Attneave (*8*). According to his model, the alternation between stable states is the result of inhibitory competition between parallel neural structures. We have explored a multistable phenomenon whose stable states are sensations of movement (element versus group) that are qualitatively different (that is, the two states cannot readily be ordered along a single perceptual dimension). By manipulating stimulus conditions, we have been able to favor either the element or the group movement sensation and, thereby, to infer some of the response properties of the neural mechanisms which underlie each stable state. The response properties parallel those of movement mechanisms studied in isolation in other experiments (*5–7*). However, by allowing the two mechanisms to compete, we can see more directly the differences in the functional characteristics of the mechanisms. In other experiments (*9*) we have selectively adapted the mechanisms that underlie the two movement sensations and have further delineated differences in their response characteristics.

ALLAN PANTLE
LUCINDA PICCIANO
Department of Psychology, Miami University, Oxford, Ohio 45056

References and Notes

1. We use the terms "element movement" and "group movement" merely as descriptive labels for the movement sensations.
2. J. Ternus [in *A Sourcebook of Gestalt Psychology*, W. D. Ellis, Transl. (Humanities Press, New York, 1950), pp. 149–160] reports his experiments on stroboscopic movement with a variety of multielement displays. One of his displays contained two stimulus frames with three dots each, whose spatial arrangement was like that of the dots in the present experiments. While Ternus does not give detailed information about the spatial and temporal characteristics of his display, he does report that his display evoked mainly the movement sensation defined as group movement in our report. Under circumstances considered special by Ternus (direct fixation of the overlapping dots, continuous illumination of the overlapping dots and rapid alternation of the third dot of each frame, or observation at very close ranges), it was possible to see the movement sensation defined as element movement in the present article. None of the stimulus variables were explored systematically by Ternus.
3. Appropriate neutral density filters were used in the binocular condition to keep stimulus luminances equal to those during dichoptic viewing with Polaroid filters.
4. When an observer arrived for the first session of the experiment, he was shown (i) a stimulus sequence with an 80-msec ISI and binocular viewing and (ii) a stimulus sequence with a 10-msec ISI and binocular viewing. After looking at each sequence, the observer was asked whether he perceived any movement of the dots, and if so, which dots moved and in what direction. All observers spontaneously reported the movement sensation defined as group movement with the 80-msec ISI and the movement sensation defined as element movement with the 10-msec ISI.
5. V. Ramachandran, V. Madhusudhan, T. Vidyasagar, *Vision Res.* **13**, 1399 (1973).
6. A. Pantle, *J. Opt. Soc. Am.* **63**, 1280A (1973).
7. S. Anstis, *Vision Res.* **10**, 1411 (1970); B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971), pp. 107–109; H. Bell and J. Lappin, *Percept. Psychophys.* **14**, 45 (1973); O. Braddick, *Vision Res.* **14**, 519 (1974).
8. F. Attneave, *Sci. Am.* **225**, 62 (December 1971).
9. J. T. Petersik and A. Pantle, in preparation. Recent work by other investigators [for example, P. Tynan and R. Sekuler, *J. Opt. Soc. Am.* **64**, 1251 (1974); B. Breitmeyer, *Vision Res.* **15**, 1411 (1975)] has shown that the processing of different spatial frequencies occurs at different temporal rates. If the spatial response properties of the element and the group movement mechanisms are different, it might be expected that the spatial characteristics of our movement display would have an important bearing on the type of movement seen.
10. Supported in part by Air Force contract F33615-74-C-4032, Wright-Patterson Air Force Base, Ohio.

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Constancy and Uniqueness in a Large Population of Small Interneurons

Abstract. *The anatomy of 61 of the smallest interneurons in the brain of the locust shows the same tendency toward uniqueness, constancy of neuropil arborizations, and frequency of occurrence of supernumerary cells as does that of 17 large interneurons; the size and number of neurons thus have no obligatory relation to the concept of the unique identifiable neuron.*

Over the past decade, and particularly with the introduction of intracellular dyes (*1*), increasing numbers of studies have described unique identified neurons. Among conspecific animals, these cells are constant and unique in axon destination, major branching patterns, soma position, and physiological properties. Although the concept of the unique identifiable neuron makes no reference to neuronal size, most studies have, for technical reasons, described large neurons in invertebrate (*2*) and vertebrate (*3*) preparations. In addition, the constancy and variability of 17 large interneurons has been evaluated in a large sample of conspecific animals (*4*). There are no accounts, however, of the constancy and variability of the small interneurons that form the bulk of the nervous system.

Table 1. The tendency toward uniqueness of the large and small ocellar interneurons. Entries are the total numbers of neurons found in particular configurations. Numbers in parentheses are the numbers of unique neurons or clusters (each with contralateral homologs). For example, 36 small interneurons found in three-cell identified clusters refers to six unique three-cell clusters, each with a complementary set of contralateral homologs.

Uniqueness of neurons (*6*)	Large interneurons	Small interneurons
Identified neuron, located along midline	1	1
Identified neuron with contralateral homolog	2 (1)	16 (8)
Identified two-cell cluster with contralateral homolog	8 (2)	8 (2)
Identified three-cell cluster with contralateral homolog	6 (1)	36 (6)
Identified cluster with more than three equivalent cells	0	0
Identified class	0	0
Total	17	61

I now report on the anatomy of 61 of the smallest interneurons in the locust brain and compare them to 17 large interneurons previously studied (*4, 5*).

That the terms "identified neuron," "identified cluster," and "identified class" have been used recently with a wide diversity of meanings by different authors suggests the need for definitions (*6, 7*). In this report, neurons are described as belonging to one of these three categories and can thus be described as occurring along a spectrum of equivalence, from large numbers of equivalent neurons (identified classes) to small numbers of equivalent neurons (identified clusters) to neurons with zero-equivalence (identified neurons) (*8*). The term "tendency toward uniqueness" refers to the tendency for cells to occur near the zero-equivalence end of the spectrum.

The neurons studied here are the small ocellar interneurons in the brain of the locust (*Schistocerca vaga*). In addition to their large compound eyes, most insects have simple eyes (dorsal ocelli). In locusts there are three ocelli, two lateral and one median; each consists of a common lens, a few hundred receptor cells, and a peripheral neuropil. In each ocellus, the receptor cells synapse peripherally with the processes of both large and small ocellar interneurons whose axons form the ocellar nerve, which extends from the ocellus to the brain. There are 17 large ocellar interneurons (*4, 5*) and at least 61 small interneurons (*9, 10*).

The anatomy of the 17 large interneurons, representing some of the largest cells in the locust central nervous system (axons, 15 μm; somata, 45 μm), has been determined by "diffusion" (*11*) of $CoCl_2$ through the distal ends of the ocellar nerves followed by subsequent precipitation of the cobalt ions as a sulfide salt (*4, 5*). The brains were then

fixed, dehydrated, embedded in paraffin, and serially sectioned at 15 μm. The cobalt-stained neurons were intensified by silver precipitation according to a modification of Timm's method (*12*) and reconstructed with a Wild drawing tube. In this study, the anatomy of 61 small interneurons, representing some of the smallest cells in the locust's central nervous system (axons, 2 μm or less; somata, 5 μm), was determined according to the same procedure. From the 61 small cells described, the anatomy of representative cells was examined in large sample sizes to ascertain their tendency toward uniqueness, constancy of neuropil arborizations, and frequency of occurrence of supernumerary cells.

The small ocellar interneurons can be characterized by the position of the axon and arborization as belonging to one of the following groups of cells: (i) unpaired identified neurons located along the midline, (ii) laterally located identified neurons and their contralateral homologs, or (iii) laterally located identified clusters with two or three equivalent cells and their contralateral homologs. As has been described for the large interneurons, the small interneurons are never found in identified classes or as identified clusters of more than three equivalent cells (Table 1). The tendency toward uniqueness of the small interneurons is indistinguishable from that of the large interneurons.

An identified neuron, MS(V)1, and a two-cell cluster, MLS(I)1-2, of small cells were reconstructed from serial sections in eight different preparations (Fig. 1) (*13*). Across preparations, the arborizations of these small cells are remarkably constant in shape and extent, especially when one considers the number of steps in the histology and serial-section reconstruction. The variability in the fine branching patterns does not exceed that observed in studies of large interneurons and motoneurons (*2, 4*).

One form of variability observed in both the large and the small interneurons was the occasional occurrence of supernumerary cells. The somata of a two-cell cluster [MLS(I)1-2] could be easily recognized and counted in more than 40 wholemount preparations. The sample size was large enough to allow the frequency of occurrence of supernumerary cells to be estimated. Normally, this cluster contains two equivalent cells (with a two-cell cluster of contralateral homologs). In three preparations, a third or supernumerary soma was revealed on one side of the brain; a serial-section reconstruction of one of these preparations shows this extra cell to be a complete anatomical duplicate of the normally occurring cells (Table 2). The frequency of supernumerary cells of the small interneurons is statistically indistinguishable from that of the large interneurons. The data suggest (i) that size and number of neurons have no obligatory relationship to the uniqueness and constancy of those neurons and (ii) that the cells within a large population of small interneurons are as constant and unique as those few large neurons previously studied.

Table 2. Frequency of occurrence of supernumerary cells of the large and small ocellar interneurons. Abbreviations: L and R, homologous clusters on the left and right sides of the brain.

Two-cell cluster (*13*)	Cell size	Animals examined	Animals with supernumerary cells
ML1-2_L	Large	41	3
ML1-2_R	Large	40	3
MLS(I)1-2_L	Small	42	1
MLS(I)1-2_R	Small	45	2

In the past, the arthropod neuropil has been broadly divided, on the basis of gross anatomical appearances, into the categories (i) "structured" (or repetitive) and (ii) "unstructured" (or nonrepetitive) (*14*). The frequent assumption was that the repetitive areas, for example the corpora pedunculata (mushroom bodies), optic lobes, and central complex, were composed of large numbers of equivalent neurons forming identified classes. However, there is increasing evidence that the number and precision of connections in these areas are constant (*15*). Furthermore, large identified interneurons are found in the central complex, corpora pedunculata, and lobula (*16*), and some of the identified small ocellar interneurons also arborize in areas of repetitive neuropil, for example the protocerebral bridge (of the central complex), corpora pedunculata, and lobula (*10*). These areas of repetitive neuropil, then, have less equivalence and a greater tendency toward uniqueness than previously suspected. With the possible exception of large classes of

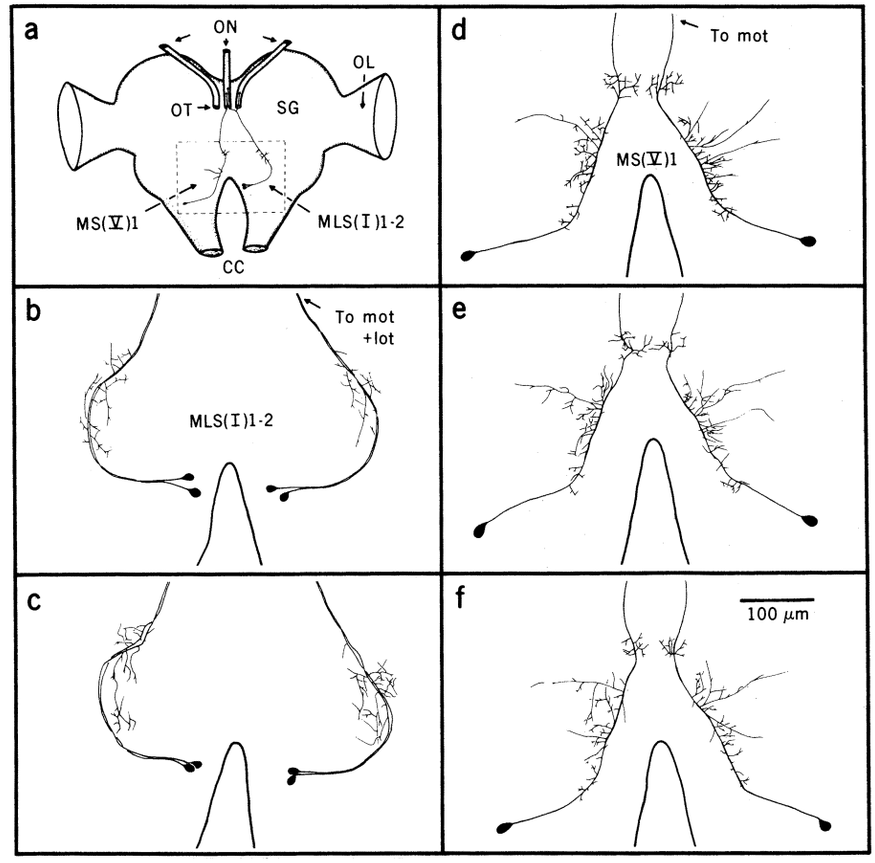

Fig. 1. Representative reconstructions showing the constancy of neuropil arborizations of the small ocellar interneurons. (a) Schematic posterior view of supraesophageal ganglion (brain); rectangle shows area viewed in (b) to (f). (b, c) Reconstructions of a two-cell cluster [MLS(I)1-2] in two animals, showing only major branches. Somata, neuropil axon, and arborizations are all drawn at twice the actual diameter. (d to f) Reconstruction of an identified neuron [MS(V)1] in three animals. Abbreviations: *OT*, ocellar tracts; *ON*, ocellar nerves (two lateral and one median); *mot*, medial ocellar tract; *lot*, lateral ocellar tract; *SG*, supraesophageal ganglion; *OL*, optic lobe; CC, circumesophageal connectives.

low-order sensory interneurons, all areas of arthropod neuropil are probably comprised entirely of identifiable neurons and clusters.

A nervous system with 10^2 neurons, such as that of a nematode (*17*), can be constituted entirely of identified neurons and clusters. My data support the notion that a nervous system with 10^5 central neurons, such as that of a locust, could also be so constituted. While studies of identified neurons and clusters in invertebrate nervous systems have progressed from giant interneurons to large interneurons and motoneurons (and now to small interneurons), our knowledge of identified neurons and clusters in vertebrate nervous systems is based solely on a few studies of giant interneurons (*3*). Although it is not possible to predict where most vertebrate neurons will occur along the spectrum of equivalence, as we investigate the central nervous systems of vertebrates with finer anatomical and physiological techniques, we will probably find less equivalence and a greater tendency toward uniqueness.

COREY GOODMAN

Department of Zoology,
University of California, Berkeley 94720

References and Notes

1. For review, see S. B. Kater and C. Nicholson, Eds., *Intracellular Staining in Neurobiology* (Springer-Verlag, New York, 1973).
2. For example, in annelids: B. Mulloney, *Science* **168**, 994 (1970); J. G. Nicholls and D. A. Baylor, *J. Neurophysiol.* **31**, 740 (1968); in mollusks: W. T. Frazier, *et al., ibid.* **30**, 1288 (1967); in arthropods: M. Burrows, *J. Comp. Physiol.* **83**, 165 (1973); M. O'Shea, C. H. F. Rowell, J. L. D. Williams, *J. Exp. Biol.* **60**, 1 (1974); M. Remler, A. Selverston, D. Kennedy, *Science* **162**, 281 (1968); J. J. Wine, J. E. Mittenthal, D. Kennedy, *J. Comp. Physiol.* **93**, 315 (1974).
3. E. J. Furshpan and T. Furukawa, *J. Neurophysiol.* **25**, 732 (1962); C. M. Rovainen, *ibid.* **30**, 1000 (1967); J. Diamond, *Fish Physiol.* **5**, 265 (1971); A. A. Auerbach and M. V. L. Bennett, *J. Gen. Physiol.* **53**, 183 (1969); P. G. Model, M. E. Spiro, M. V. L. Bennett, *Brain Res.* **45**, 288 (1972).
4. C. S. Goodman, *J. Comp. Physiol.* **95**, 185 (1974).
5. ———, *Cell Tissue Res.*, in press.
6. An *identified neuron* is a unique neuron (a single cell with no other equivalent cells) that has a constant anatomy and physiology in conspecific animals, in that it can be repeatably recognized from animal to animal and distinguished from all other neurons. An *identified cluster* is a unique cluster (a fixed number of equivalent cells with no other equivalent cells) with a constant anatomy and physiology in conspecific animals; these clusters often contain only a small (numerically fixed) number of equivalent neurons. Two neurons are defined as equivalent when any single cell, considered alone and out of context, cannot be anatomically or physiologically distinguished from the other cell. Theoretically, an identified cluster is numerically invariant (just as an identified neuron is always a single cell). In practice, however, one can occasionally observe a supernumerary cell (anatomical duplicate of normally occurring cell) occurring as an equivalent (or duplicate) cell of an identified neuron (*7*) or as an additional equivalent cell within an identified cluster (*4, 7*). An *identified class* comprises equivalent neurons and does not imply that the number of these neurons is constant; these classes often contain a large (numerically variable) number of equivalent neurons.
7. D. P. Kuffler and K. J. Muller, *J. Neurobiol.* **5**, 331 (1974).
8. The concept of a spectrum of equivalence, with neurons that are unique having zero-equivalence, comes from T. H. Bullock, in *The Neurosciences; Third Study Program*, F. O. Schmitt and F. G. Worden, Eds. (MIT Press, Cambridge, Mass., 1974), pp. 343–346. In this report I follow that usage of the term "unique."
9. For a description of the arborization of all 61 small cells in eight specific areas of brain neuropil, see (*10*).
10. C. S. Goodman and J. L. D. Williams, *Cell Tissue Res.*, in press.
11. Although the term "diffusion" is commonly used, it has not been shown whether the uptake of cobalt ions by the cut ends of the axons is an active or a passive process.
12. N. M. Tyrer and E. M. Bell, *Brain Res.* **73**, 151 (1974); as further modified (*5*).
13. The designations are part of a standardized nomenclature used to describe 61 small ocellar interneurons (*10*) and 17 large ocellar interneurons (*4, 5*).
14. D. Maynard, *Am. Zool.* **2**, 79 (1962); for a review of arthropod brain anatomy, see T. H. Bullock and G. A. Horridge [*Structure and Function in the Nervous System of Invertebrates* (Freeman, San Francisco, 1965)].
15. G. A. Horridge and I. A. Meinertzhagen, *Z. Vgl. Physiol.* **66**, 369 (1970); J. L. D. Williams, *J. Zool.* **176**, 67 (1975).
16. J. L. D. Williams, thesis, University of Wales (1972); M. J. Weiss, *J. Morphol.* **142**, 21 (1974); M. O'Shea and J. L. D. Williams, *J. Comp. Physiol.* **91**, 257 (1974).
17. R. Goldschmidt, *Z. Wiss. Zool.* **90**, 73 (1908); *ibid.* **92**, 306 (1909).
18. I thank D. Bentley, M. O'Shea, K. Pearson, and C. H. F. Rowell for criticizing the manuscript; J. L. D. Williams for helpful discussions and assistance; D. Kennedy and R. Roth for the use of facilities; and B. Bacher for assistance. Supported by NIH grant NS 09404-05 to C. H. F. Rowell and NSF predoctoral fellowship to C. S. Goodman.

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Abolition of Direction Selectivity in the Visual Cortex of the Cat

Abstract. *Cats were reared in a stroboscopically illuminated environment, which deprived them of experience with visual movement but allowed them form vision. In these cats, neurons of the visual cortex displayed normal orientation selectivity, but direction selectivity was virtually abolished. The effect remained unaltered by long periods of normal visual exposure.*

The response characteristics of single cells in the cat visual cortex can be profoundly modified by rearing animals in special visual environments (*1, 2*). Since, in everyday life, visual stimuli are in constant motion on the retinae, interest has been focused on the consequences of restricted experience with visual movement for cortical development. Rearing animals in stroboscopic illumination (strobe rearing), which deprives them of experience with movement but allows them patterned visual input, results in reduced orientation and direction selectivity among cortical neurons (*3*). The low-frequency stroboscopic environment used in previous experiments (one flash every 2 seconds) can be made progressively more like the normal environment by increasing the frequency of the flashes. As the frequency was increased, we were able to examine the emergence of characteristic cortical properties. We now report that strobe rearing at an intermediate frequency (eight flashes per second) results in a cortex containing neurons with orientation selectivity but rarely with direction selectivity.

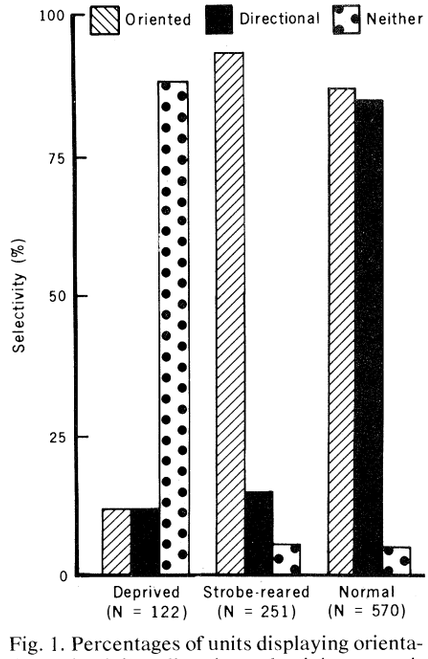

Fig. 1. Percentages of units displaying orientation selectivity, direction selectivity, or neither property in cats reared in the dark, strobe-reared, and reared normally. For each group, *N* represents the total number of units studied in the various groups of cats. Data for normal and deprived cats were derived from Cynader, Berman, and Hein (*5*).

Five kittens served as subjects in these experiments. They were raised from birth in a lighttight enclosure in which the only illumination source was a strobe light flashing eight times per second. The 10-μsec flash duration ensured a series of stationary retinal images. The human subjective experience is that of a series of jerky images, reminiscent of the early motion pictures. After 4 to 6 months, we studied the visual responses of single neurons in the striate cortex according to methods and criteria that have been described elsewhere (*4, 5*). Responses in strobe-reared kittens were compared with responses of kittens reared in the dark and those of normal cats. We classified units as orientation selective if