

invariants that can be computed in parallel represent a straightforward answer to the gestaltists: The things that naturally organize are just those that have explicit small-parameter descriptions.

Given these advantages, let us consider some alternatives. One alternative is a Von Neumann-like design, but we can reject this as being too slow when built in neural circuitry. Parallel Von Neumann computers are also not feasible, owing to the difficulty in satisfying property 2. One of the big current problems with networks of Von Neumann machines is the time taken in interpreting different message protocols.

A second alternative is variable encoding. Analog computers are designed on this principle, and there is no reason why differential equations could not be directly encoded in neural circuitry. Current models of the eye-movement-control circuitry are based on analog servomechanisms and have made several important predictions (Robinson 1978). The advantage of the analog encoding is that it is more compact than the value unit encoding (but probably only by about a factor of 10^2 , since the firing rate is extremely band-limited). Variable units have two important disadvantages: (a) only one value of a variable can be accessed at a time, and (b) the circuitry tends to be more delicate (adding or removing pieces affects performance unpredictably). Nonetheless, just as the thalamus uses some value encoding, the cortex could use some variable encoding. However, most single-cell electrophysiological recording data would rule out variable units.

One controversial aspect of the value unit hypothesis is the encoding of values in a few units. This has become known as the "localist" hypothesis, as opposed to the "distributed" hypothesis, which suggests that encodings involve many hundreds or more units. The N^k argument sharpens this debate. Naturally, many hundreds of units will be involved in a percept; the crucial question is: how are small groups of parameters handled? Keeping the number of units that represent a parameter vector small will facilitate parallel computations, since nearby values do not interfere, and may simplify the connection problem, since another network that requires the value need only connect to a few units. Besides these advantages, single-cell recording data seems to be in favor of a localist encoding. This is certainly true for the highly retinotopic areas such as V1 and V2. We argue that once the correct parameters are identified it will extend to other extrastriate areas as well.

What are the advantages of locality? In connectionist terms, to implement the useful relationships among sensory and motor parameters, it is enormously useful that value units *similar in value* be *physically proximal*. However, as the value units become increasingly abstract, the notion of value locality becomes vaguer and the physical locality becomes less imperative. Extremely abstract units may form a diffuse network that is scattered throughout the cortex and follows no regular pattern. In this case, the primary-secondary indexing concept may not be useful, but we believe the concepts of value units and topological locality could still prove useful. Skimpy evidence comes from patients with lesions of the corpus callosum who exhibit very discrete functional losses (e.g., Dimond, Scammell, Brouwers & Weeks 1977).

To conclude on a less technical note, for a long time

strictly computational models have not had a significant interaction with basic studies in the neurosciences. However, new discoveries in both these areas are leading to a renaissance of attempts to bridge these disciplines. We hope that this paper will spark additional interest in interdisciplinary studies.

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NOTE

1. Traditionally, the receptive field of a neuron has been defined with respect to a stimulus. This has the unfortunate effect of making it dependent on a particular experiment. In our model we define the receptive field as the response to *all* the neurons' inputs, some of which may be feedback connections from neurons in more abstract cortical areas.

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Value, variable, and coarse coding by posterior parietal neurons

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Ballard's connectionist approach is very satisfying to a neurophysiologist, since it presents models constrained by what we know about the brain as well as by the physical world from which the brain must extract information. I would like to comment first on the variable and value-encoding schemes that appear to be mixed at a single-neuron level in some cortical areas, particularly those involved in sensorimotor integration. Second, I will discuss the possible use by the inferior parietal lobule of a coarse-coding approach to specify the locations of visual stimuli in space.

Neurons in the caudal aspect of the inferior parietal lobule in the medial superior temporal area (MST), lateral intraparietal area (LIP), and area 7a respond to visual stimuli and have large

retinal receptive fields (Robinson, Goldberg & Stanton 1978; Siegel, Andersen, Essick & Asanuma; Van Essen, Maunsell & Bixby 1981; Yin & Mountcastle 1977). Thus, these cells meet the spatial-coding criteria for value coding outlined in the target article. However, these cells also have activity related to oculomotor behavior and encode eye position, eye velocity during smooth pursuit, and head velocity from vestibular stimulation (Andersen, Essick & Siegel 1985a; Kawano, Mitsuyoshi & Yamashita 1984; Lynch, Mountcastle, Talbot & Yin 1977; Mountcastle, Lynch, Georgopoulos & Sakata 1975; Sakata, Shibutani & Kawano 1983; Wurtz & Newsome 1985). These parameters are generally encoded in monotonic frequency-of-firing response profiles and thus qualify as examples of variable encoding. Since many of these oculomotor-related responses could be a result of artifactual visual stimulation during eye movements, we and others have designed extensive controls to separate visual from eye-movement responses (Andersen et al. 1985a; Sakata et al. 1983; Wurtz & Newsome 1985). The general result is that many of these cells receive both visual and oculomotor signals.

Why should two encoding schemes be present in the activity of single neurons? One possibility is that such combinations are required for sensorimotor integration. One example of such a process may be found in those cells of the inferior parietal cortex which receive both eye-position and retinal visual signals.

Recent work on the oculomotor system has shown that at least some types of saccadic eye movements are programmed to positions in head-centered space rather than to locations in retinal coordinates, providing evidence for nonretinal representations of visual space in the brain (Becker & Jurgens 1979; Hallet & Lightstone 1976; Mays & Sparks 1980). Some current models maintain that in order to generate eye movements to a target the oculomotor system subtracts location of the eyes from the head-centered representation of the target location to create a motor error signal; the distance and direction the eyes must move to foveate the target (Becker & Jurgens 1979; Fuchs, Kaneko & Scudder 1985; Robinson 1975). The superior colliculus and frontal eye fields together are essential for the generation of saccades (Schiller, True & Conway 1980). Both of these structures contain motor error signals, suggesting that spatial representations of target positions must lie closer to sensory pathways than these areas (Bruce & Goldberg 1985; Mays & Sparks 1980). The inferior parietal lobule (IPL) projects strongly to both the superior colliculus and the frontal eye fields (Andersen, Siegel, Essick & Asanuma 1985; Barbus & Mesulam 1981; Lynch & Graybiel 1983). The visually evoked activity of many IPL cells is the product of the retinal receptive field of the cell and a gain factor that is a function of eye position (Andersen et al. 1985c). This operation creates an eye-position-dependent tuning for locations of visual stimuli in head-centered space.

Although these cells show a tuning for spatial locations that is eye-position-dependent, the system as a whole acts in an eye-position-independent fashion. Using a coarse-tuning approach somewhat similar to the overlapping receptive field strategy described in the target article, it can be shown that spatial-location information independent of eye position is contained in the population response of IPL neurons (Andersen, Siegel & Crick, unpublished).

In Figure 1 three cells are represented which each have different best angles of gaze (the eye position represented by the black dot at which the gain of the visual response is maximum) and different retinal receptive fields (represented by the hollow circles). The line connecting the best gaze location and the receptive field indicates that the receptive fields are retinotopic; that is, they move with the eyes. These cells are considered a group because the combination of their best gaze position and receptive field position results in their all being tuned to the same approximate location in head-centered space. The output of these cells is simply summed and compared to the outputs of similar groups constructed for other spatial locations. If a stim-

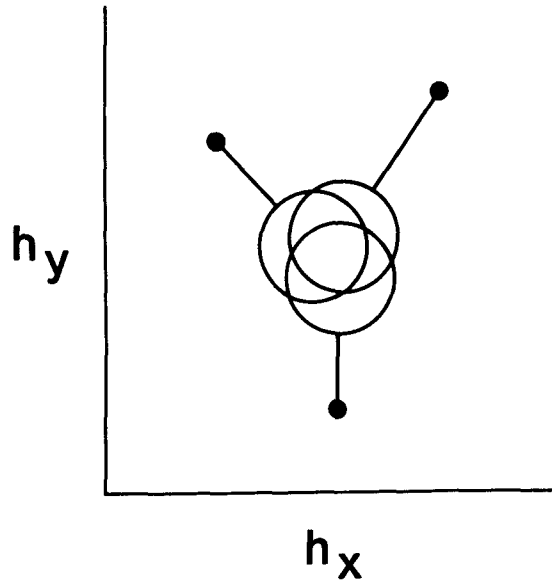


Figure 1. (Andersen). Schematic representation of how populations of light-sensitive neurons whose activity is modified by eye position might encode spatial location independent of eye position. H_x and H_y refer to horizontal and vertical coordinates in a head-centered coordinate system.

ulus falls within the space defined by this group, its summed output is greater than that of any of the other groups. A topographic representation based on spatial tuning would be one way in which the brain could recognize which group of neurons encodes a particular spatial location; we have some preliminary evidence that such an organization may exist in area 7a.

As Ballard points out, this class of models requires very few cells for implementation. The simple model outlined above also predicts that it is necessary to have some eye position gains that do not increase monotonically with eye deviation but rather have peaks at intermediate eye positions. These types of gain fields (which in fact look more like value codes than variable codes) are found in at least one-fourth of the cells we have examined in area 7a (Andersen, Essick & Siegel 1985b). The coarse-coding approach may explain the seemingly paradoxical situation that the area of the brain most strongly implicated in spatial perception from lesion studies has cells with such large visual receptive fields. As pointed out in the target article, this approach has poor resolution for distinguishing the spatial location of two objects. Since we rarely make movements to more than one object at a time, this may not prove to be a problem if attention suppresses other inputs to the map. IPL cells are significantly modulated by attention, but it remains to be seen whether such additional processes can refine the behavior of this presumably coarse system.

Value encoding of patterns and variable encoding of transformations?

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It was not until the last century that people seriously linked perceptual experience with hypothetical physiological mechanisms. It soon became obvious that certain perceptual experi-