tion that myofilaments are located near the luminal membrane only.

Additional evidence that the luminal and extraluminal membranes have different properties was derived by comparing the response of the myocardium to alterations in the intraluminal and extraluminal ionic media. Application of isotonic solutions containing high concentrations of KCl (60 to 200 m*M*) to the luminal surface elicited maintained tension (contracture) and rendered the heart unresponsive to current passed in either direction. Exposure of the extraluminal membrane to 100 to 200 m*M* KCl, on the other hand, failed to produce contractures and did not alter the contractile response to current passed in either direction (Fig. 3). Direct measurement of intracellular potential with glass microelectrodes filled with 3*M* KCl showed that the resting potential of the myocardial cells (− 65 ± 5 mv) was unaffected by changes in the concentration of extraluminal KCl, whereas the cells promptly depolarized in response to increased luminal KCl. As described above, variation of intraluminal Ca^{2+} and Mg^{2+} altered the contractile response, whereas changes in concentration of these ions extraluminally had no effect on contraction. These observations provide additional evidence that only the luminal membrane actively participates in the excitation-contraction coupling process; the extraluminal membrane appears to be electrically passive and is effectively clamped by the luminal membrane.

Consistent with these findings, direct measurements of intracellular potential in another species (*Chelyosoma productum*) showed that only the luminal membrane is capable of generating an action potential (*4*). In contrast to our findings, Kriebel (*4*) reported that the extraluminal membrane of the myocardial cells depolarized completely when exposed to isotonic 480 m*M* KCl, producing a potential difference of 8 to 15 mv (lumen positive), without eliciting a contracture or any apparent alterations in excitability. If the extraluminal membrane is completely depolarized, any transcellular potential difference recorded must reflect the potential difference across the luminal membrane exclusively. Since the electrically measured threshold for excitation (and resulting contraction) of these myocardial cells is about − 50 mv (*4*), it is inconsistent that depolarization of the luminal membrane above the mechanical threshold should not elicit contraction. If, on the other hand, the extracellular membrane is actually insensitive to KCl, as in the sea potato, it is not clear why a transcellular potential was recordable.

In the sea potato, no transcellular potential difference could be measured, even when the luminal or extraluminal surfaces were exposed to 100 m*M* KCl. This finding suggests that the 40- to 50-mv depolarization observed directly with microelectrodes upon exposure of only the intraluminal surface to KCl was being short-circuited through a low-resistance pathway. To test this hypothesis, we measured the transcellular resistance by passing short current pulses (5 msec) between two Ag/AgCl electrodes and recording the voltage difference across another set of Ag/AgCl electrodes. Both ends of the preparation were immersed in oil to insulate the areas of the preparation damaged by the ligatures from the rest of the myocardium. These experiments confirmed a low transcellular resistivity of 200 ohm cm^2. Morphologically, the low-resistance "shunt" pathway may correspond either to extracellular channels between myocardial cells or to the raphe of the heart, where the heart cells are joined together with connective tissue. The presence on electron micrographs of specialized junctions which appear to isolate the luminal from the extraluminal surface may favor the latter possibility. Kriebel (*5*) obtained a similar value for transcellular resistivity in other species of tunicates in which he cut the heart along the raphe to form a sheet and concluded that the tight junctions have an electrically high transverse resistance.

The experiments outlined above show that the heart of the sea potato consists of a single layer of myocardial cells sharing many of the electromechanical properties of vertebrate myocardial tissue. In addition, these experiments strongly suggest that only the luminal membrane of the heart plays an active role in excitation-contraction coupling processes. It appears that the extraluminal membrane has no role in the activation of the contractile apparatus, and its potential is effectively clamped by the luminal membrane. The existence of myofilaments only on the luminal side provides the structural basis for the electromechanical measurements. These properties of this single-layered heart with one active membrane makes it an ideal preparation for a variety of electrophysiological and radioisotope studies.

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4 June 1974

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Visual Detection of Line Segments: An Object-Superiority Effect

Abstract. *Observers identified a briefly flashed line segment more accurately when it was part of a drawing that looked unitary and three-dimensional than when the line was in one of several less coherent flat designs.*

Many cells in the mammalian visual cortex respond best to straight line segments with a particular orientation in a particular location on the retina (*1*). A number of theoretical models for pattern recognition employ similar oriented-line detectors as an early stage in a hierarchical feature-identification process (*2*).

Our visual detection task used stimuli appropriate for such line detectors: four line segments differing in orientation and location relative to a fixation point, as shown in Fig. 1, a–d. On each trial, one of these target lines, together with one of several context patterns such as Fig. 1e, was flashed briefly on a computer-controlled cathode-ray tube screen, producing the compound patterns shown in Fig. 2.

The viewer's task was always to identify which one of the four diagonal line segments was present in the briefly flashed display. None of the context pat-

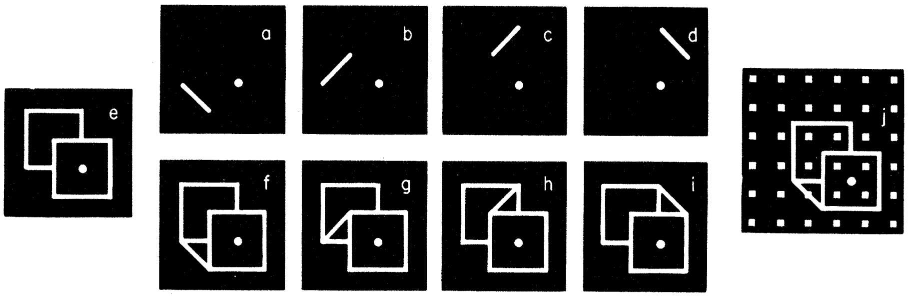

Fig. 1. Briefly flashed stimuli used in two experiments. The subject's task on each trial was always to indicate which one of the four line segments *a–d* (differing in orientation and location relative to the continuously visible fixation point) was present. The target line was always accompanied by context lines, such as the squares in *e*, producing compound patterns such as *f–i*. Each stimulus flash was followed immediately by a 100-msec dotted masking stimulus, shown in *j* superimposed on a stimulus pattern.

terns provided any clue about which of the four target lines was present; in principle, a viewer could ignore the context and attend only to the target lines, without sacrificing accuracy (*3*).

We found that the visual context nevertheless had a marked effect: viewers identified the diagonal target line better when it was combined with the two overlapping squares shown in Fig. 1e than with any other comparable context pattern that we have tried. Unlike the other patterns in Fig. 2, the overlapping squares combine with each target line to portray a distinctive and convincing, though not particularly familiar, three-dimensional object (Fig. 1, f–i).

The influence of context on a simple visual detection task seems inconsistent, at first sight, with a class of pattern recognition models in which elementary features are detected first and then overall structure is ascertained from the identified features (*4*). (Our stimuli were designed to bear most directly on detection of single oriented line segments. However, comparisons among the patterns in Fig. 2 suggest that a similar conclusion holds for more complex, multiple-line features such as angles or T-intersections.)

What kinds of model would be consistent with an effect of overall structure on detection of components? Among the many possibilities, three broad classes are particularly interesting. First, figure recognition might be a global, holistic process that deals simultaneously with an entire pattern, and does so more effectively for certain sorts of figure; local, component features could then be deduced from the overall configuration. A second possibility is that there are both simple-feature detectors and detectors for certain sorts of more complex patterns; elements could be detected by the feature detectors in any context, but accuracy would be better when more complex detectors are also activated. A third alternative would involve recurrent loops instead of a serial hierarchy; meaning or structure could enhance the sensitivity of pertinent feature detectors. Although our findings do not distinguish among such alternatives, they may make possible further experiments that will.

Details of our experimental procedure were as follows. The stimuli were composed of luminous dots briefly displayed on a cathode-ray tube (P4 phosphor), which the subject viewed binocularly in a dark room. To initiate a trial, the subject depressed a foot switch. One of the four target lines (Fig. 1, a–d), accompanied by one of the context patterns (as in Fig. 2, a–f), was then displayed randomly for one of three durations. The three display durations were selected for each subject on the basis of pretests and previous performance, to yield accuracies of roughly 50, 60, and 70 percent correct for Fig. 2a (chance accuracy would be 25 percent). The durations used ranged from 5 to 44 msec. The target display was followed immediately by a 100-msec masking stimulus composed of large square dots (Fig. 1j), to curtail persistence of a visual image. The subject pressed one of four response keys to identify which target line had been seen. Throughout the session, a luminous fixation point was visible, except when briefly replaced by a plus or minus sign that indicated whether the subject's response was right or wrong.

All of the context patterns contained the same eight vertical and horizontal line segments, with only their arrangement varied. The length of each of the long lines was approximately 0.7 degree of visual angle. The contexts were designed to equate, or permit evaluation of, a number of potential influences on accuracy, such as the presence of angles and T-intersections, information about location of target-line end points, local masking by adjacent lines, masking by more distant lines with similar orientations, confusability and redundancy of the context, number of lines, and amount of irrelevant light on the screen.

All possible combinations of target line, context, and duration appeared equally often and randomly intermixed, five times each per daily session. In one experiment, six subjects each completed six sessions, using the four contexts shown in Fig. 2, a–c and e. In a second experiment, nine subjects (five of whom had served in the previous study) each completed seven sessions with the three contexts shown in Fig. 2, a, d, and f.

The main finding was that when a target line was part of a configuration that looks unitary and three-dimensional (Fig. 2a) it was identified more accurately than when in any other context. The last column in Fig. 2 gives the mean differences between percentage correct with the context of Fig. 2a and with each of the other contexts. All differences are within-subject differences, averaged across the subject's three target exposure durations. (In the first experiment, with six subjects, the mean accuracy with context 2a was 62.8 percent; in the second experiment, 68.7 percent. This difference is not meaningful, since different stimulus durations were used for each subject.)

Two analyses of variance showed a significant main effect of context for both the first ($P < .05$) and second experiments ($P < .01$). The findings of significance held both for raw data (percentage correct) and for an arc sine transformation. All analyses used the usual error terms for repeated measures (subject interactions). The only other significant effects were stimulus duration ($P < .01$ in both experiments) and a duration by context interaction ($P < .05$) in the first experiment (the range of accuracies was larger with the longest stimulus duration than with the shorter ones).

Accuracy with the three-dimensional figures (Fig. 2a) was significantly different from accuracy with contexts 2d, 2e, and 2f according to Dunnett's mul-

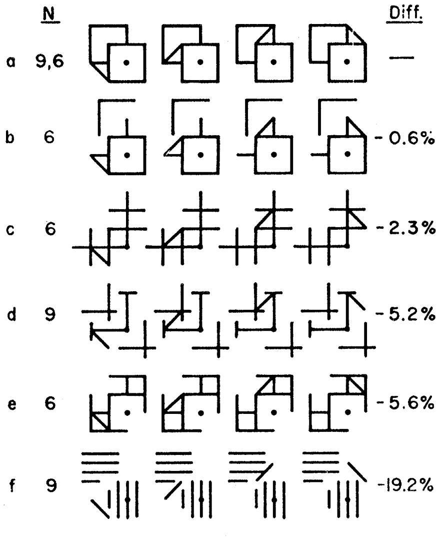

Fig. 2. Relative accuracy in identifying line segments when presented in various contexts. All contexts, *a–f*, contain the same set of lines and give no information about which of the four diagonal target lines (Fig. 1, *a–d*) is included. ***Diff.*** is the mean deficit in accuracy with each context as compared to context *a*. *N* is the number of subjects tested with each context, 360 or 420 trials per subject with each context.

tiple comparison test, $P < .01$, two-sided (*5*). All subjects were more accurate with 2a than with 2d, 2e, or 2f. The mean accuracy across subjects was greater with 2a than with 2d, 2e, or 2f at each of the three stimulus durations. Although in these experiments subjects were not significantly more accurate with context 2a than with 2b or 2c, larger differences between 2a and both 2b and 2c can be found with a suitably modified display procedure.

Figure 3 shows data from one practiced subject when the masking dots were displayed 40 msec after the end of the 40-msec stimulus (instead of immediately after). The display intensity, stimulus duration, and delay of masking dots were all selected for this subject on the basis of exploratory sessions with varied intensities, durations, and delays. The procedure was otherwise similar to that in the first two experiments, except that a more haphazard pattern was substituted for 2f and all six contexts were intermixed within each session. After the initial session, the data are remarkably consistent and show that accuracy for pattern 3a exceeded that for patterns 3b–3f by an average of 9.7, 14.7, 9.7, 16.7, and 19.7 percent, respectively. All of these differences were statistically reliable by Dunnett's test, $P < .01$.

The finding that lines were easier to identify in a unitary three-dimensional picture than in less well-structured patterns is reminiscent of the "word-superiority effect": a briefly flashed letter is easier to identify in a pronounceable word than in an unpronounceable string of letters (*6*). In both cases, a constituent element (letter or line segment) is perceived better when the context creates a well-formed unit, even if the context provides no clues about the correct choice on a given trial, and even though the identity of the whole configuration depends on the identity of its components (letters or line segments). One might propose that a special, efficient linguistic mechanism comes into play when pronounceable words are viewed (*6*); similarly, the visual system may have special, efficient mechanisms for forming representations of coherent scenes (*7*). Perhaps recognition of both words and objects depends on more general processes that make use of structural rules and meaning to determine perception. In any case, we have demonstrated a visual effect that seems analogous to the word-superiority effect but is not restricted to specific linguistic mechanisms or to elements as arbitrary as letters.

There is a difference between the effects of context on letters and on line segments. A letter is often detected better when it is part of a well-structured letter-string than when it occurs alone [the "word-letter effect" (*8*)]. We have found, however, that diagonal target lines were detected better when presented alone than when accompanied by other lines. In fact, using a variety of context patterns, we found that accuracy decreased as total line-length in the context increased. The decline in accuracy with increasing amounts of irrelevant stimulation is in line with the usual findings in experiments on simultaneous masking, reduced signal-to-noise ratio, and the like. For this reason, two of the contexts used in the first experiment are omitted from Fig. 2, since they had fewer lines than the other contexts.

We cannot yet specify the sources of the different effects of different contexts, but further experiments should prove informative. Gregory Ozog, working with us at Bell Laboratories, used a different detection task and a different set of six contexts and also found that accuracy with his three-dimensional drawing was significantly better than with any other context. Comparisons among Ozog's patterns support the impression given by our patterns, that accuracy is improved both by closure of the context and by three-dimensional appearance.

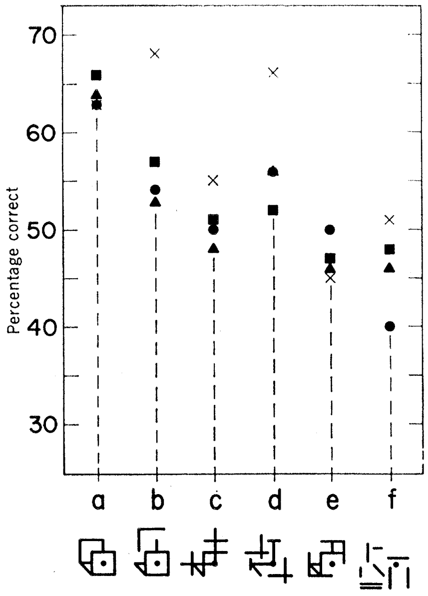

Fig. 3. Accuracy in identifying line segments when the masking dots were delayed. Data are from a practiced observer, who had 180 trials per context in each of four sessions (×, day 1; ●, day 2; ▲, day 3; ■, day 4). Accuracy by chance would be 25 percent.

In the light of such remarkable perceptual abilities as the capacity to read rapidly (*9*) or to make sense of our visual surroundings "at a glance" (*7*), it is not surprising that appropriate context aids perception. But how context plays its role is still unclear. Our demonstration, which uses line segments rather than more complex stimuli like letters or objects in a realistic scene, should provide a useful tool for characterizing the processes through which context influences perception.

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3. But see J. C. Johnston and J. L. McClelland, *Science* **184**, 1192 (1974).
4. It is sometimes difficult to determine from published descriptions whether a given model actually falls into this class. However, writing in 1972 about computer programs for analysis of visual scenes, M. B. Clowes said: "All the scene analysis programs described to date . . . have accomplished an analysis by first reducing the TV image to a line diagram where each line is presumed to correspond to an edge. . . . The production of this line diagram is independent of its subsequent analysis and *vice versa*." [M. B. Clowes, in *Machine Perception of Patterns and Pictures*

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9. U. Neisser, *Cognitive Psychology* (Appleton-Century-Crofts, New York, 1968), pp. 105–137.

10. We thank P. H. Winston for his important role in inspiring our experiments, and M. G. Ruddy for computer programming and data collection. We also thank K. Ainslie, V. Blaisdell, A. S. Coriell, B. Gates, G. Ozog, and R. Szoc for assistance with these experiments or related pilot studies, and M. Allyn and D. E. Meyer for extensive comments on the manuscript. This work was carried out while N.W. was on sabbatical leave from Loyola University of Chicago. It was supported in part by PHS grant R01EY00143 to N.W.

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21 June 1974 ■

Development of Mollusk Shells

We wish to contribute perspective to Clark's (*1*) report on the growth and shape development of bivalve shells. Our examination of representative species among the various pelecypod (bivalve) families indicates that, as a general case, the periostracum forms a topologically continuous sheath completely enclosing each growing shell. On the outer surface it becomes a tough cuticle (*2*). The Pectenidae (scallops) and Cardiidae (cockles) seem atypical in the apparent absence of this continuous periostracum.

It is not clear from the text or the electron micrographs in (*1*) whether the periostracum in *Pecten diegensis* forms a similar enclosing sheath, but it does appear that the periostracum is present, although extremely thin, and continuous over at least the margin of the advancing shell. Shell growth is probably not by extension of the advancing shell margin into the aqueous medium, but is more like the picture of a man in a sheet who extends his arms. All the sequential biochemical events are thus contained within this protective membrane, which is continuous and maintains a controlled environment. It would be valuable to follow the periostracum with the scanning electron microscope over the entire outer surface to the hinge to establish its continuity. If continuity were established, the shell development of *Pecten diegensis* would be consistent with that of many animals in other pelecypod families.

The layering observed by Clark in the deposition of new shell material suggests a biological rhythm, possibly the same rhythm which is responsible for the concentric lines normal to the direction of growth which are common to all of the pelecypods. If the periostracum were continuous over the tops of the growth ridges described by Clark, the interspaces might be due to loss of matrix during handling and treatment of the sections or perhaps partial delamination of the layers. The shells of the scallops and cockles are convoluted, and this may be related to the invisible (or missing) periostracum on the outer shell surface.

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References and Notes

1. G. R. Clark, *Science* **183**, 968 (1974).
2. In freshwater mussels of northern California this cuticle has a protective function, so that injury to this covering allows leaching and perforation of the shell matrix. Shell integrity seems essential, as all healthy individuals had intact shells, while all individuals found with perforations were dead and in many instances filled with mud.

26 March 1974

I appreciate the interest of Gainey and Morris in my recent report (*1*), and welcome the opportunity to broaden the perspective of the discussion.

Gainey and Morris devote most of their comment to a discussion of the function and limited distribution of the periostracum in bivalves. They correctly note two functions of the periostracum, the first being as a protective covering for the entire shell and the second being as a mechanism for isolating the calcification of the shell margin from the sea. They also note that in some groups of bivalves the periostracum is not obvious as a covering on the entire shell and suggest that scanning electron microscopy should be used to see whether it is, in fact, present in areas other than the shell margin. Here they seem to be arguing that the protective function is the original function of the periostracum, whereas current theory and the very evidence they cite suggest strongly that the periostracum evolved to satisfy the needs of calcification and the protective function evolved later in certain groups. These concepts are scattered throughout the literature of the past 25 years (*2*), and will be discussed at some length in a paper now in press (*3*).

Gainey and Morris also present some speculations on layering and delamination, but further discussion might best await at least one supportive fact.

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1. G. R. Clark II, *Science* **183**, 968 (1974).
2. For a beginning, see references in (*1*).
3. G. R. Clark II, *Am. Zool.*, in press.

9 September 1974 ■

Niobium for Superconducting Alternating-Current Power Transmission

Suenaga and Garber (*1*) have reported low a-c losses for samples of Nb$_3$Sn conductor tested at 4.2 K and 60 hertz. Their results are significant because they demonstrate that the a-c losses of this material are not high enough to preclude its consideration for use as a commercial superconducting cable. However, their concluding sentence, "Such cables would have marked advantages with respect to higher operating temperature and fault current capability than cables employing a niobium conductor, and with the same or lower a-c loss," is not fully supported by the data in their report, nor is it supported by experimental work carried out and reported elsewhere (*2–7*).

Suenaga and Garber compare the a-c losses at 4.2 K of "composite" and "tin dipped" Nb$_3$Sn with the niobium a-c losses at 4.2 K reported by the Linde Division of Union Carbide Cor-