A Hypothesis-Based Approach to Clinical Psychophysics and to the Design of Visual Tests
The Proctor Lecture

David Regan

Over the past 30 years or so, it has become increasingly clear that even gross defects of visual function can be hidden from detection by classic clinical tests. In this lecture, I have outlined a hypothesis of visual processing that offers a guide to the design of tests for revealing forms of visual loss that are hidden from detection by the classic tests of visual function and have given examples of the application of the hypothesis.

A further point bears on the growing involvement of ophthalmologists and vision scientists in developing screening tests for individuals who must perform tasks that require high skills in visually guided motor action, such as driving a car or truck, flying a passenger aircraft, flying a medical emergency helicopter, and providing visual surveillance in air-sea rescue operations. The hypothesis can guide the design of screening tests that are specific for the task to be performed.1–3

At one time, basic research on the detection of objects and discriminations of their shapes and configurations was restricted to luminance-defined form. However, recent findings indicate that rather than containing only one subsystem for the early processing of the spatial attributes of objects, the visual system contains five parallel subsystems, the performances of three of which compare well with that for luminance-defined form, except only for fine detail and sharp edges (reviewed in Ref. 4). In the second half of this article is discussed the implications of these findings for clinical psychophysics.

Psychophysics Is Not Physiology: Mathematical Versus Structural Models of the Visual System

Almost all current research on the visual system falls under the general heading of systems analysis. The nature of a psychophysical model can be understood in terms of the following distinction made in systems analysis: between (1) the mathematical (i.e., functional) model of a system that allows the system's output for any arbitrary input to be predicted and (2) the structural model of the same system (i.e., a description of the system's physical parts and their interconnections).5–7 The force of the distinction is that, for a system composed of multiple interconnected nonlinear parts, the system as a whole may have system properties—functional properties that may be qualitatively different from those of any of its parts. A psychophysical model is an example of what is meant by a mathematical or functional model in the context of systems analysis. In this sense, psychophysical and structural models of the visual system are complementary descriptions of the same nonlinear system.

A psychophysical model that is framed entirely in terms of sequential stages of processing lumps together the effects of the profuse feedback, feedforward, and lateral neural connections within the visual system, including interactions between individual cortical areas and between cortical areas and the (at least 20) subcortical nuclei that are connected to the cortex.8–10 Among the consequences for psychophysics are the following: (1) Because the physical basis of a system property cannot be assigned a discrete location within the system, it follows that, for visual functions that are system properties, the question of where the function is performed within the visual system may not be meaningful. (2) The sequence of processing stages in a psychophysical model may be exceedingly difficult to relate to the structural level of description and, in particular, to the hierarchical organization of cortical areas.

Thus, in principle, the value of a psychophysical model may be diminished if it is forced into the straightjacket of being framed entirely in terms of presently known physiological entities. Relevant to this is Westheimer's statement that such writings portray "the preoccupation of current psychologists with the interim findings of physiology instead of concentrating on their birthright."11

Filters

In psychophysics, the theoretical construct of a filter that passes only part of the incoming information dates back to the trichromatic theory of color vision, as does the notion of independent operation of parallel filters.12 Over the past 40 years, the discovery that adaptation can produce a temporary loss of sensitivity to luminance contrast that is selective for spatial frequency and orientation13–16 triggered a large number of attempts to extend the notion of parallel filters to the early processing of luminance-defined form. The hypothesis was that (at least for near-threshold contrasts) the first stage of processing luminance-defined form can be modeled as a parallel array of filters, each of which passes only a narrow range of spatial frequencies and orientations and whose properties are affected neither by the spatial content of the visual scene nor by the observer's psychophysical task (reviewed in Ref. 17). Any given first-stage spatial filter is supposed to have a strictly localized receptive field.

More recently, the spatial filtering concept has been extended to spatial filters for motion-defined form, texture-defined form, and cyclopean form (reviewed in Refs. 2,4,18). Because any of these three kinds of filter receives input from an array of spatial filters for luminance-defined form, the processing of motion-defined, texture-defined, and cyclopean forms is comparatively degraded for very fine detail and sharp edges.

Hering's theory of color vision incorporates the following ideas: (1) Because the sensitivity profiles of the three color
filters overlap considerably, wavelength information can be represented in terms of the relative activation of the three color filters; (2) this information can be recovered at an opponent-processing stage. The just-noticeable difference in wavelength is far smaller than the wavelength bandwidth of any of the color filters—a consequence of the low noise level in the filters’ outputs combined with the “relative activity” encoding of wavelength just mentioned. This concept of broad-band filtering followed by opponent processing has recently been extended from color vision to psychophysical models for the processing of spatial frequency, orientation, sensitivity to relative position, the direction of motion in depth, motion within a frontoparallel plane, and changing size.

The “Sets of Filters” Hypothesis

If, on the one hand, it were the case that an observer’s response to a designated input variable did not depend only on the designated variable, but rather was strongly affected by other variables, then the task of the psychophysical modeler would be forbiddingly difficult. On the other hand, if early visual processing can, at least partially, be modeled in accordance with the hypothesis illustrated in Figure 1, then the hypothesis could provide a guide to the design of psychophysical tests.

According to Figure 1, the early processing of at least some kinds of visual information is through sets of filters that, to a first approximation, operate independently and are free from crosstalk. (The theoretical construct “set of filters” is quite different from the theoretical construct “filter.” For example, the sensitivity profiles of the filters within a set commonly overlap. By definition, this is not so for sets of filters). At least for the processing of small changes, there are several candidate sets of filters, including ones for the rate of change of size, rate of change of binocular disparity, time to collision, and direction of motion in depth (reviewed in Refs. 2, 4, 39).

How does one test whether a candidate set of filters obeys the crucial independent-processing requirement? Illustrating one method, Figure 2 shows that observers can discriminate independently the time to collision (TTC) with an approaching object.

**FIGURE 1.** The “sets of filters” hypothesis. The dashed lines indicate that descending task-dependent signals might affect the properties of some sets of filters. Adapted, with permission, from Regan D. Visual information channeling in normal and disordered vision. Psychol Rev. 1982;89:407–444.

**FIGURE 2.** Plots of response probability versus the task-relevant variable (A, D) and a task-irrelevant variable (B, C). The time to collision (TTC) with an object approaching the eye at constant speed is given by: TTC \(=\) (object’s instantaneous angular size)/(rate of increase of angular size). Adapted, with permission, from Regan D, Hamstra S. Dissociation of discrimination thresholds for time to contact and for rate of angular expansion. Vision Res. 1993;33:447–462.
sphere and its rate of increase of angular size. (These two variables had zero correlation within the stimulus set.)

For the organism, one advantage of analyzing those kinds of visual information that are important for visually guided motor action through parallel, independently functioning sets of filters, is that the operation of any given set of filters would be the same in different visual environments. Thus, a skill learned in one visual environment would transfer to other visual environments.

Note that the dashed lines in Figure 1 depict the possibility that the properties of any given set of filters may not be invariant, but rather may be controlled by descending signals that vary the properties of the filters according to the visual task at any given moment. The exception is the uppermost (A) set of filters that subserve color vision.

In the context of the psychophysically based hypothesis illustrated in Figure 1, the possibilities of visual dysfunction include the following: (1) sensitivity loss for an entire set of filters; (2) sensitivity loss for only some filters within a set; (3) broadening of the bandwidths of individual filters within a set; (4) elevation of discrimination threshold, either indirectly consequent on (2) or (3), or directly caused at the opponent-process stage; (5) a partial or total failure of independence between the processing performed by two or more sets of filters. The dashed lines in Figure 1 suggest that a given visual dysfunction may reflect either abnormality within a set of filters or abnormality in the task-dependent descending signal. (Note that these are distinctions based on psychophysical modeling. To relate the kinds of dysfunction just described to physiological or neurochemical disorders would require convergent information, including the correlation of psychophysical test results with medication in patients and rigorous psychophysical–physiological bridging experiments in alert, behaving, nonhuman primates.)

In the sections to follow, I describe examples of possibilities (1), (2), and (4). Possibility (5) seems so far to have been explored only in the context of pilots flying high-performance jet aircraft.

Implications for Clinical Psychophysics

Suppose that only one set of filters is dysfunctional. Even if the defect is gross, it will not be detected by a clinical test unless the test assesses the functioning of the affected set of filters. For example, many individuals have areas of the binocular visual field where a rate of change of disparity produces no sensation of motion in depth (stereomotion scotomata), although clinical stereoaucity, visual acuity, and even sensitivity to motion parallel to the frontal plane are all normal.31–35 Figures 3A and 3B illustrate this point. Figure 3A shows a stereomotion field for depth (disparity) oscillations. A horse-shoe-shaped region of total blindness to stereomotion is evident. (Depth oscillations are not perceived, even when the viewing time is long.) Figure 3B shows thresholds along a horizontal line passing through the center of the fovea. Although the threshold for stereomotion (open symbols) is extremely high within the stereomotion scotoma, thresholds for monocular (filled symbols) and binocular (stars) motion within a frontoparallel plane are unaffected, as is the threshold for a difference in static depth. This finding added to previous evidence that stereomotion is processed independently of motion parallel to the frontal plane.24–31 A common finding with stereosomatotop is that they are different for far and near disparities. Furthermore, sensitivity to approaching and receding motion can be lost independently of one another.

A clinical test that assesses only certain filters within a set may fail to detect even a gross loss of function in other filters within the set. The groundwork for the following illustration of this point was laid by psychophysical evidence discussed earlier that luminance-defined spatial form is processed through multiple parallel filters, each of which is tuned to a narrow range of spatial frequencies and orientations.13–15 This psychophysical evidence was, however, restricted to near-threshold (i.e., just visible) levels of luminance contrast. Human brain-evoked potential studies subsequently showed that spatial filtering also occurs at contrast levels far above the contrast-detection threshold.40–45 Figure 4A plots brain signals evoked by a single vertical grating. The spatial frequency tuning is broadband independent of the grating’s contrast (15%–100%). In Figure 4B a second vertical grating was superimposed on the first grating, and its spatial frequency was varied. The variable grating suppressed the response evoked by the fixed grating, but only when its spatial frequency was close to that of the fixed grating. The result of only one experiment is shown in Figure 4B, but similar results were obtained independently of the spatial frequency of the fixed grating. The bandwidth of this nonlinear suppression was 0.4 to 1.0 octaves, in good agreement with channel bandwidths estimated from psychophysical data. In Figure 4C the spatial frequency of the variable...
The lines of fundamental research just reviewed provided a basis for understanding why in some patients with multiple sclerosis the Snellen high-contrast letter test shows normal acuity, even though sensitivity for gratings of low and/or intermediate spatial frequencies be reduced more than fivefold.\(^{46-48}\) Figures 5A and 5B demonstrate that a blurring lens selectively attenuates visual sensitivity to high spatial frequencies. Results in the patient with multiple sclerosis shown in Figures 5C and 5D exhibit a mirror-image pattern of loss. The selective loss of sensitivity to intermediate spatial frequencies experienced by a second patient (Figs. 5E, 5F) has been attributed to dysfunction of intermediate-spatial-frequency channels.\(^{46,49-50}\) This intermediate-frequency loss is often selective for orientation,\(^{57-58}\) can occur in patches within the visual field,\(^{58}\) and is commonly selective for temporal as well as spatial frequency.\(^{48}\) Although monocular diplopia of optical origin can cause a selective loss of sensitivity to intermediate spatial frequencies that is tuned to orientation,\(^{51-52}\) the frequency tuning is considerably sharper than in Figures 5E and 5F,\(^{52}\) and it is difficult to see how such loss could be tuned to temporal frequency. It is a puzzle how the pattern of loss just described could be caused by plaques of demyelination.

A similar pattern of loss can be caused by Parkinson disease.\(^{53-56}\) A patient with Parkinson disease who experienced a large loss of contrast sensitivity after overnight withdrawal of medication, exhibited a recovery of contrast sensitivity within 1 hour of taking oral medication.\(^{57}\)

To allow the kinds of subtle visual loss shown in Figures 5C through 5F to be conveniently detected in the clinic, we introduced a range of low-contrast acuity charts that differ from the familiar Snellen chart in that, rather than near-100% contrast, the letters are either 50%, 25%, 10%, or 4% contrast.\(^{58-59}\) Figures 6A and 6B compare one of the low-contrast charts with a near-100% contrast chart. An abnormally high ratio of high-contrast acuity to low-contrast acuity effectively distinguishes between an entirely optical (front of the eye) cause of visual loss and a retinal and/or central visual system component. An alternative approach is to use letters of constant size but variable contrast.\(^{50}\)

Low-contrast acuity charts also provide a sensitive means of quantifying an individual’s susceptibility to glare.\(^{61,62}\) Glare susceptibility measurement may be useful in assessing visual disability experienced by patients with early cataract of any given type, because it assesses the contrast-diluting effect of light scattered onto the retina rather than the light scattered out of the pupil\(^{55}\) and must surely have a future role in assessing an individual’s suitability for driving a vehicle at night.

As mentioned earlier, some patients experience a loss of discrimination that is distinct from a loss of sensitivity. For example, a patient’s spatial-frequency discrimination was unaffected at low frequencies at which contrast sensitivity was depressed, but was very poor at high spatial frequencies at which contrast sensitivity was unaffected.\(^{54}\) This patient’s vision cannot be described as blurred; rather, her perception was distorted. This loss of ability to distinguish between gratings of different bar widths is exactly what would be expected if, as suggested previously on different grounds, spatial frequency discrimination threshold is determined by opponent processing.\(^{19}\) A similar discrimination loss (although short-lived) can be produced by adapting to a high-contrast grating.\(^{20}\)

Evidence that orientation discrimination threshold is also based on opponent processing\(^{11,12}\) is shown in Figure 7. Adapting to a vertical high-contrast grating elevates contrast detection threshold for near-vertical test gratings (open symbols).\(^{15}\) But orientation discrimination threshold is elevated for
test grating tilted by approximately 11° to 17° from vertical (solid symbols), as would be expected if orientation discrimination threshold were based on opponency between orientation-tuned elements.

If visual acuity for a line chart (Fig. 6B) is lower than for a repeat-letter chart (Fig. 6C) then acuity is limited by the accuracy of gaze selection or control, rather than by resolution or lateral interactions between contours. The development of visual acuity in some children is limited by gaze accuracy. In a group of amblyopic children undergoing treatment, 20% had defective gaze selection or control. This percentage rose to 53 in a group of adults who had been unsuccessfully treated for amblyopia. We suggested that the repeat-letter test could identify children whose amblyopia was less likely to respond to


Figure 6. (A) One of the four Regan low-contrast acuity charts. (B) High-contrast acuity chart. (C) Repeat-letter chart.
of quite different area was briefly distorted. This aspect ratio aftereffect transfers from luminance-defined shape to a cyclopean shape\textsuperscript{3,25} and to a color-defined shape.\textsuperscript{76}

A Multiplicity of Visual Fields

The realization that useful clinical information can be obtained by plotting the distribution of visual sensitivity throughout the visual field dates back at least to von Graefe, Bjerrum, and Traquair. But clinical fields have largely been restricted to testing gross visual sensitivity to the presence of an object, commonly the ability to detect a static or moving bright light.

Some of the early essays regarding nonclassic perimetry focused on the temporal properties of visual processing. For example, we found that, in some patients with multiple sclerosis, visual fields for the delay in perceiving onset or offset of light showed islands of increased delay,\textsuperscript{77–79} and visual fields for double-flash resolution revealed areas of degraded temporal resolution.\textsuperscript{80,81} These temporal measures tracked increases and decreases of the body temperature of patients in whom temperature changes model increasing demyelination and remyelination ( Uhthoff syndrome).\textsuperscript{82,83} The rationale for these studies of temporal factors was that animal models of demyelination had shown that transmission delay and reduced spike firing frequency precede blockade.\textsuperscript{84} Others adopted a frequency-domain rather than a time-domain approach by measuring fields for flicker-fusion frequency\textsuperscript{85} and by demonstrating field defects in patients with ocular hypertension (OHT) using flicker perimetry.\textsuperscript{86}

The hypothesis illustrated in Figure 1 is that visual information from any small area of the visual field is processed through parallel, independently functioning sets of channels. Although comparatively little has so far been firmly established regarding the clinical value of measuring visual fields based on this hypothesis, a number of preliminary reports have been published. We have already seen (Fig. 3) that stereomotion fields can provide quite different information from that provided by clinical fields, stereoacuity fields, or even fields for motion within a frontoparallel plane.\textsuperscript{31–33} Curiously, although visual fields for stereomotion commonly show defects in normally sighted individuals, visual fields for the motion-in-depth sensation produced by changing size and fields for associated judg

Visual Processing of Two-Dimensional Images

Next, I discuss the hypothesis that there are visual dysfunctions that cannot be detected by test stimuli whose contrast varies along only one dimension (e.g., gratings, Gabors), because the dysfunction is restricted to the processing of image two dimensionality. In Figure 4C, nonlinear suppression of the fixed grating’s response was almost as strong when the gratings were orthogonal as when they were parallel. Thus, the response to a two-dimensional image could not be explained entirely in terms of the response to a single grating. Psychophysical evidence for this point was obtained by instructing observers to discriminate small variations in the aspect ratio (i.e., height/width) of an ellipse around some mean value. The trial-to-trial variations in aspect ratio were accompanied by large trial-to-trial variations in area, thus removing height alone or width alone as reliable cues to aspect ratio.\textsuperscript{75} Observers were exquisitely sensitive to departures from circularity. Figure 8 shows that discrimination threshold fell to approximately 1% at an aspect ratio near 1.0 which, for an area of 1.0\textsuperscript{2} was a hyperacuity as defined by Westheimer\textsuperscript{74} in a previous Proctor lecture. This experiment provided evidence for a mechanism that compared the height and width of a figure with great precision, while being somewhat insensitive to the area of the figure and to the retinal locations of its boundaries—a so-called global process. Further evidence for this mechanism for processing two dimensionality is that, after adapting to a rectangle, the perceived aspect ratio of a subsequently viewed test figure


Another question yet to be addressed is whether patients can experience selective disruption of long-distance interactions in the early processing of luminance-defined\textsuperscript{67–70} cyclopean,\textsuperscript{71} and motion-defined\textsuperscript{72} forms.

The dotted line in Figure 7 shows the postadaptation threshold elevations (solid line) and for contrast detection (dotted line) for orientation discrimination. 1316 Regan

FIGURE 8. The just-detectable percentage change in aspect ratio (i.e., height/width) for outlined ellipses of different mean aspect ratios. Adapted, with permission, from Regan D, Hamstra S. Shape discrimination and the judgement of perfect symmetry: dissociation of shape from size. \textit{Vision Res.} 1992;52:1845–1864.
ments of time to collision can both be intact, even within a stereomotion scotoma.87 Thus, the behavioral consequences of stereoscotomata for collision avoidance on the highway are evident presumably only when monocular information about time to collision and the direction of motion in depth is unavailable or corrupt, as, for example, when the approaching object is very small88 or (more commonly) when the approaching object’s retinal image changes shape as it grows larger.89

When contrast sensitivity fields for temporally modulated gratings of 2 or 5 cdcdeg were measured in a group of patients with OHT, 50% showed field defects, even though clinical fields (Goldmann; or Octopus, Interzeag, Schlieren, Switzerland) and grating acuity fields were normal. We suggest that our test procedures revealed selective dysfunction in neurons with large receptive fields, whose function was not effectively tested by either Octopus or Goldmann targets.90,91 These psychophysical findings might be explained by subsequent physiological evidence that ganglion cells with large-diameter axons are preferentially damaged in glaucoma.92 In recent years there has been considerable interest in attempting to develop techniques to distinguish between the functioning of different kinds of retinal cell.93–98

Motion-Defined Form

Animals who are eaten by other animals are commonly adept at remaining absolutely motionless, because motion can break camouflage, rendering the hitherto-hidden prey visible to the predator. As already mentioned, the early processing of motion-defined form occurs within one of the five subsystems for spatial form.

Although everyday object motion confounds several possible cues to object visibility,99 by arranging that a target’s outline is stationary while texture elements within the image and outside the target’s image move in opposite directions at the same speed, the target’s camouflage is broken by almost pure motion contrast. In the situation depicted in Figure 9B, threshold for detecting the letter is determined by the speed difference of the texture elements inside and outside the letter, and the appearance and disappearance of texture at the object’s boundaries plays a negligible role.100

The (motion) contrast sensitivity function for a motion-defined grating differs from the luminance-contrast sensitivity curve, in that it does not extend to such high spatial frequencies and grating acuity is only 5 to 10 cdcdeg.101 By analogy with the contrast sensitivity function for luminance-defined form, it may be that the motion contrast curve is the envelope of narrow-bandwidth (approximately 1.5 octaves) tuning curves of spatial-frequency filters for motion-defined form.102 Receptive field size for such filters has been estimated at 0.2° to 2°.103–106

To explain why a motion-defined boundary can look much sharper than would be expected from either grating acuity or receptive field size, it has been suggested that perceived sharpness is determined by the pattern of activity among receptive fields for relative motions that straddle the boundary.106 Acuity for relative position (vernier step threshold) is also puzzlingly acute for motion-defined form (27–45 arc sec).99 It is comparable to that for luminance-defined form of matched spatial sampling (i.e., the same number of dots per degree of subtense), perhaps for the reason just mentioned. An alternative explanation (if the vernier task can be regarded as an orientation discrimination task) is that orientation discrimination threshold for motion-defined form is remarkably low, as low as for luminance-defined form of matched spatial sampling (approximately 0.5°).107 To account for the finding that orientation discrimination for motion-defined form is even sharper than the orientation tuning curves of even the most sharply

Figure 9. Motion-defined letters. (A–D) Photographic time exposures of a computer monitor. (A) A letter is perfectly camouflaged within a pattern of stationary dots. (B) Dots inside and outside the letter move at the same speed but in opposite directions. Although the letter is rendered visible by texture contrast. Adapted, with permission, from Regan D, Hong X. Visual acuity for optotypes made visible by relative motion. Optom Vis Sci. 1990;67:49–55.
tuned cortical cells. I suggested that filters for motion-defined form are tuned to orientation and that discrimination threshold is determined by the pattern of activity among such filters. Turning to the processing of two-dimensional form, aspect ratio discrimination for motion-defined rectangles is, at approximately 2%, similar to that for luminance-defined rectangles of matched spatial sampling. In summary, the spatial discrimination thresholds so far reported for motion-defined form are, providing spatial sampling is matched, little if at all inferior to the corresponding thresholds for luminance-defined form.

To facilitate the testing of this visual subsystem for motion-defined form in patients, we developed a test based on the familiar Snellen test (Fig. 9). Ten different letters were presented at high dot speed, then at lower dot speed, and so on. A plot of the patient’s percentage of correct letter recognitions versus dot speed gave a psychometric function that allowed the dot speed that gave a 55% correct score to be estimated (55% is halfway between chance and 100% correct).

The ability to read motion-defined letters seems to be an especially sensitive indicator of dysfunction and provides complementary information to standard clinical tests. As might be expected from this last point, the developmental time course of the ability to read motion-defined letters differs from that of visual acuity for luminance-defined letters. The ability to read motion-defined letters seems to be an especially sensitive indicator of visual dysfunction. This may seem surprising, given that a loss of sensitivity to motion per se is exceedingly rare and may point to a failure in the spatially integrative (global) processing required to extract the letter’s shape. A considerable proportion of patients with multiple sclerosis (~70%) have abnormal recognition scores for motion-defined letters, including many patients whose scores on both high-contrast (Snellen) and low-contrast luminance-defined letter charts are normal and who show no other visual abnormality. In a group of patients who had been successfully treated for unilateral amblyopia, results in 95% of treated eyes and 80% of fellow eyes were abnormal on the motion-defined letter test.

\[ \text{Texture-Defined Form} \]

Because demyelinating plaques are typically scattered throughout white matter, our studies in patients with multiple sclerosis gave no indication of whether a single circumscribed lesion could cause the pattern of visual loss just described. Therefore, we studied a series of 13 patients who had undergone neurosurgery to remove unilateral lesions and who had normal visual acuity and central visual fields and normal ability to detect and to discriminate the direction of dot motion. Figure 10 shows that seven patients had extensive lesions in parietotemporal white matter. These seven patients were unable to recognize motion-defined letters. The black areas (Figs. 10B, 10C, arrows) are the region of overlap in five patients. The ability to recognize motion-defined letters was normal in the remaining six patients, in none of whom the lesion extended into the area of overlap shown in Figure 10. Neurons sensitive to oppositely directed motion are required to extract motion-defined form, and animal evidence indicates that these are not found before area middle temporal (MT), far along the so-called motion pathway, and long after its branching from the so-called form–color pathway. We suggested that the failure to read motion-defined letters reflects a disruption of one specific spatiotemporal pattern of activity within a large volume of brain and, in particular, is caused by the severing of connections, perhaps between cortical areas in the two pathways, or connections from homologues of medial superior temporal (MST)/MT to V1, or connections between cortical areas and (at least) subcortical structures.

\[ \text{Figure 10. The outlines mark lesion boundaries delineated by CT (computed tomography) in seven patients with unilateral damage. All lesions are plotted onto one hemisphere. Reprinted, with permission, from Regan D, Giaschi D, Sharpe JA, Hong KH. Visual processing of motion-defined form: selective failure in patients with parieto-temporal lesions. J Neurosci. 1992;12:2198–2210.} \]
along a horizontal axis but are constant along any vertical axis. Below approximately six samples per degree (six short lines per degree in this case), visual sensitivity to an OTD grating is contaminated by spatial sampling effects, but, providing this limitation is respected, the (texture) contrast sensitivity function for an OTD grating is approximately flat over the 60:1 range between 0.07 cyc/deg and approximately 4.0 cyc/deg with a grating acuity of approximately 10 cyc/deg. The corresponding function for a luminance-defined grating of matched spatial sampling peaks at approximately 2 cyc/deg and does not fall until beyond 20 cyc/deg.119 Spatial-frequency discrimination thresholds for the two kinds of grating are identical from 0.07 to 0.4 cyc/deg—that is, over this 6:1 range, sensitivity to differences in the spatial scale of scene content is identical. Discrimination does not fail until beyond 7 cyc/deg for an OTD grating but extends to at least 20 cyc/deg for a luminance-defined grating.119

Acuity for the relative position of an OTD boundary (vernier step threshold and bisection threshold) is the same or only slightly inferior to that of the luminance-defined form of matched sampling frequency up to a spatial sampling frequency of approximately 20 per degree, beyond which the processing of an OTD boundary is necessarily inferior.120 Orientation discrimination threshold for an OTD bar (0.57°) is only slightly inferior to that for a luminance-defined bar of matched sampling121 and is much lower than the orientation-tuning bandwidth of the most sharply tuned cortical cells.108 To account for this finding, I suggested that the human visual system contains filters that are selective for the orientation of OTD form and that orientation discrimination threshold is determined by the pattern of activation among filters.121 (Evidence for such filters was subsequently reported: Adapting to an OTD grating produces an orientation-specific reduction in sensitivity to OTD test gratings.125) Regarding the processing of two-dimensional form, the aspect ratio discrimination threshold for OTD rectangles is, at 2.5% to 5%, comparable with that for matched luminance-defined form.123 In summary, the spatial discrimination thresholds for OTD form so far reported are only slightly, if at all, inferior to corresponding thresholds for luminance-defined form, provided that the number of spatial samples per degree is the same for both kinds of form and is not too high.

To facilitate the testing of the texture-defined form subsystem in patients, we developed a letter-reading test using the same 10 letters as are used in the motion-defined letter test.124 Short lines within an OTD letter were horizontal, and lines outside the letter were vertical (or vice versa), thus rendering the letter visible by orientation–texture contrast only (Fig. 11A). To reduce letter visibility in a progressive manner, we added either one, two (Fig. 11B), three, four (Fig. 11C), and so on, randomly placed dots for each texture line. In each trial, two patterns were presented. One contained a letter and the other contained only horizontal or only vertical lines. Thus, we could quantify both letter detection and letter recognition. By presenting all 10 letters with one noise dot, then with two noise dots, and so on, we were able to construct psychometric functions for OTD letter detection and recognition. The solid symbols in Figures 12A and 12B plot such data averaged over a group of control subjects. The continuous lines show the percentage of correct detections and recognitions predicted by a computational model whose schematic is depicted in Figure 13.125 This multichannel model has a double-opponent stage. It is similar to several previous models126–131 except for the last stage, which allows quantitative predictions of experimental data—namely, the percentage of correct letter detections and recognitions. The image shown in Figure 11A is the result of passing the Figure 11A pattern up to this stage. Reprinted, with permission, from Regan D, Hong XH. Two models of the recognition and detection of texture-defined letters compared. Biol Cybern. 1995;72:389–396.

FIGURE 11. Texture-defined letters of high (A) and progressively degraded visibility (B, C). (D) Result of passing pattern A through the first five stages of the Figure 13 model. Reprinted, with permission, from Regan D, Hong XH. Two models of the recognition and detection of texture-defined letters compared. Biol Cybern. 1995;72:389–396.

nonlinear, stage (stage 4) a nonlinear lateral interaction (NLI) enhances the boundaries of the OTD letter. Figure 11D shows the result of processing the Figure 11A pattern up to this stage.
This process was repeated for the other nine letters to give 10 templates that were cross-correlated with the processed results of the 110 noise-degraded letters, to give the letter-recognized probabilities shown in Figure 12B. The model’s predictions failed when the NLI stage was omitted.

Letter recognition data in a group of 25 patients with multiple sclerosis with normal visual acuities were compared with data in control subjects. Results in some patients were abnormal on the OTD letter test, but not on the motion-defined letter test, whereas results in others were abnormal on motion-defined letters but not on OTD letters. To account for this dissociation we suggested that the NLI stage in Figure 13 corresponds to long-range myelinated fibers in the primary visual cortex and that demyelination of these fibers disrupts the recognition of OTD letters, whereas, as mentioned earlier, lesions in a quite different region (Fig. 10) disrupt the recognition of motion-defined letters.

**SUMMARY**

Psychophysics can provide knowledge of visual function that cannot in practice be inferred from either cellular-level or molecular-level physiological data. Psychophysical (mathematical) models of the visual system exist in a world different from that of structural (physical) models. The difficulties that restrict a psychophysical level of understanding would be reduced if the following experimentally testable hypothesis were valid: Aspects of the retinal image that are important in visually guided action are processed through sets of filters that operate approximately independently of one another. Several candidate sets of filters have been identified in the early processing of luminance-defined form. In the broader context, there are five parallel subsystems in the early processing of the spatial aspect of the retinal image, and the spatial discriminations supported by the subsystems for motion-defined, texture-defined, and cyclopean forms are little if at all inferior to those for luminance-defined form except for very fine detail and sharp edges. Examples are given of how the hypothesis just stated can guide the design of visual tests to aid the diagnosis and investigation of a number of ophthalmological and neurologic disorders.

**Acknowledgments**

The research in the author’s laboratory has been performed in collaboration with colleagues, both vision researchers and physicians, who have contributed greatly to the work described herein. They include Ken Beverley, Han Colliewij, Max Cynader, Caspar Erkelens, Bernie Fresco, Debbie Giaschi, Rob Gray, Stan Hamstra, Xiang-Hua Hong, Peter Kaiser, Radha Kohly, Angela Kothe, Stephen Kraft, Ron Kruk, Lorinda Kwan, Raymond LeBlanc, Barry Lee, Charles Maxner, Michael Morgan, Jock Murray, David Neima, Christine Portfors, Paul Price, Jane Raymond, Marian Regan, Whitman Richards, James Sharpe, Trevford Simpson, Henk Spekreijse, Graham Trope, Christopher Tyler, Henk van der Tweel, Alex Vincent, and Hugh Wilson. The author thanks Derek Harnanansingh for valuable technical assistance and the National Eye Institute, National Sciences and Research Council (NSERC), Medical Research Councils (MRC) of the United Kingdom and Canada, Air Force Office of Scientific Research (AFOSR), and Centre for Research in Earth and Space Technology (CRESTech) for support and sponsorship. DR is the NSERC/CAE Chair in Vision and Aviation (CAE, Saint-Laurent, Quebec, Canada, is a provider of simulation technologies for training in aerospace).


