IEEE Trans. Pattern Anal. Mach. Intell.* 11, 717–728
23 Manjunath, B.S. and Chellapa, R. (1991) *Proceedings of the IEEE Computer Society Conference on Computer Vision and Pattern Recognition* (IEEE Computer Society, ed.), pp. 358–363, IEEE Computer Society Press
24 De Valois, L. and De Valois, K.K. (1988) *Spatial Vision*, Oxford University Press
25 Daugman, J.G. (1989) *IEEE Trans. Biomed. Eng.* 36, 107–114
26 Field, D.J. (1987) *J. Opt. Soc. Am.* A4, 2379–2394
27 Pentand, A.P. (1984) *IEEE Trans. Pattern Anal. Mach. Intell.* 6, 661–674
28 Godfrey, D., Lythgoe, J.N. and Rumball, D.R. (1987) *Biol. J. Linn. Soc.* 32, 427–433
29 Nakayama, K. (1985) *Vision Res.* 25, 625–660
30 Reichardt, W. and Poggio, T. (1979) *Biol. Cybern.* 35, 81–100
31 Ramachandran, V.S. (1987) in *The Perception of Illusory Contours* (Petry, S. and Meyer, G.E., eds), pp. 93–108, Springer-Verlag
32 Yuille, A.L. and Grzywacz, N.M. (1988) *Nature* 333, 71–74
33 Bülthoff, H.H., Little J.J. and Poggio, T. (1989) in *Proceedings of a Workshop on Visual Motion* (IEEE Computer Society, ed.), pp. 212–238, IEEE Computer Society Press
34 Pough, F.H. (1976) *Copeia* 1976, 834–836
35 Jackson, J.F., Ingram III, W. and Campbell, H.W. (1976) *Am. Nat.* 110, 1029–1053
36 Endler, J.A. (1990) *Biol. J. Linn. Soc.* 41, 315–352
37 Braddick, O.J. (1985) in *The Senses* (Barlow, H.B. and Mollon, J.D., eds), pp. 192–211, Cambridge University Press
38 Braddick, O.J. and Atkinson, J. (1985) in *The Senses* (Barlow, H.B. and Mollon, J.D., eds), pp. 212–238, Cambridge University Press
39 Blakemore, C. and Cooper, G.F. (1970) *Nature* 228, 477–478