"Novelty" cells in association cortex of cat ¹

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Responses of single neurons in the suprasylvian cortical association areas of the chloralosed cat to auditory, tactile and visual stimuli were studied. All cells responded to all modalities of stimulation. A number of cells showed complex integrative effects to polysensory combinations of stimuli. These cells also exhibited a "novelty" effect: cell discharge probability increased as interstimulus interval was increased, in some instances up to 30 sec or more. Stimulus combinations and variations of interstimulus interval interacted in a complex manner in their effects on cell discharge probability.

Several lines of evidence support the view that association response areas of the cerebral cortex of cat play a special role in attentive aspects of behavior, particularly in tasks involving processing of information from more than one modality of stimulation (e.g., Thompson & Kramer, 1965; Thompson & Shaw, 1965). Gross evoked response analysis of these regions in the chloralosed cat indicated that they are activated in a nonspecific manner by auditory, visual, and tactile stimuli (Thompson, Johnson, & Hoopes, 1963). However, in studies of single unit activity in these regions it has been reported that many cells, particularly in the suprasylvian association areas, do not respond to more than one modality of stimulation (e.g., Bental & Bihari, 1963; Dubner & Rutledge, 1964). We have undertaken a large scale analysis of the response properties of cells in the middle suprasylvian gyrus, partly to determine the degree of polysensory convergence. In the course of this study we have encountered a number of cells that exhibit complex integrative and interactive properties as a function of the nature and recency of polysensory stimulation—properties that appear to resemble behavioral "attention" or response to "novelty." Characteristics of these complex novelty cells are described in this report.

Method

Cats were anesthetized with chloralose (50-70 mg/kg IP) and paralyzed with Flaxedil. The left middle suprasylvian gyrus was exposed and single neuron responses were recorded extracellularly with tungsten microelectrodes using standard techniques. All data were recorded on film. Peripheral stimuli were free field click, light flash, and single shock pulse to ipsilateral forepaw. A standard interstimulus interval (ISI) of 2 sec was routinely employed during preliminary exploration.

Results

All of the approximately 200 cells studied to date responded to all modalities of stimulation. There

were marked variations in latency of response to various stimuli between different cells. Thus, one cell might exhibit latencies of between 30 and 40 msec to all stimuli (see Fig. 1), another might show 30 msec latency to flash, 50 msec to click, and 180 msec latency to forepaw shock, and so on. However, for any given cell the particular latencies were reliable. At least 10 percent of the cells studied (i.e., more than 20 cells to date) exhibited the complex integrative properties to be described here.

"Integrative" cells typically respond relatively infrequently when single stimuli of a given modality are presented at the standard 2 sec ISI. However, they respond more frequently when combinations of two stimuli are presented simultaneously every 2 sec, and discharge even more frequently to a stimulus complex consisting of all three stimuli given simultaneously. An example of such a cell is shown in Fig. 1. The stimulus is indicated to the left of each trace, together with the probability of response (proportion of times cell discharged to a series of stimuli, e.g., 30 percent to clicks, 80 percent to flashes, etc.). Response probabilities for a given cell were stable over time. Note in Fig. 1 that although the response probabilities are low for auditory and tactile stimuli given separately, the probability of response is high for a combined auditory-tactile stimulus.

Many of these integrative cells exhibit what might be termed a "novelty" effect to variation of the ISI. Thus a given cell might respond infrequently or not

Fig. 1. Responses of single neuron in suprasylvian gyrus of chloralosed cat to auditory (A=click), visual (V=flash), or tactile (T=forepaw shock) stimulation, given singly (left column) and in simultaneous combinations (right column) every 2 sec. Number to left of each trace indicates probability of response. Upward deflections are positive; the stimuli occur at beginning of trace. (Time calibration 25 msec)

Fig 2. Probability of response of unit in suprasylvian gyrus to stimuli alone and in combinations plotted as a function of interstimulus interval.

at all to a particular stimulus presented at the standard 2 sec ISI. However, as the time between stimuli is increased, the probability of response increases. For some cells this relationship holds for ISIs up to 30 sec or longer. Results of parametric study of a novelty cell are illustrated in Fig. 2. Discharge probability is plotted against ISI for all stimuli, singly and in combinations. All three stimuli evoked little or no activity in the cell at the 2 sec ISI. However, for every type of stimulus and stimulus complex, discharge probability increases as ISI increases. The integrative actions of stimulus combinations are clearly seen in this cell. Although each stimulus alone yields a low response probability at the 2 sec ISI (auditory, .13; tactile, 0; visual, 0), some stimulus combinations yield high response probabilities at this same ISI (auditory-tactile, .67; auditory-visual-tactile, .89).

These data also illustrate interaction effects between stimulus combinations and ISIs. At the 2 sec ISI the response probability is low for all stimuli given singly and for the auditory-visual combination, but the auditory-tactile combination gives a high response probability. However, at the 4 sec ISI both the auditory-tactile and the auditory-visual stimulus combinations yield high response probabilities.

Discussion

On the basis of the data presented here, it may be inferred that cells in the association response areas of the suprasylvian gyrus of the cat are truly

polysensory, responding to auditory, visual, and tactile stimulation (and possibly other modalities as well). Earlier conclusions that many cells in these regions are not polysensory (e.g., Dubner & Rutledge, 1964) may be due in part to the very long response latencies exhibited by some cells to some types of stimuli, and in part to the fact that only short ISIs were used. If only the 2 sec ISI had been used in the cell illustrated in Fig. 2, for example, it would be concluded that the cell responds infrequently to auditory stimulation and not at all to tactile or visual stimulation. In fact, at the 6.3 sec ISI the cell responds frequently to all types of stimulation.

The integrative properties of many of these cells are striking. The effects of simultaneous stimulation by more than one modality on cell discharge probability are often much more than additive (see Fig. 2). The novelty effect is particularly clear: The less frequently the stimulus is given, the more frequently the cell responds, even up to intervals of more than half a minute, which is a very long period of lability for cortical cells in anesthetized preparations. Furthermore, combinations of stimuli and interstimulus intervals yield complex interaction effects on cell discharge probability. It may be suggested that cells of this type might, in the normal animal, code degree of stimulus novelty both in terms of stimulus quality and stimulus recency.

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Notes

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