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Psychophysical studies of visual cortical function

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13. ABSTRACT (Maximum 200 words)

Our goal has been to understand visual cortical function using psychophysical techniques. In particular, we examined visual attention, visual search, visual surface representation and color filling in. In visual attention, we found evidence to suggest two components of focal attention, a transient and a sustained process. We also provided evidence for the role of attention in saccadic eye movements by showing rapid deployment of attention in the "gap" paradigm. In visual search, we found a particular situation where increasing distractor number led to decreasing reaction times, suggesting a different role for attention in such tasks. In visual surface representation, we outlined the role of surface encoding (border ownership, modal and amodal completion, transparency) in many visual tasks. From these studies we postulated the principle of generic image sampling, a hypothesis which provides a geometric tool to understand visual surface learning. We also have investigated the perception of depth from unpaired points (DaVinci stereopsis), showing that such points lead to depth and subjective contours. In color filling in, we have explored spatial-temporal dynamics and have created a neural model.

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During the recently completed grant period, considerable progress has been made in a variety of project areas. We divide our research accomplishments into several broad areas: Visual surface representation, visual attention and visual search, plus a smaller project on brightness and color filling in as well as tilt-after-effects with real and subjective contours. We briefly summarize progress in each area in turn.

Visual surface representation:

The main bulk of this work on surface representation has been done in collaboration with Shinsuke Shimojo, originally a post-doctoral fellow in my laboratory in San Francisco and now Associate Professor of Psychology, University of Tokyo. Our joint work deals with three related areas, all concerned with the multiple representation of surfaces. Our findings were published as 7 refereed papers and two book chapters, one honoring Torsten Wiesel in a Festschrift volume, plus a summary chapter appearing in the recent Cold Spring Harbor Symposium on Quantitative Biology, volume 55: the Brain.

First, we covered topics in the completion of "invisible" surfaces behind occluders (Nakayama, Shimojo, and Silverman, 1989; Shimojo, Silverman and Nakayama, 1989; Shimojo and Nakayama, 1990, Nakayama and Shimojo, 1991). In these papers, using both with static and moving images, we addressed the issue of boundedness of surfaces and the termination of lines. We asserted that a bounded surface in an image could be either surrounded by an intrinsic border (reflecting the outline of the surface itself) or it could be bounded as a result of occlusion. Likewise for lines. A line can terminate because it really does come to an end in the real world, or it could terminate because of occlusion. In a similar vein, such a line can have either an intrinsic or extrinsic terminator. To deal with such a possibility, we hypothesized that the visual system treats borders separating one image region and another in a one-sided way (Nakayama and Shimojo, 1991). What we mean is that ordinarily the border will "belong" to either one region or the other, not both. Furthermore, in our experiments, we show that depth plays a decisive role in determining which region "owns" the border. Ordinarily, it belongs to the closer surface. The assignment of border ownership is decisive in a number of visual tasks, in perceptual grouping and pattern recognition (Nakayama, Shimojo, and Silverman, 1989), in solving the aperture problem for motion (Shimojo, Silverman, and Nakayama, 1989) and for determining motion correspondence in apparent movement displays (Shimojo and Nakayama, 1990).

We show that if an image region does not "own" its bounding contour, it is effectively unbounded there and can thus link up with other unbounded image regions to aid in the perception of surfaces which are literally hidden behind other surfaces. This completion of surfaces behind closer surfaces (called amodal completion by Michotte and Kanisza) powerfully effects a variety of seemingly primitive visual functions. As such, we suggest that it is

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implemented relatively early in visual processing. In fact, we suggest that it is not inconceivable that it could be mediated by combinations of signals arising from cell types in the striate cortex with known receptive field properties. Thus, to encode line continuation or termination of lines in the real world, we hypothesize that hypercomplex cells (end stopped cells) could be gated by disparity sensitive cells coding depth in the region of image line termination (see Shimojo and Nakayama, 1988).

Second, we have explored the problem of occlusion in relation to binocular vision. Capitalizing on the fact that there is a very specific pattern of unpaired monocular points in the binocular image, we have outlined and systematized a number of important phenomenon which we label under the rubric of DaVinci stereopsis. We summarize these results in a number of publications (Shimojo, Silverman, and Nakayama, 1988; Shimojo and Nakayama, 1989; Nakayama and Shimojo, 1990; Nakayama and Shimojo, 1991). In this work, we show that instead of seeing binocular rivalry when viewing these unmatched points, our visual system is remarkably adaptive, providing us with reliable depth from such points. Even more surprising is the fact that the presence of such unpaired points can give rise to the formation of subjective occluding contours and subjective occluding surfaces (Shimojo and Nakayama, 1991). In all our experimental work, we find that perception is critically dependent on which eye receives the unpaired points. For example, lack of rivalry and appropriate perceived depth of these points requires that only "ecologically valid" configurations of disparity and unpaired points will be used. In addition, the location of subjective occluding contours is critically dependent on which eye is stimulated; it appears to the immediate left of right-eye-only points and to the immediate right of left-eye-only points. Because eye-of-origin information is only explicit in V1 and disappears in higher extra-striate cortical areas (Hubel and Wiesel, 1968; van Essen, 1985), it suggests that the processing of this form of occlusion is mediated either in the striate cortex or in areas receiving direct projections from striate cortex. The results also reinforce the view that subjective contours are the result of an early cortical process, occurring at least by V2 (see von der Heydt et al, 1983). We also argue that DaVinci stereopsis is likely to be learned, built up over many exposures of unpaired points and occluding contours.

Third, we have explored and are continuing to explore the curious emergence of perceived transparency in a number of simple untextured stereograms. In Nakayama, Shimojo, and Ramachandran (1991) we outlined the conditions under which perceived transparency is triggered as well as showing that when it is triggered, seemingly more primitive features can be drastically altered. Thus when perceived transparency is triggered, we see color spreading into otherwise uncolored areas, subjective contours appearing in some sections of the image and removed in others, depth of regions is radically altered, and object shapes are dramatically changed because of the

reversal of figure and ground. We hypothesize that there are 3 critical variables important in the perception of transparency. These are depth, luminance and the presence of collinearity.

Visual attention and visual search

Work in this area has been done in two separate collaborative efforts, one with Manfred Mackeben, the other with Mary Bravo. Each is described in turn.

Cued attention experiments

In our experiments on spatially directed visual attention done in collaboration with M. Mackeben at Smith Kettlewell Eye Research Institute, we elucidated a transient and a sustained component of visual attention using a discrimination paradigm. We found a large difference in visual performance as a function of cue lead time for visual discrimination tasks where the target could not act as its own cue (see Nakayama and Mackeben, 1989). Our conclusion was that there were two distinct components of focal visual attention, a sustained component more likely to be under voluntary control and a transient component, more likely to be shaped by earlier visual properties. A series of control experiments revealed, however, that the transient component could not be attributed to any known property of the visual system, such as transient cells, or the like.

More recently, we completed an additional study on "express attentional" shifts. Our goal was to test Burkart Fischer's hypothesis that express saccades are caused by a rapid deployment of attention to the target site (Fischer, 1987). Using the "gap" paradigm which favors the appearance of express saccades, we predicted and found that the attentional shift to a peripheral target was much more rapid for gap times comparable to those which elicit express saccades. Control experiments ruled out competing explanations and supported the view that the "gap" paradigm (as used by Fischer and others), facilitates an attentional shift to the periphery because it enables an attentional disengagement from the fovea. As such, our study provided important missing data to link attention to saccadic eye movements. This paper (Mackeben and Nakayama, 1992) has just been accepted for Vision Research.

Visual search experiments

In visual search experiments, conducted largely in collaboration with Dr. Mary Bravo, our starting point was to think about the allocation of focal attention in visual search displays. Seriously considering various theories of attentional guidance (Koch and Ullman, 1985; Treisman, 1985; Julesz, 1985), we made a somewhat counterintuitive set of predictions. Under some circumstances, we predicted that reaction times should **decrease** with increasing numbers of distractors in a visual search task, rather than increase as has generally been the case. Our approach was to use tasks where attentional focussing to the target was required, asking the observer to make a

speeded forced-choice discrimination of a non-cue feature of the target. Because this feature was also present in the distractors, it required that the observer focus attention on the target. For most of the experiments, we used colored cues and had the observer make a discrimination as to the shape of the odd colored target. Two primary paradigms were used. In one case, the colors of the distractor could reverse from trial to trial (the mixed case). In the other case, target and distractor color remained constant throughout a block of trials. As predicted from a consideration of "top down" vs "bottom up" theories, only in the mixed case did reaction times decrease with increasing numbers of distractors. In addition, when using the more usual present-vs-absent task employed by others, the reaction time vs distractor number function was also flat, as expected. We draw a number of rather somewhat unusual conclusions from this data. Most important, and contrary to the conclusions drawn by others, we hypothesize that ordinary visual search tasks do not reveal properties of preattentive vision exclusively, but are more likely to reflect post attentive processing. (this paper will shortly appear in Perception and Psychophysics).

In addition to this empirical work just described, we also mention our speculative theory entitled the "Iconic bottleneck" (Nakayama, 1991), written in 1986. This was outlined in the previous proposal and is yet to appear in print, delayed as a book chapter edited by Colin Blakemore.

Color filling in

In collaboration with Dr. Michael Paradiso, a post-doctoral fellow in my lab in San Francisco, we have completed both empirical and theoretical studies of color filling-in. Our first goal was to see whether filling-in, hypothesized to occur in stabilized vision and in patients with retinal lesions, might also be seen in normal everyday vision. Our stimulus was a homogeneous disk, presented briefly. When viewed in isolation, it appeared as just that, a homogeneous disk. However, when it was followed by various patterns, either in the same or the other eye, a dramatical reduction in brightness in the center of the disk could be seen. Our original working hypothesis was that a hypothetical color-filling process had been interrupted. By varying the distance of a circular pattern following the disk and its onset relative to the disk, we were able to characterize the process as one of spatial propagation with a relatively high velocity. Early modeling of the phenomenon outlined a process of a filling in, more akin to fluid originating at contour boundaries and rushing in to the unfilled regions. This model was presented as Paradiso and Nakayama (1989). An additional set of psychophysical experiments, however, suggested that such a model may be inadequate. In these later experiments, we constructed a circular mask with very large gaps in the circle's perimeter, ones that should be essentially transparent to brightness filling. Surprisingly, such masks also had a great effect in preventing color filling, something that would not be easily expected if we took the filling idea as being analogous to fluid flow. As a result of these last experiments, we have now constructed a very different type model,

inspired more by concepts of "smoothness" rather than fluid flow. Such a filling process might be understood more as a fabric whose edges are quickly raised by the presentation of a disk and the middle of which is raised quickly and ballistically, in response to the elevation of the perimeter. The action of the pattern mask, therefore, is to tack down the fabric, preventing it from rising. The psychophysical findings are presented Paradiso and Nakayama (1991). In addition, the revised model was presented at the 1990 ARVO meeting and a manuscript of this theoretical work is in preparation.

Interaction of real and subjective contours

Also in collaboration with Dr. Paradiso and Shimojo, we found that there was an asymmetric interaction between real and subjective contours when studying the tilt after effect. We found that adapting to subjective contours could only alter perceived orientation of subjective contours; whereas, the adaptation to real contours could alter the perceived orientation of both real and subjective contours. Furthermore, we found that the interocular transfer of this after-effect was much higher for subjective contours than for real contours. Both findings taken together indicate that subjective contours are encoded later than real contours in cortical areas where the proportion of binocular cells is higher. Yet, their critical and similar dependence on orientation differences suggests that illusory contours are subject to the same interactions as cortical neurons coding real edges. As such, it suggests that the locus of subjective contour representation must be sufficiently low to be governed by the same rules as orientation tuned cells. This contrasts sharply to earlier views suggesting that illusory contours are higher order cognitive processes because ordinarily we wouldn't expect such higher order processes to show orientation tuning. This paper has been published as Paradiso, Shimojo, and Nakayama (1989).

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Papers in press or under review

14. Mackeben, M. and Nakayama, K. Express attentional saccades (*Vision Research*, In Press)
15. Bravo, M. and Nakayama, K. The role of attention in differeng forms of search tasks (*Perception and Psychophysics*, in press).
16. Nakayama, K. and Shimojo, S. Visual Surface Perception. Invited manuscript for Science. (under review)
17. Shimojo, S. and Nakayama, K. Interocularly Unpaired Zones Escape Local Binocular Matching, *Nature* (under review).