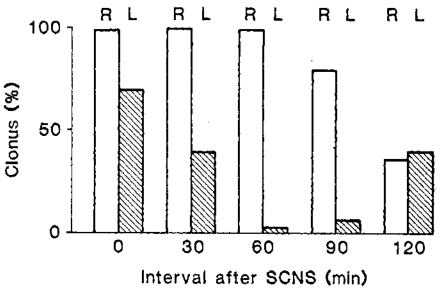

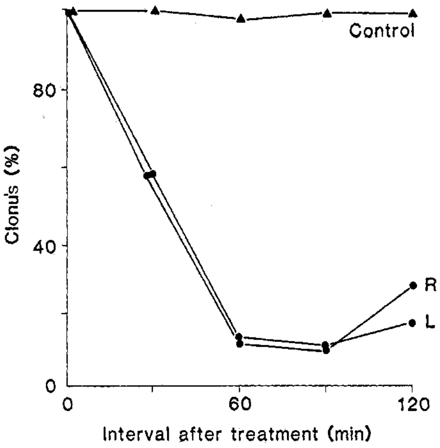

Fig. 3 (left). Laterality of SCNS-induced suppression of clonus. Fig. 4 (right). Stimulation of radial and median nerves suppressed ankle clonus, demonstrating that the mechanism mediating this response is suprasegmental.

nerves) for 1 hour twice daily for 1 week. Ankle clonus was elicited by patellar stretch by a physician who did not know the purpose of the study. The SCNS suppressed clonus for 2 hours on the first trial in all subjects, whereas none of the subjects given control stimulation responded (Fig. 2). With SCNS, slight inhibition was immediately observable, but maximum suppression did not occur until 1 hour after the treatment ended. This delay occurred in all instances and suggests the need for "processing time." Inhibition lasted for 3 hours and was observed in every subject.

The SCNS-induced clonus suppression did not depend on analgesia, as all subjects were pain-free at the time of the experiment. Clonus was inhibited but not abolished by the stimulation, as was demonstrated by the observation that it could be elicited, to a minor degree after multiple attempts, indicating that the threshold for eliciting the reflex was markedly raised. These results imply that SCNS decreases neural excitability and raises the threshold for clonus.

Administering SCNS to the right median, radial, and saphenous nerves produced clonus inhibition on the left side for as long as 90 minutes after treatment ended (Fig. 3), but inhibition occurred bilaterally for 2 hours after treatment. (Stimulation on the left side produced the opposite pattern of response.) Thus, SCNS did not produce its effect by global psychogenic factors such as sedation. The precise neuroanatomical pathways subserving altered excitability are not known, but these results imply that SCNS can be used as a tool to map functionally intact but latent human synaptic connections.

The SCNS suppresses clonus by dampening the oscillations in firing of alpha motoneurons either through segmental or suprasegmental inhibition. At the segmental level, a decrease in the excitability of muscle spindles or an increase in the potency of recurrent inhibition from Renshaw cells may decrease excitability of the basic stretch reflex. At the suprasegmental level, diverse brain regions regulate the threshold of alpha motoneurons by way of gamma efferents (*5*). In order to discern whether the suppression of clonus is the result of centrifugal inhibition, I stimulated the radial and median nerves bilaterally. Stimulation of the nerves in the wrists completely inhibited ankle clonus, indicating that stimulating neurons at the level of the sixth to eighth cervical segments suppresses neurons in the lumbosacral segments.

Spasticity is a global term covering phenomena as diverse as rigidity, clonus, hyperreflexia, overadduction of legs and ankles "scissoring," and the dorsiflexion of the toes. All of these signs are due to the release of spinal cord reflex mechanisms from inhibition by higher brain centers. The relative contribution of different brain areas in modulating postural reflexes is still unknown, but most authors agree that the analogy of spasticity to animal decerebrate rigidity is inadequate. The latter refers to an increase in extensor tone immediately after intercollicular transection; this increase in tone is transient in the case of animals, whereas human spasticity is permanent.

In this report, I document a decrease in clonus subsequent to SCNS. Rigidity also decreases, but I have been unable to find any change in the extent of scissoring, hyperreflexia, or the Babinski sign. Similar dissociation of the behavioral components of spasticity has been reported after administration of Baclofen (*6*). SCNS may provide an analytical tool for dissecting the various behavioral components of spasticity. In conjunction with metabolic mapping techniques such as positron emission, it may provide a clue to the identity of brain regions mediating the individual behavioral components.

Suppression of clonus is reminiscent of "consolidation," defined here as the time-dependent transfer of information across diverse regions of the central nervous system. One example of this phenomenon is the fixation of postural asymmetry (*7*): transection of the spinal cord of 45 minutes after a unilateral cerebellar lesion abolishes asymmetry, whereas later transection does not. To my knowledge, this is the first demonstration that any procedure can abolish a grossly observable spinal reflex in an awake, intact animal.

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8. I thank E. Eldred and J. Beatty for critical review of this manuscript.

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Receptive Fields and the Optimal Stimulus

Albrecht *et al.* (*1*) have suggested that the "spatial frequency channel" hypothesis provides more insight into the functional nature of visual cortical neurons than does the bar-width, or "size" view. They also pointed out that their results—that such cortical cells in both the cat and the monkey are more sharply tuned to gratings than to bars—are consistent with an opponent center-surround receptive field (RF) with subsidiary disinhibitory flanks.

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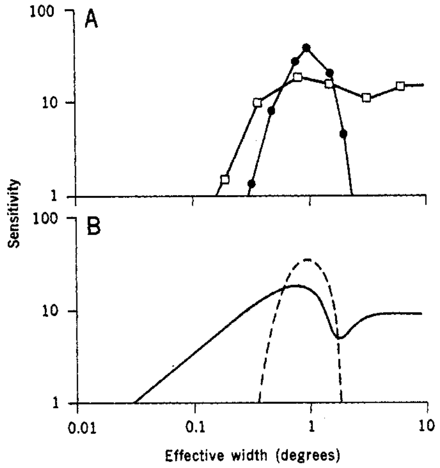

Fig. 1. (A) Sensitivity for bars (squares) and gratings (circles) for a complex cell in the striate cortex of a cat [from (*1*)]. (B) Theoretical functions.

We convolved a simple, one-dimensional RF, such as they suggested, with bars and gratings. The computer-generated curves contain virtually all the salient features of the Albrecht *et al.* data (relative bandwidths and amplitudes, lack of drop-off of bar sensitivity at large effective widths, and so forth) (Fig. 1). The overall concordance between experiment and theory suggests that "frequency channels" and "bar detectors" imply each other, and that a cell's response might also be well characterized in terms of the RF directly.

Albrecht *et al.* stated, "The optimum stimulus for a cell is conventionally considered to be that which evokes the largest response." They, and others, searched for this largest response on the basis of the constraint of constant stimulus contrast, or equivalently (for a linear system), they vary the contrast until a criterion response is elicited. Motivated by the significance of the RF itself, we suggest an alternate constraint, that of constant "energy," E, defined (in analogy to the energy in a physical wave) as:

$$E = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} |s(x,t)|^2 \, dx \, dt$$

where $s(x,t)$ gives the deviation of the luminance from its mean value as a function of position and time (*2*). The stimulus that maximizes response under this constraint, we call the "optimal stimulus."

The virtue of this criterion is that the optimal stimulus gives quantitatively the detailed spatial and temporal properties of the RF: Its spatial distribution is that of the RF, and its temporal history (reversed in time) "matches" the system's impulse response function (*3*). Thus, by successive approximations through a set of trial stimuli, or appropriate response-stimulus feedback loop, the spatiotemporal properties of the system can be deduced (*4*). These properties include phase information, which is not revealed by grating and flicker sensitivity curves.

In short, the frequency channel and optimal stimulus (or RF) descriptions are compatible and both should be in the repertoire of the physiologist and psychophysicist.

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4. Since submission of the original version of this comment, A. Watson, H. Barlow, and J. Robson reported optimal stimuli for humans, determined psychophysically (paper presented to the annual meeting of the Association for Research in Vision and Ophthalmology, Sarasota, Fla., 26 April to 1 May 1981).
5. This work was supported by grant EY01640 from the National Institutes of Health. We would like to thank D. S. Falk and R. M. Steinman for helpful comments.

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Using a relatively simple set of geometric patterns (lines, edges, spots), Hubel and Wiesel (*1*) were able to derive the spatial receptive field (RF) properties of visual cortical neurons. We and others (*2*, *3*) have since characterized the spatial properties through the use of spatial frequency grating patterns. In a linear system, these two descriptions (space domain and frequency domain) are mathematically equivalent; we have in fact demonstrated the equivalence of these two descriptions for simple cells (*4*). Thus, while not surprising, it is nevertheless reassuring to know that Stork and Levinson (*5*) were able to generate theoretical predictions (based upon linear assumptions and a receptive field structure such as the one we, and others, have demonstrated) in agreement with the results of our experiments (*6*).

However, it is erroneous to equate the space domain description of striate cells (the spatial RF) with the term "bar detector" (an error Hubel and Wiesel were careful *not* to make). It must be emphasized that a linear spatial filter with tuning comparable to what is found in the striate cortex would make an extremely poor bar detector, providing totally ambiguous information concerning bar width. The main point of our experiment was the demonstration that cortical cells are simply not selective along the dimension of bar width. An adequate bar detector would require a different type of RF structure than what is found in the visual cortex. This fact is evident in the empirical results of our study as well as the theoretical results of Stork and Levinson.

When considering the functional significance of the spatial-analytic capabilities of striate cells, one must keep in mind the idealized nature of these mathematical descriptions: no physical system can span the infinite distance required to isolate a single sine wave for a pure frequency domain description, and similarly no physical system can isolate an infinitesimal spatial impulse for a pure space domain description. Practical considerations force the essential dual characteristic. An ideal system should provide maximum conjoint localization in both domains—space and frequency—comparable to the spatial tuning of visual cortical neurons (*7*). We certainly agree that the analytic tools of vision research should include both descriptions: spatial receptive fields and spatial frequency tuning.

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6. In (*3*), we emphasized that our results were consistent with the notion of "linear summation of excitation and inhibition within receptive fields with spatially antagonistic regions" (p. 88); we have shown elsewhere (*4*) that the linear filter predictions are in accord with the measured bar versus grating responses; further, we interpreted our data within both the space domain and the frequency domain perspectives (*3*, p. 90).
7. Guided by analogies to quantum mechanics, Gabor has investigated this dual characteristic of an information sampling system and has provided an elegant and rigorous discussion of the basic issues [D. Gabor, *J. Inst. Elect. Eng.* **93** (Part 3), 429 (1946)]; Marcelja has clearly demonstrated the relevance of Gabor's "theory of communication" to visual cortical function [S. Marcelja, *J. Opt. Soc. Am.* **70**, 1297 (1980)].

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