

THE anterior superior temporal polysensory area (STPa) has been hypothesized to be an integration site for signals coming from the dorsal and ventral visual pathways. To determine whether neurons in STPa were selective for simple two-dimensional geometrical shapes and whether this area might integrate different visual cues, cells were tested with motion- and luminance-defined shapes. Many neurons were activated by the shape stimuli under at least one condition; however, very few showed selectivity for a particular shape under either condition. Only one neuron responded selectively to shapes defined by both cues. Thus selectivity for simple shapes is not a prevalent property of STPa neurons and the integration of luminance and motion signals does not appear to occur at the single neuron level in STPa. *NeuroReport* 9: 2063–2070 © 1998 Rapid Science Ltd.

Key words Shape-from-luminance; Shape-from-motion; Single-unit recording; Macaque; Temporal cortex; Visual pathways

Lack of selectivity for simple shapes defined by motion and luminance in STPa of the behaving macaque

Kathleen C. Anderson
and Ralph M. Siegel^{CA}

Center for Molecular and Behavioral
Neuroscience, Rutgers University, 197
University Avenue, Newark, NJ 07102, USA

^{CA}Corresponding Author

Introduction

Visual function in primates is subserved at the cortical level by a large number of areas that have been grouped functionally into two separate processing streams.¹ Areas involved in object recognition form a pathway originating in striate cortex (VI) and extending ventrally to V4 and into intertemporal cortical area TEO and TE. The activity of neurons within this ventral pathway has been shown to be selective for wavelength, color, orientation, and shape.^{2–5} Areas involved in spatial and motion processing comprise a pathway projecting from VI to the middle temporal (MT) and medial superior temporal (MST) areas in the upper bank and floor of the posterior superior temporal sulcus (STS), and then up to inferior parietal areas 7a, and the ventral and lateral intraparietal areas (VIP and LIP).⁵ Neurons within these dorsal areas have been shown to selectively respond to both the direction and type of motion, as well as to the spatial location of stimuli (see Ref. 7 for a recent review). Despite this detailed knowledge of the physiological properties of visual cortical neurons, it is still largely unknown how different aspects of the visual scene become integrated or where this integration takes place.

Regions in both the parietal cortex and inferior temporal cortex project to the rostral portion of the superior temporal polysensory area (STPa) and to prefrontal cortex.^{8–10} Based on their anatomical inputs, both STPa and prefrontal cortex have been

proposed as possible areas of convergence and integration for signals coming from the two visual pathways.¹¹ The role of prefrontal cortex in the processing of different types of visual information has been the focus of many recent studies,^{12,13} whereas STPa has received relatively little attention. Neurons in STPa have large bilateral receptive fields. Most cells respond well to moving stimuli and many cells show direction selectivity, implicating this area in motion processing.^{14,15} Some neurons in STPa are selective for specific combinations of body forms and direction of movement.^{16,17} These physiological results provide evidence that neurons in STPa are capable of integrating information about form and motion, at least for this highly specialized class of biologically relevant stimuli.

In addition to selectivity for moving bodies, it has also been shown that some neurons in STPa respond selectively for both real and two-dimensional representations of faces.^{14,18–22} These findings have prompted some investigators to suggest that STPa contains a region specific for face processing.^{19,20} However, lesions of STP produce visual discrimination deficits for both face and non-face stimuli.²³

The first goal of this study was to determine whether neurons in STPa selectively respond to more general, non-biological stimuli, such as simple shapes. As cue-invariant neuronal responses have been shown for areas in both the dorsal and ventral visual streams,^{24,25} the second goal of these experiments was to assess whether selectivity for a particular shape is

maintained regardless of whether the shape is defined by motion or luminance. The results of the present study indicate that STPa neurons do not show a high degree of selectivity for the simple shapes used in these experiments, and furthermore, that motion and luminance are not integrated by single neurons in this area.

Materials and Methods

Subjects, surgeries, and recording techniques: Single unit extracellular recordings were made from two hemispheres of two monkeys (*Macaca mulatta*) trained to fixate and respond to visual stimuli. All experimental and surgical procedures were carried out in accordance with the NIH Guide for the Care and Use of Laboratory Animals. The surgical and recording techniques have been described in detail previously.²⁶ Briefly, a recording chamber (16 mm diameter) was placed over the cortex ~15–16 mm anterior to the interaural plane and 19–20 mm lateral to the midline. These coordinates were based on pre-operative MRI sections of each monkey's brain. STPa lies 20–25 mm below these coordinates, just ventral to the auditory association cortex. After a 2-week recovery period, recording sessions were initiated. Neuronal signals were amplified, filtered and displayed on an oscilloscope, and only units showing activity greater than twice the amplitude of the background were isolated. Interspike intervals were measured and displayed on-line during recording sessions.

For verification of the location of the recording sites, electrolytic lesions (4 μ A for 4 s) were made on the last few days of recording for one animal. The animal was perfused and lesion sites were identified using standard histological procedures.²⁶ All lesions sites were located in the upper bank and fundus of the rostral portion of the superior temporal sulcus (STS). The second animal is still being used in experimental work. The placement of the electrode was localized in this animal during the experiments by taking frontal and lateral X-ray images while the electrode was in the brain. The general recording region was identified by comparison with MRI sections taken at the same anterior–posterior coordinates.

Stimulus displays: To study neuronal response to shapes in a controlled manner, shape-from-motion and shape-from-luminance stimuli similar to those of Britten *et al.*²⁷ and Sary *et al.*²⁵ were used. Eight two-dimensional geometrical figures, matched for area, were chosen to test shape selectivity in STPa. Each shape subtended $5 \times 5^\circ$ of visual angle and was plotted on a 10° circular background in both

conditions. In the luminance condition, dim white shapes (8.7 cd/m^2) were plotted on a gray background (4.9 cd/m^2). The motion-defined shapes were made up of 128 white dots (0.1° in diameter, 32 cd/m^2 , visible for 533 ms), translating to the left at $12^\circ/\text{s}$. The dots comprising the shape were embedded in a background also containing the same number of dots and moving at the same speed but in the opposite direction. Once a dot in the motion displays disappeared, it was wrapped around to the edge of the shape to maintain equal density in the background and shape. Consequently, density cues that could account for differential responses to the displays were eliminated. Both types of displays were presented on a dark screen (1.0 cd/m^2). Figure 1 illustrates the two types of stimuli and shows the eight shapes that were

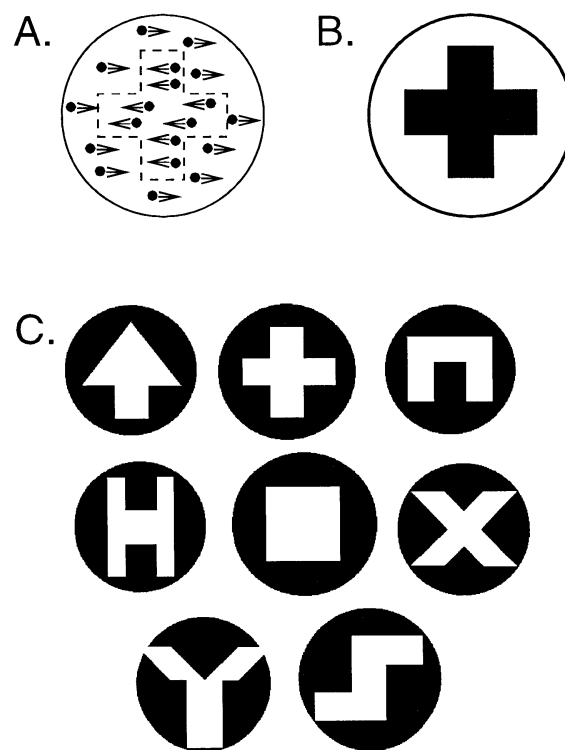


FIG. 1. Illustration of the displays used to test shape selectivity and cue invariance in STPa. The shapes subtended $5 \times 5^\circ$ of visual angle and were plotted on a circular background 10° in diameter. (A) Shape-from-motion displays. These displays were made up of a total 256 white dots (32 cd/m^2). The shapes contained 128 dots that moved in the leftward direction and the background contained 128 points moving to the right. The dots moved at $12^\circ/\text{s}$. The average luminance (integrated over area) of the motion-defined displays was 140.5 cd/m^2 . (B) Shape-from-luminance displays. These displays were made up of white shapes (8.7 cd/m^2) plotted on a gray circular background (4.9 cd/m^2). The luminance integrated over the area of these displays was 479.2 cd/m^2 . Both the motion and luminance displays were plotted on a dark screen that had a luminance of 1.0 cd/m^2 . Note that for the luminance displays there were three different levels of luminance, the shape itself, the circular background, and the screen. The motion displays contained only two levels, that of the dots and that of the screen. (C) The eight shapes used in this study. All shapes were matched for total area ($5 \times 5^\circ$).

used in this experiment. The luminance-defined and motion-defined shapes were grouped into separate blocks for presentation during recording sessions. Data were collected for eight presentations of each shape within each block.

The luminance-defined shapes were made as dim as possible without making them impossible for humans observers to detect. Nevertheless, the luminance-defined shapes had a larger integrated luminance than the motion-defined shapes. This was because a total of 256 pixels were activated in the motion displays whereas 7850 pixels were activated in the luminance displays. The integrated luminance of the motion displays was 3.4 times smaller than the luminance displays. A further difference in the two displays was their contrast. The motion displays had a contrast ($(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$) of 0.94 while the luminance displays had a contrast of 0.28. These contrast and luminance differences preclude direct comparison of the firing rate across the motion and luminance stimuli. However, these differences should not present a problem for the interpretation of the results since it is the relative response of the neuron to the individual shapes *within* each condition that is compared (see *Statistical Analysis*).

The displays were generated on an IBM/PC 33 MHz 486 computer at a resolution of 640×480 pixels using a Number Nine Corporation Sergeant Pepper graphics board. The stimuli were presented on a video monitor (Mitsubishi XC3315C; 84 cm diagonal) at a refresh rate of 60 Hz.

Behavioral task: The monkey was seated 57 cm from the monitor with his head fixed to the chair. The onset of a red fixation point in the center of the screen signaled the beginning of a trial. The monkey was required to fixate the point and pull back a lever. Two seconds later, a visual display appeared at the center of the screen. The monkey was required to maintain fixation and release the key within 800 ms after the disappearance of the shape which occurred at a random time between 1500 and 4000 ms following the onset of the display. For the motion-defined stimuli, the shape disappeared when the dots comprising the shape changed direction and moved in the same direction as the background dots. In the luminance condition, the shape was dimmed to the same gray as the background and thus became invisible. Thus the animal was required to attend to the shapes in both conditions and respond to their disappearance. The animal was rewarded with a drop of juice for correct performance while maintaining fixation throughout the trial. Eye position was monitored with an infrared eye tracker (ISCAN Co., RK-416) and fixation was within a window of 1° .

Statistical analysis: Neuronal activity was averaged over eight trials for each display within a block and firing rates were calculated for the 500 ms before the onset of a display (baseline) and the 500 ms immediately after. A two-way analysis of variance (ANOVA) was performed to determine the effect of the onset of the stimuli (ONSET factor, two levels, before and after) and the effect of the eight individual shapes (SHAPE factor, eight levels) on the activity of the neurons. Responses were evaluated at the $p < 0.05$ significance level. An ANOVA was performed on the neuronal response to each block of displays. Neuronal responses that showed an effect of ONSET alone indicated that the neuron was sensitive to the onset of the stimuli, but responded equally to all of the shapes within a block. An effect of SHAPE or an interaction between ONSET and SHAPE indicated that the neuron responded differentially across the shapes and the neuron was classified as selective for shape. Responses that did not show a significant effect of either factor, nor an interaction, were classified as non-responsive. This statistical design has been described and justified.²⁶ If a neuron showed a selective response under both conditions, selectivity in each block was qualitatively compared to determine whether it was for the same shape(s). Overall responses to the two blocks of displays were not directly compared due to the differences in luminance and contrast of the two types of shapes described above. Differences in the firing rate between the two conditions could reflect these differences in the displays rather than the cues used to define the shapes.

Results

The response of 118 neurons was tested with both the shape-from-motion and shape-from-luminance stimuli. Sixty-six percent (78/118) responded significantly above baseline to at least one of the stimuli and comprise the visually responsive neurons in this study.

The most surprising finding was the relative lack of selectivity to shapes defined by either the motion or the luminance cue. Fifty-eight of the 118 neurons, or three-quarters of the visually responsive cells, only responded significantly to the *onset* of the motion and/or luminance stimuli, without regard to their shape (Figs 2,3). Thus these neurons were responding equally to all of the shapes within a block. Some of these cells (15/118) responded significantly to the onset of both the motion- and luminance-defined shapes (Fig. 2). Although we did not quantitatively compare the responses to the two blocks of stimuli, it was clear that there were differences in the magnitude of responses to the two blocks of shapes for

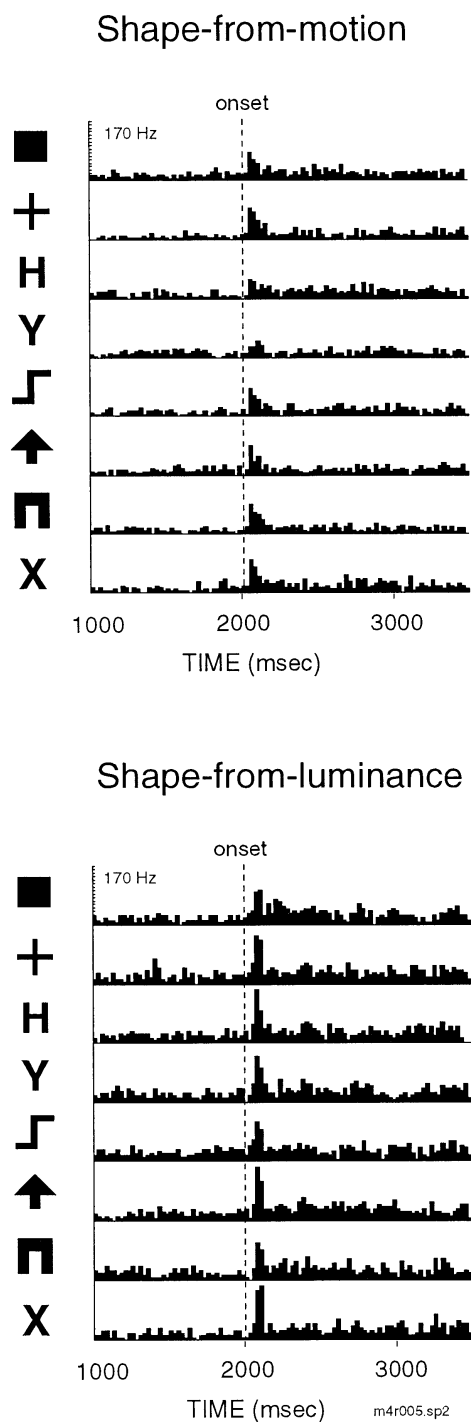


FIG. 2. Response of a cell that was significantly activated by the onset of shape-from-motion displays (top panel) and the shape-from-luminance displays (bottom panel). Peristimulus time histograms represent the mean response over eight presentations of each shape. The response to each shape is plotted in each row of the histogram and the icons to the left of each row represent the shape. The vertical dotted line in both histograms indicates the onset of the shape stimulus. This cell responded more strongly to the luminance-defined shapes but did not show a selective response for a particular shape in either block. The Y-axis represents the firing rate of the cell averaged across eight trials (spikes/s). The X-axis represents time (ms). Bin size 25 ms.

some of the neurons (Fig. 2). This difference in activity might reflect differences in neuronal response to luminance- and motion-defined shape. However, these differences could simply be due to differences in the overall luminance or contrast of the displays. Another group of neurons (23/118 or 19%) responded to the onset of the shapes only when they were defined by motion, but not when they were defined by luminance (Fig. 3a). A similar number of neurons (20/118 or 17%) responded significantly to the onset of the shapes only when they were defined by luminance but not by motion (Fig. 3b). Thus, while these three groups of neurons were responsive to the onset of the shapes under one or both of the conditions, they did not show selective responses for a particular shape under either condition.

A small group of neurons (19/118 or 16%) responded selectively to the shapes defined by luminance or the shapes defined by motion, but not both. The response of these cells varied across different shapes. The majority of these cells (14) were selective for shapes when they were defined by luminance, but not by motion (Fig. 4b). Five cells responded selectively to the shapes when they were defined by motion, but not by luminance (Fig. 4a). Only one cell showed a selective response to both the luminance- and motion-defined shapes (Fig. 5). However, the selectivity was not for the same shape in the two conditions.

Discussion

The results of these experiments indicate that very few neurons in STPa show selectivity for simple, two-dimensional shapes. The neurons that did show shape selectivity were not tuned to one specific shape, but usually responded to more than one shape (see Figs 4b,5). In most of these cases, it was difficult to determine which particular shape evoked the strongest response from the neuron. These results also indicate that shape selectivity for individual neurons in STPa is not cue-invariant, as none of the cells tested showed selectivity for the same shapes under both the luminance and motion conditions.

Negative findings need to be carefully assessed before drawing any conclusions. In this study of STPa, there are several possibilities for the relative lack of shape selectivity of the neurons. First, it is possible that the stimulus set used was too simple or too limited. A larger number of stimuli (or a different set) may have evoked selective responses from a higher proportion of neurons. However, similar stimuli have been used to show shape selectivity in IT and in the parietal cortex,^{5,25,28} which are considered high level visual association areas. As STPa is

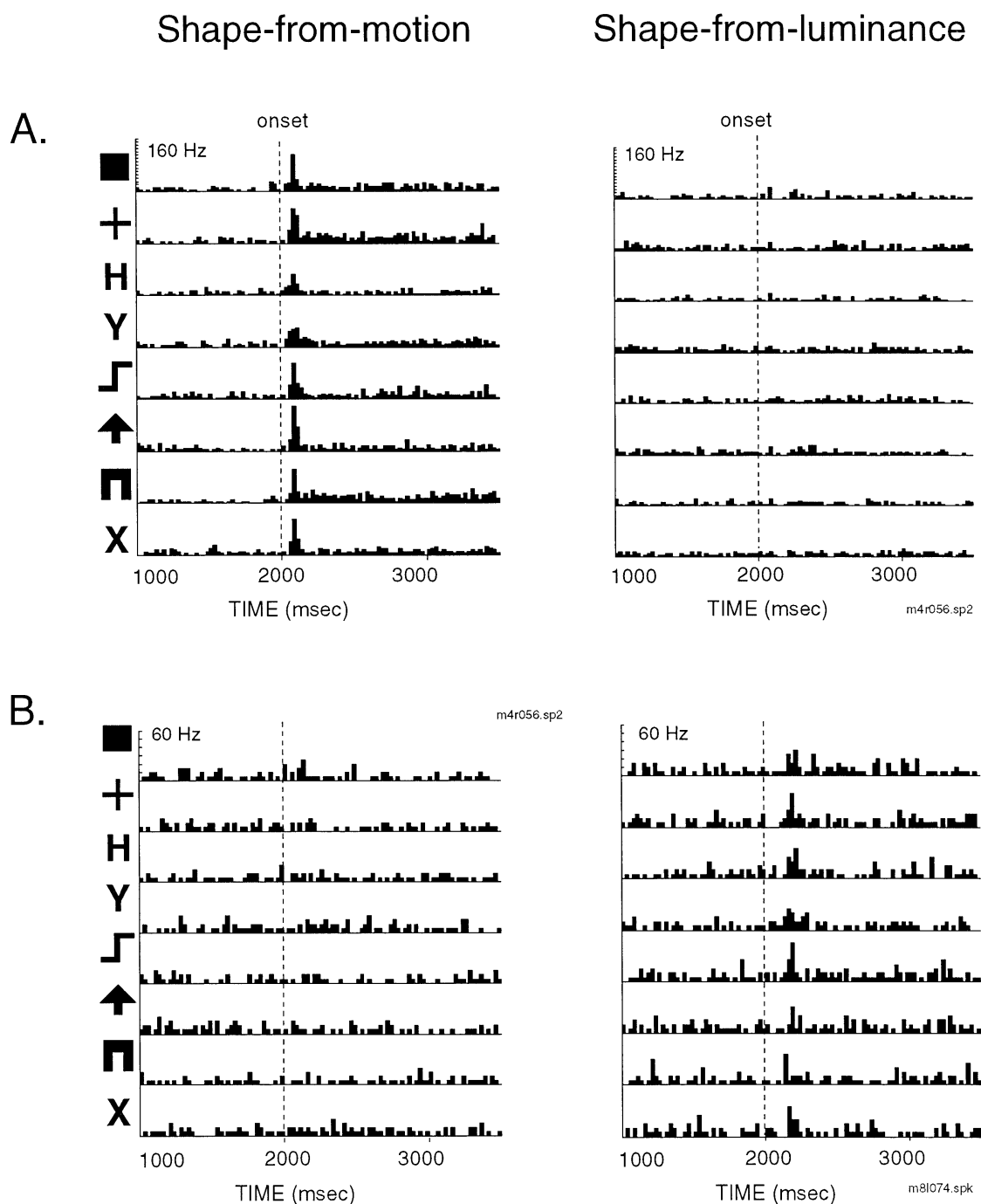


FIG. 3. Two neurons that responded to the shapes in one but not the other condition. Same conventions as in Fig. 2. (A) This cell responded significantly to the onset of the shape-from-motion displays (left) but not to the shape-from-luminance displays (right). The response to the shape-from-motion displays was equal for each of the eight shapes. (B) This cell responded significantly to the shape-from-luminance (right) displays but not to the shape from motion displays (left). As with the cell in (A) the response was not selective for a particular shape in the luminance condition.

also a high level association area, this set of stimuli appeared to be a reasonable choice to test the selectivity of neurons in this area.

A second possibility for the lack of shape selectivity in this study of STPa is the small sample size. Selectivity for non-face shapes in STPa occurs in a small percentages of neurons, varying between 5 and

26% of all cells tested.^{14,22} Moreover, face and body selectivity is reported in only a small percentage of the total neurons tested.^{14,15,20,21,29} For instance, 5–20% of 2000 neurons tested in both the upper and lower banks of STPa responded selectively to faces with even fewer showing selectivity for non-face shapes.²²

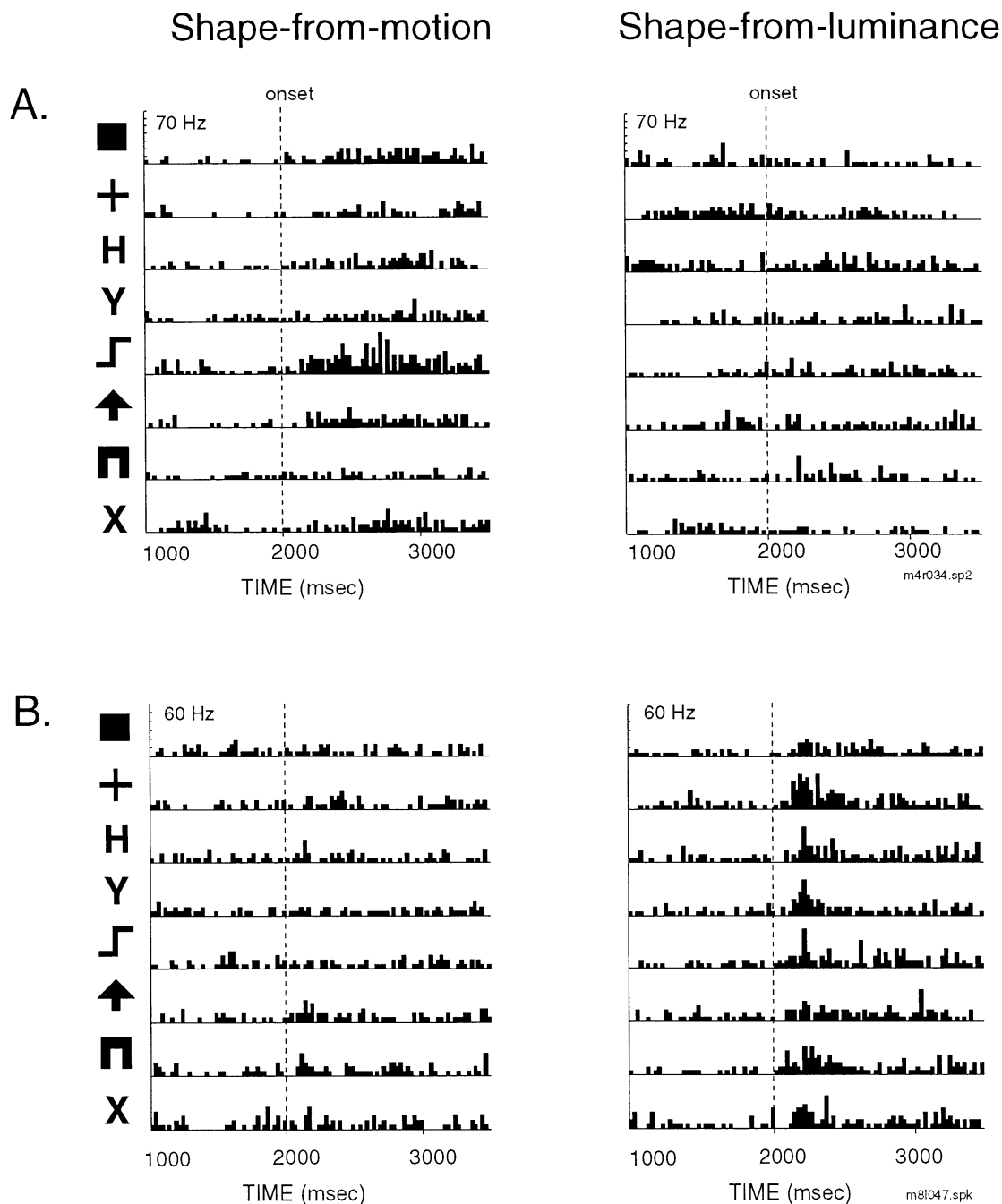


FIG. 4. Two cells that responded selectively for a shape under one or the other condition but not both are shown here. Conventions are the same as in Fig. 2. (A) This cell responded selectively for a shape (the backwards "Z", row 5) in the motion-defined block (left) but did not significantly respond to the onset of any of the luminance-defined shapes (right). (B) This cell showed the opposite response pattern than the cell in (A). This cell responded selectively for the luminance-defined shapes (right) but non-selectively for the motion-defined shapes (left). While the cell responded to all of the shapes in the luminance condition it was significantly more activated by the "+" shape (row 2) and was thus classified as selective. This cell had a weak but significant response to the onset of the motion-defined shapes (left), but this response was statistically equal for all of the motion-defined shapes.

A related possibility for the lack of shape selectivity is that sub-regions containing shape selective cells in STPa may not have been sampled in this study. Neurons that respond selectively to face stimuli have been identified in some, but not all regions of STP. We sampled neurons randomly

throughout the recording chamber and did not attempt to focus on areas more selective for shape or other stimuli. Furthermore, our recordings were confined to the upper bank of the anterior STS whereas some of the earlier studies included cells in the lower bank, an area typically considered to be

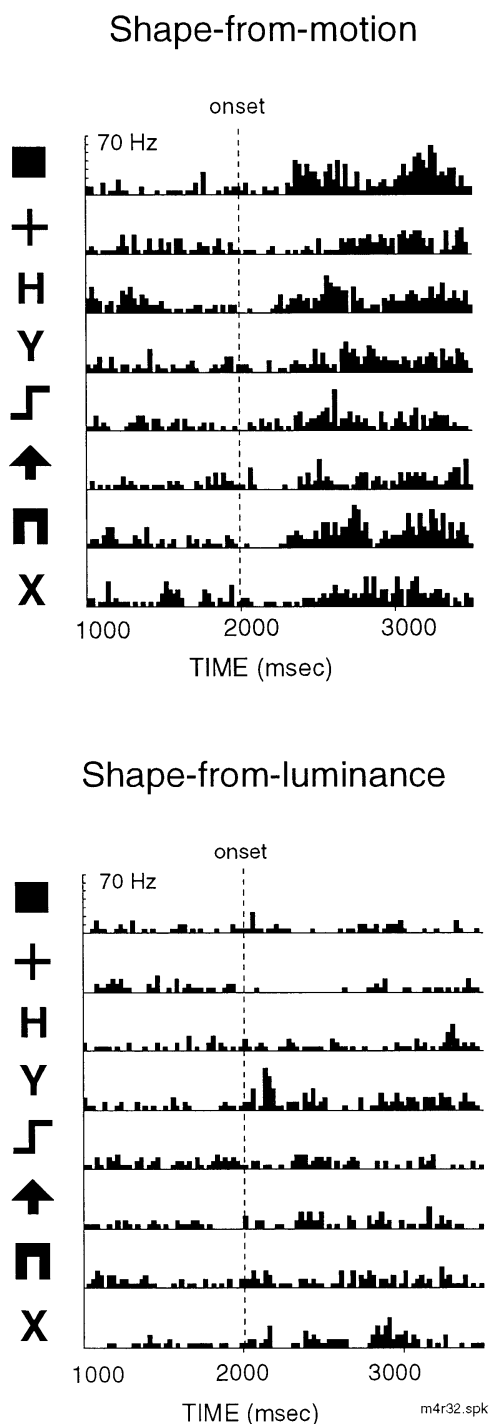


FIG. 5. The one cell that showed a selective response for shape under both conditions. The selectivity of the cell was different for the two types of shapes. The top panel represents the response of the cell to the motion-defined shapes. In this condition the activity of the cell varied significantly across the shapes. Thus while the cell responded to all of the shapes, it was more responsive to some than others (e.g. compare the response to the "+" and the ■). The bottom panel shows the response of the same cell to the luminance-defined shapes. This cell was more responsive to the onset of the "Y" shape than to the other shapes within the luminance block. Note that this cell had unusually long latencies for the motion-defined stimuli (top panel). Latencies of this magnitude were not seen for the response of any other cells in this study.

part of the inferotemporal cortex.³⁰ Thus it is possible, although unlikely, that our recording sites missed a restricted area containing a high percentage of cells selective for shape or face stimuli.

A final possibility to account for the lack of shape selectivity is that the animal was not required to discriminate the actual shape of the stimuli, but only needed to respond when the shape disappeared. The monkey could have responded to changes in the direction of motion, changes in the luminance, the disappearance of the contours of the shape, or to the shape itself. Neither the motion nor the luminance condition required that the monkey actually *detect* and respond to the shape. Using a task that required the animal to discriminate the shape of the stimulus may increase the selective responses of the neurons in this area. It should be noted, however, that STPa neurons with shape (and face) selectivity have been reported in anesthetized animals.¹⁴ Furthermore, in many studies reporting face selectivity in this area, the animals were not required to discriminate the stimuli, but had to respond only to a central fixation stimulus.^{19,21,22}

No support was found for the hypothesis that the selectivity of STPa neurons for simple shapes was invariant for luminance and motion cues. The lack of cue-invariance reported here may only reflect the relatively small number of neurons showing selectivity in general, and merits further investigation. Cue-invariant neuronal selectivity has been reported for other extrastriate areas including MT,²⁴ MST³¹ and IT.²⁵ Therefore it is reasonable to speculate that this would be a property of STPa neurons given its anatomical inputs. In addition, many of the neurons in STPa that are selective for faces and bodies maintain this selectivity over a range of stimulus transformations including size, position, orientation, spatial frequency, color, contrast, expression and view, although the degree to which selectivity is maintained varies (see Ref. 32 for a review). Studies in our laboratory have shown that some neurons in STPa are size and orientation invariant for rotating spheres.³³ Thus it is possible that STPa neurons can show some cue-invariant responses if tested with other stimuli.

Conclusion

Within the constraints of the limited stimulus set, the extent of sampled cortex, and the behavioral task, it is concluded that selectivity for *simple* shapes is not a predominant feature of STPa neurons. Given prior reports of face and body selectivity in STPa, form selectivity in this area may be limited to a specialized class of biologically relevant shapes. Furthermore, the lack of selectivity for specific shapes

does not support the hypothesis that STPa is an integration site for motion and object signals that define simple shapes.

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