

## Frontal units of the monkey coding the associative significance of visual and auditory stimuli

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**Summary.** Two monkeys were trained on both visual and auditory association tasks. Single unit activity of the frontal (prefrontal and post-arcuate premotor) cortex was recorded in these monkeys to investigate the convergence of visual and auditory inputs and to examine whether the frontal units are involved in coding the meaning (associative significance) of the stimulus, independent of its modality. A total of 289 units showed changes in firing rate after the cue presentation on the visual and/or auditory tasks and were examined on both modalities of tasks, 175 of them showing *differential* activity in relation to either the associative significance and/or physical properties of the visual and/or auditory cues. Of the 289 units, 136 (47.0%) were responsive only to the visual cue (76 of them showing cue-related differential activity), 13 units (4.5%) only to the auditory cue (6 of them showing cue-related differential activity) and the remaining 140 units (48.5%) to both modalities of cues (18 of them showing visual, 7 of them showing auditory and 68 showing both modalities of cue-related differential activity). Fifty of the 68 bimodal differential units showed changes in firing in relation to the associative significance of both modalities of cues independent of the cue's physical properties, and are considered to be involved in the crossmodal coding of the associative significance of the stimulus. The proportion of bimodal differential units was higher in the pre- and post-arcuate areas than in the principalis and inferior convexity areas of the frontal cortex. The results indicate that some frontal units participate in the crossmodal coding of the associative significance of the stimulus independent of its physical properties, and most frontal units play different roles depending on the modality of the stimulus.

**Key words:** Bimodal unit – Prefrontal cortex – Premotor cortex – Associative significance – Monkey

### Introduction

Anatomical studies have shown that the prefrontal cortex (PFC) and the cortex of the superior temporal sulcus (STS) receive convergent inputs from inferotemporal, superior temporal and posterior parietal association cortices; the two areas are thus considered to be sensory convergence areas (Jones and Powell 1970; Chavis and Pandya 1976; Pandya and Selzer 1982). These two polysensory areas have also been shown to be mutually interconnected (Jones and Powell 1970; Seltzer and Pandya 1989). Furthermore, certain parts of the posterior association cortex projecting to particular areas of the PFC, may also send fibers to those parts of the STS area which project to the same PFC areas (Kawamura and Naito 1984).

Physiological studies have shown that there are polysensory units which respond to stimuli of two or three kinds of sensory modalities in the PFC (Benevento et al. 1977; Wollberg and Sela 1980; Bruce and Goldberg 1985) and in the STS (Benevento et al. 1977; Desimone and Gross 1979; Bruce et al. 1981; Baylis et al. 1987; Hikosaka et al. 1988) although Azuma and Suzuki (1984) found no PFC unit which responded to both visual and auditory stimuli. Polysensory units in the PFC and STS were usually examined in the anesthetized preparation or in an awake animal passively exposed to irrelevant stimuli of several modalities. The functional significance of the convergence of several modalities of sensory inputs in the PFC and STS has not been clarified.

The bimodal properties of PFC unit activity have begun to be examined in the awake behaving monkey. Thorpe et al. (1983) described units in the monkey orbitofrontal cortex which responded to both the sight and taste of a particular food such as a banana. These orbitofrontal units are considered to be involved in the formation of crossmodal associations between visual and taste stimuli. Some pre- and post-arcuate frontal units were reported which were very similar in spatial tuning for the auditory and visual localization (Vaadia et al. 1986). Those units may participate in space localization, independently of the modality of the spatial cue.

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Some PFC units are related to the 'associative significance' of a visual stimulus, e.g., whether or not a specific visual stimulus is associated with a reward (Watanabe 1990). If the convergence of several modalities of inputs in the PFC has functional significance for crossmodal association, then one might expect to find PFC units that code the associative significance of the stimulus independent of its modality. Therefore, in this experiment, different modalities (both visual and auditory) of cues were associated with the juice reward. Unit activity was studied during both the visual and auditory tasks, in order to verify the existence of bimodal units in the PFC and to clarify whether there are PFC units which might be involved in the crossmodal coding of the associative significance of the cue. Post-arcuate premotor (PM) unit activity was also recorded inadvertently from one hemisphere of one monkey.

Consistent with the anatomical and physiological evidence described above, many frontal (PFC and PM) units were responsive to both visual and auditory cues. Some frontal units appeared to code the associative significance of the cue independent of its modality. Most frontal units behaved quite differently when the modality of the cue was changed. Preliminary reports have appeared elsewhere (Watanabe 1989).

## Material and methods

### Subjects

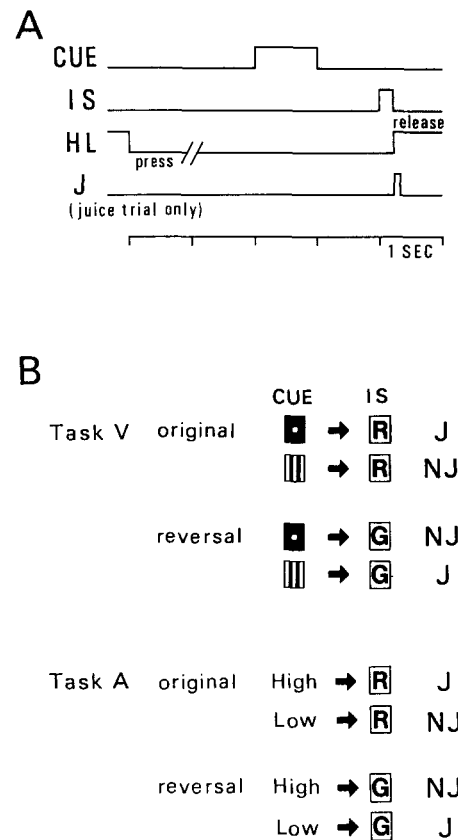
Subjects were the same two monkeys as described in the previous paper (Watanabe 1990).

### Apparatus

Each monkey was seated in a primate chair and faced a panel which contained a central window (8 cm high and 6 cm wide) above a hold lever (HL; 5 cm wide and protruded 5 cm). Visual stimuli were presented within the window. Auditory stimuli were presented by binaural headphones (Pioneer, SE-305) situated on an upper restraining plate of the primate chair. The headphone was very close to, but not attached to each ear of the animal, providing a sound source about 3 cm from each ear.

### Behavioral training

The animal was trained on a lever-release response task (Fig. 1A). In this task the animal first had to depress the hold lever (HL). After a variable time of intertrial interval (ITI; 4.5–6.5 s, Mean = 5.6 s), a visual or auditory cue was presented for 1 s followed by a delay period of 1 s. If the animal continued to depress the HL, a red or green light was presented on the window as an imperative stimulus (IS). When the animal released the HL within 1 s after the IS presentation, the IS light was turned off, with or without a drop of fruit juice (0.2 ml), depending on the previously presented cue. If the animal released the HL before the IS presentation, the animal had to resume the trial from the beginning. If the animal did not release the HL within 1 s after the IS presentation, the IS light was turned off without juice reward and the animal had to resume the trial, which presented the same cue as in the preceding (no release) trial. The animal had to release the HL even on the no juice trial to advance to



**Fig. 1.** A Sequence and timing of events in the lever-release response task. Abbreviations; IS, Imperative Stimulus; HL, Hold Lever, J, Juice. B Cue and IS presented for both original and reversal situations on Task V and Task A. "R" indicates red light and "G" indicates green light. "J" indicates juice delivery while "NJ" indicates no juice delivery

the next trial. Juice (J) and no juice (NJ) trials appeared in a predetermined semi-random sequence.

The animal was trained on both *original* and *reversal* tasks. On the original task, a red light was used as an IS and a circle pattern (visual) or high tone (auditory; 1500 HZ pure tone, 85 dB(A) at the ear level) indicated that juice delivery would follow an adequate release response whereas stripes (visual) or low tone (auditory; 10 HZ pulse train, 60 dB(A) at the ear level) indicated no juice delivery even after the adequate release response. On the reversal task, a green IS was used and stripes or low tone indicated juice delivery whereas a circle or high tone indicated no juice delivery (Fig. 1B). The cue did not indicate the response the animal should perform ("behavioral significance") since the animal had to perform the release response on both J and NJ trials; instead the cue indicated whether juice would be given or not to the release response and thus was expected to gain "associative significance" for the juice delivery. In other words, the lever-release response task coincided with a differential classical conditioning procedure, in which the cue was a CS and juice was the UCS.

The animal was first trained on the original task (red IS) and then on the reversal task (green IS). Then blocks of 50 trials in original and reversal tasks were presented alternately during about 2500 trials of daily training. One monkey was first trained on the visual task (Task V) and then on the auditory task (Task A) while the other monkey was trained in the opposite order. It took 1 to 2 months for the animal to be well trained (achieving significant differentiation in reaction time between J and NJ trials) on Task V and 3 to 4 months on Task A.

The experiment was controlled by a microcomputer (NEC TK-85).

### *Surgery, unit recording, data analysis and histology*

Details were presented in a previous paper (Watanabe 1990). Unit activity was recorded either on Task V or on Task A, and these tasks were interchanged about every 100 trials. Unit recording was done in the principalis, arcuate and inferior convexity areas of the PFC, and some post-arcuate PM units were also recorded inadvertently (see Fig. 10 and its legend). Only those units which showed clear changes in firing in relation to the task event(s) were selected, by visual inspection of the inkwriter record, for later off-line analysis. A search of units was done more intensively in the vicinity of those units which showed clear cue-related activity changes. Thus, there is a sampling bias in the present experiment.

When a unit was found which showed clear cue-related activity changes on either task, it was examined on both original and reversal situations of both modalities of tasks, to clarify the characteristics of its cue-related activity. When a cue-related unit was found which showed a different kind of or a different magnitude of activity changes between Task V and Task A, it was further examined by simultaneously presenting visual and auditory cues which had the same associative significance.

## Results

### *Behavioral data*

Reaction time (RT) of both animals on visual (Task V) and auditory (Task A) tasks is presented in Table 1. RT was significantly shorter on J trials than on NJ trials on both tasks. Furthermore, RT was significantly longer on Task A than on Task V for both J and NJ trials.

### *Cue-related unit activity*

A total of 316 PFC and 123 PM units showed changes in firing rate in relation to one or more of the events of Task V and/or Task A. Unit activity observed on Task V was presented separately in a previous paper (Watanabe 1990). A total of 339 task-related units obtained on Task A were classified depending on the period when the activity changes were observed; (1) cue (and/or delay) periods, (2) response period and (3) post-trial period. Classification of task-related units on Task A is presented in Table 2 as well as the classification of those on Task V for the sake of comparison. Since the main aim of the present study was to examine bimodal responsiveness of the frontal units, this paper focuses on units with cue-related activity, that is changes in activity occurring just after the presentation of the visual and/or auditory cues. The database consists of 289 frontal units that showed cue-related activity on at least one task and were examined on both original and reversal situations of both modalities of tasks, with 136 (47.0%) having only visual cue activity, 13 (4.5%) having only auditory cue activity and 140 (48.5%) having both visual and auditory cue activity.

Among the 289 cue-related units, this paper more specifically focuses on 175 units which showed *differential* activity; i.e., which responded to the two cues of Task V or

**Table 1.** Reaction time of both animals on the visual (Task V) and auditory (Task A) tasks (in ms, 108 trials each)

<i>Monkey no 1</i>			
<i>Task V</i>	original	J	200.1 (SD = 73.8)
		NJ	372.5 (SD = 112.8)
	reversal	J	191.1 (SD = 75.6)
		NJ	387.0 (SD = 106.2)
<i>Task A</i>	original	J	292.4 (SD = 90.3)
		NJ	426.5 (SD = 129.4)
	reversal	J	291.5 (SD = 63.3)
		NJ	422.4 (SD = 99.0)
<i>Monkey no 2</i>			
<i>Task V</i>	original	J	234.6 (SD = 85.6)
		NJ	405.1 (SD = 124.4)
	reversal	J	223.8 (SD = 86.9)
		NJ	432.9 (SD = 130.6)
<i>Task A</i>	original	J	312.2 (SD = 75.9)
		NJ	496.7 (SD = 142.2)
	reversal	J	328.0 (SD = 82.9)
		NJ	498.7 (SD = 130.5)

**Table 2.** Classification of units which showed task-related activity changes on Task A and on Task V. Numbers in parentheses indicate the number of units which showed *differential* activity in relation to the difference of the cue and/or the response. Note that the same unit is counted twice as Task V-related and Task A-related when it showed changes in activity on both tasks

	(Number)	
	<i>Task A</i>	<i>Task V</i>
Cue-related only	41 (29)	57 (48)
Response (R)-related only	142 (23)	67 (14)
Post trial (PT)-related only	20 (12)	31 (25)
cue + R related	95 (51)	214 (115)
cue + PT related	13 (11)	22 (19)
R + PT related	17 (17)	12 (12)
cue + R + PT related	11 ( 8)	20 (20)
Total	339 (151)	423 (253)

Task A in different magnitude of firing, since such units may play more important roles in coding the cue than those units which do not show differential activity (76 of 136 visual units and 6 of 13 auditory units were 'differential' and of the 140 bimodal units, 18 had differential visual responses, 7 had differential auditory responses, and 68 were differentially responsive in both modalities). Cue-related differential unit activity was divided into three types; *Type P*, *Type M* and *Type MP*. *Type P* activity was related to the cue's physical properties – i.e., whether the cue was a high tone or low tone (whether the cue was a circle or stripes in the case of Task V) irrespective of whether the task situation was original or reversal, *Type M* activity to the cue's meaning – i.e., whether the cue indicated juice delivery or not independent of its physical properties (and thus is considered to be related to coding the associative significance of the cue) and *Type MP*

activity to both aspects of the cue. On the other hand, when a unit did not respond to the cue, it was classified as "Type 0 (zero)" and when it responded to the cue but did not show *differential* activity in relation to the different cues, it was classified as "Type N". Table 3 shows the numbers of cue-related units grouped according to the type of activity observed on each (visual vs. auditory) task. Hereafter, each group of units will be called *VX-AY* units where X indicates the type of activity on Task V and Y indicates the type of activity on Task A.

One hundred and fourteen of the 289 cue-related units did not show differential activity and showed their non-differential (Type N) activity changes either on one modality of task (Task V:  $n=60$ ; Task A:  $n=7$ ) or on both modalities of tasks ( $n=47$ ). These Type N activities may be related to coding that a cue has been presented, irrespective of its nature.

Among 175 differential units, 107 showed their cue-related differential activity only on Task V ( $n=94$ ) or only on Task A ( $n=13$ ). Figure 2 shows an example of a unit which showed cue-related differential activity only on Task V. This *VM-AN* unit observed in the principalis area showed a higher rate of firing to the J cue than to the NJ cue independent of cue's physical properties on Task V but showed nondifferential activation to the two tones on Task A. Thus, this unit is considered to be involved in coding the associative significance of the visual cue. Figure 3 shows an example of a unit which showed cue-related differential activity only on Task A. This arcuate *VO-AM* unit showed a higher rate of firing to the J cue than to the NJ cue on Task A whereas there was almost no change in activity to either J or NJ cues on Task V, and thus this unit is considered to be involved in coding the associative significance of the auditory cue only. In this unit, changes in firing before the release-response were observed only on J trials and the magnitude of the pre-response activity changes was larger than that observed after the J cue presentation on Task A (the pre-response

activity changes are considered to be related to anticipation of the reward). Furthermore, pre-cue base-line activity was greater and changes in activity during the delay preceding the release-response on J trials appeared much earlier on Task A than on Task V. Such differences in pre-cue base-line activity and/or in pre-response activity between Task V and Task A were observed in 52 frontal units.

In 68 of the 175 differential units, cue-related differential activity was observed on both Task V and Task A. And 50 of these 68 bimodal differential units showed Type M activity on both Task V and Task A (*VM-AM* units). An example of this type of unit is shown in Fig. 4. This PM unit was activated when the visual cue indicated forthcoming juice delivery during both the cue and the following delay periods, and did not show noticeable change in activity to the NJ cue on Task V. On Task A, this unit also showed a higher rate of firing to the J cue than to the NJ cue. Thus, the activity of this unit was not dependent on the physical properties of the stimulus (i.e., whether it was a circle or stripes, or whether it was a high tone or low tone) but was considered to be related to the associative significance of both modalities of cues. Among 50 units of this type, 29 units showed a similar level of base-line activity and similar magnitude of cue-related changes in activity on both tasks as illustrated by the unit in Fig. 4. Among them, ten (five of them PM) units showed set-related activity changes (Weinrich and Wise 1982), with sustained activity changes from the cue presentation to the lever-release response.

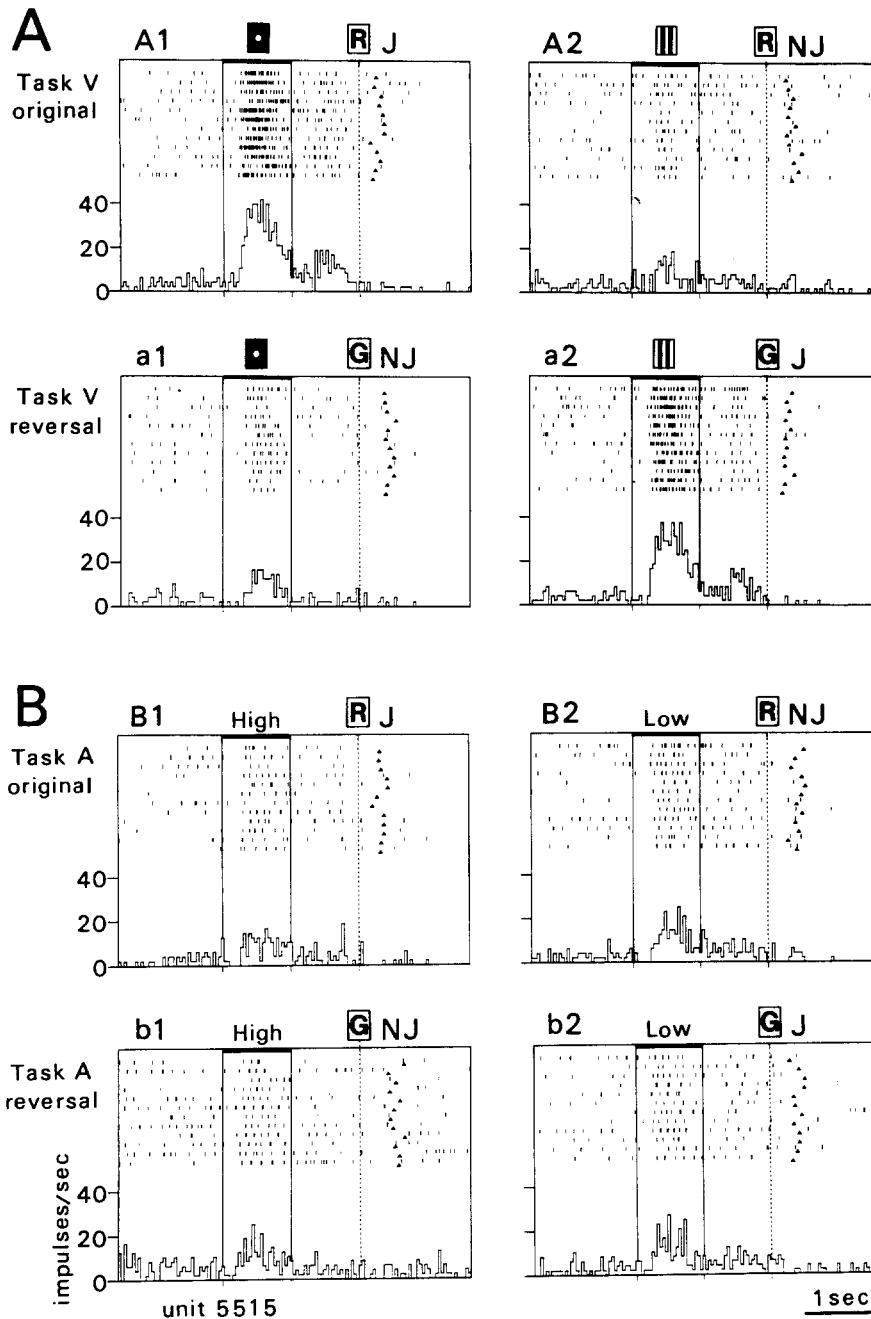
On the other hand in the remaining 21 of the 50 *VM-AM* units, base-line activity, the magnitude of cue-related changes in activity and/or latency of cue-related activity changes were significantly different between the two kinds of tasks as illustrated by the unit in Fig. 5. This PM unit showed a higher rate of firing on J trials than on NJ trials after the cue presentation on both Task V and Task A. However, pre-cue base-line activity level and the magnitude of pre-response activity changes were different between the two modalities. Furthermore, cue-related activity changes on J trials appeared much earlier on Task A than on Task V, and there were two peaks in the cue-related activity on Task A.

No unit was found which showed Type P activity on both modalities of tasks whereas 4 of the 68 bimodal differential units showed Type MP activity on both tasks (*VMP-AMP* units). In all 4 units, the characteristics of the differential activity were different between the two tasks as is the case for the unit in Fig. 6. This principalis unit showed the highest rate of firing after the striped cue presentation in the reversal situation (a2) and the second highest rate of firing after the circle cue presentation in the original situation (A1) showing similar changes in firing in the other situations (A2 and a1) on Task V (*Type MP*). On Task A, this unit showed a higher and similar rate of firing to high and low tones in the original situation (B1 and B2) and showed a decrease in firing rate after the high tone presentation in the reversal situation (b1) (*Type MP*).

In 14 of the 68 bimodal differential units, the type of cue-related differential activity was different between the two kinds of tasks (4 *VM-AP* units; 1 *VMP-AP* unit; 5

**Table 3.** Numbers of cue-related units grouped according to the type of activity observed on each of visual and auditory task. In this table, VO (AO), VN (AN), VP (AP), VM (AM), VMP (AMP) indicate respectively, no activity change, nondifferential activity change, Type P, Type M and Type MP activity change observed on Task V (Task A). For example, the number which is asterisked indicates the number of *VM-AP* units (which showed Type M activity on Task V and Type P activity on Task A) (An example is shown in Fig. 7). It should be noted that the proportion of *VO-AN*, *VN-AO* and *VN-AN* units may be underestimated since unit activity was recorded more intensively in the vicinity of the area where cue-related differential units were observed

(Type on auditory task)	(Type on visual task)					Sum
	VO	VN	VP	VM	VMP	
AO	/	60	9	38	29	136
AN	7	47	1	11	6	72
AP	3	2	0	4*	1	10
AM	3	3	0	50	5	61
AMP	0	2	1	3	4	10
Sum	13	114	11	106	45	289



**Fig. 2A, B.** An example of the activity of a *VM-AN* unit recorded in the principalis area on Task V (**A**) and on Task A (**B**). For **A** and **B**, the upper two rasters and histogram displays are for trials in the original situation (red IS) and the lower two displays are for trials in the reversal situation (green IS) (The data on the first and the second trials after the reversal of the associative significance of the stimulus are omitted). Left side displays are for trials when a circle (**A**) or high tone (**B**) was presented as a cue and right side displays are for trials when stripes (**A**) or low tone (**B**) was presented as a cue. A1 and B1 indicates the activity on the original J trials, A2 and B2, on the original NJ trials, a1 and b1, on the reversal NJ trials and a2 and b2 on the reversal J trials. For each raster and histogram display, the second vertical line from the left indicates the time of the cue presentation and the third line indicates the end of the cue presentation (and the beginning of the delay period). A horizontal black bar indicates the period when a cue was being presented (1 s), and above the bar is shown the cue which was actually presented ('high' indicates high tone and 'low' indicates low tone in **B**). A vertical dotted line indicates the time of the IS (imperative stimulus) presentation and above that line is shown the color of the stimulus which was actually presented as an IS (R indicates red and G indicates green). J or NJ mark above each display indicates whether juice was given (J) or not (NJ) to the animal's release response of the lever. In raster displays, each row indicates the unit activity for 5.12 s and each pulse indicates the occurrence of spike discharge(s) in a 10 ms time bin. Small upward triangles indicate the time of the release response of the lever (and the time of the juice delivery on the J trials). Each histogram indicates the sum of spike discharges shown above in the raster display for 12 trials in 40 ms time bins. In this and the following figures, only the data when the animal responded within 1 s after the IS presentation are presented

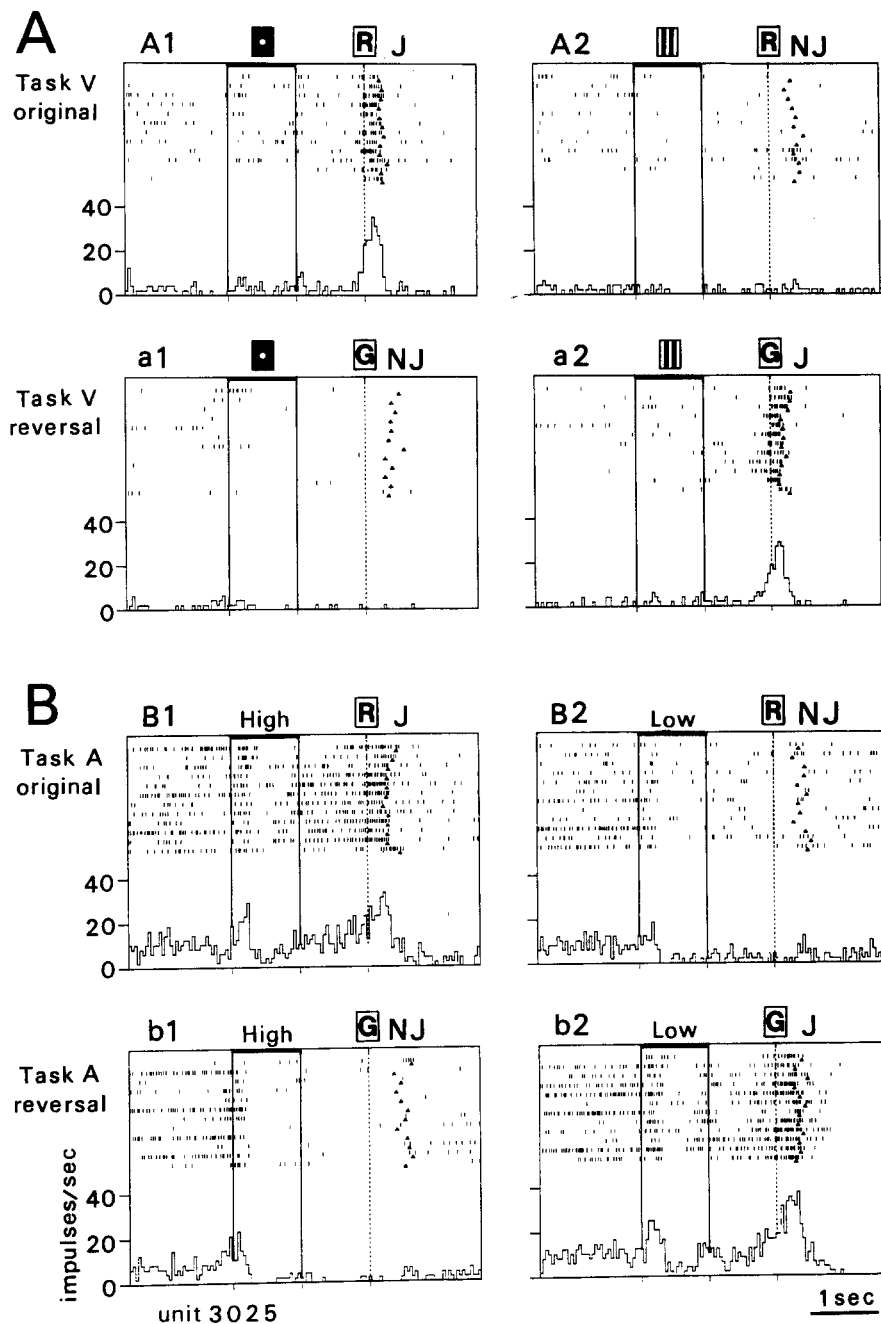
*VMP-AM* units; 1 *VP-AMP* unit; 3 *VM-AMP* units). Figure 7 shows an example of *VM-AP* unit found in the inferior convexity area. This unit showed Type M activity on Task V with a higher rate of firing on NJ trials than on J trials during both the cue and the following delay periods. On the other hand, this unit showed Type P activity on Task A with an activation to the high tone on both original and reversal situations during both the cue and the following delay periods while showing almost no change in activity to the low tone. Thus, this unit is considered to be involved in coding the associative significance of the visual cue and the physical properties of the auditory cue.

Figure 8 shows an example of *VMP-AM* unit found in the arcuate area. On Task V, this unit showed a highest

rate of firing to the circle cue in the reversal situation (a1) and showed the second highest rate of firing to the striped cue in the original situation (A2) showing the least activation to the circle cue in the original situation (A1) (*Type MP*). On Task A, the magnitude of cue-related activity changes was smaller than that on Task V, and this unit showed a higher rate of firing to the NJ cue than to the J cue (*Type M*).

#### *Interaction of visual and auditory stimuli*

The effect of simultaneous presentation of visual and auditory cues which have the same associative significance was examined on 16 cue-related differential units which



**Fig. 3.** An example of the activity of an arcuate VO-AM unit. Conventions are the same as in Fig. 2

showed either a different type of differential activity or a different magnitude of activity changes, between the visual and auditory tasks. They showed either Type M or Type MP activity on Task V and showed Type P, M, MP or nondifferential (Type N) activity on Task A. Figure 9 shows an example. This principalis VM-AP unit showed Type M activity on Task V and showed a higher rate of firing to the NJ cue than to the J cue (Fig. 9A) while this unit showed Type P activity on Task A showing a higher rate of firing to a low tone than to the high tone on both the original and reversal situations (Fig. 9B). When visual and auditory cues were presented simultaneously (Task V + A), this unit showed Type M activity changes (Fig. 9C).

The behavioral RT was not different between Task V and Task V + A. The effect of presentation of the auditory cue was masked in this way by the visual response on all the 16 units examined, with most units showing little difference between the activity changes observed on Task V and those on Task V + A.

#### *Locations of bimodal units*

The distribution of each group of cue-related units in the frontal cortex is shown in Table 4. Table 5 shows the proportion of bimodal units among cue-related (both

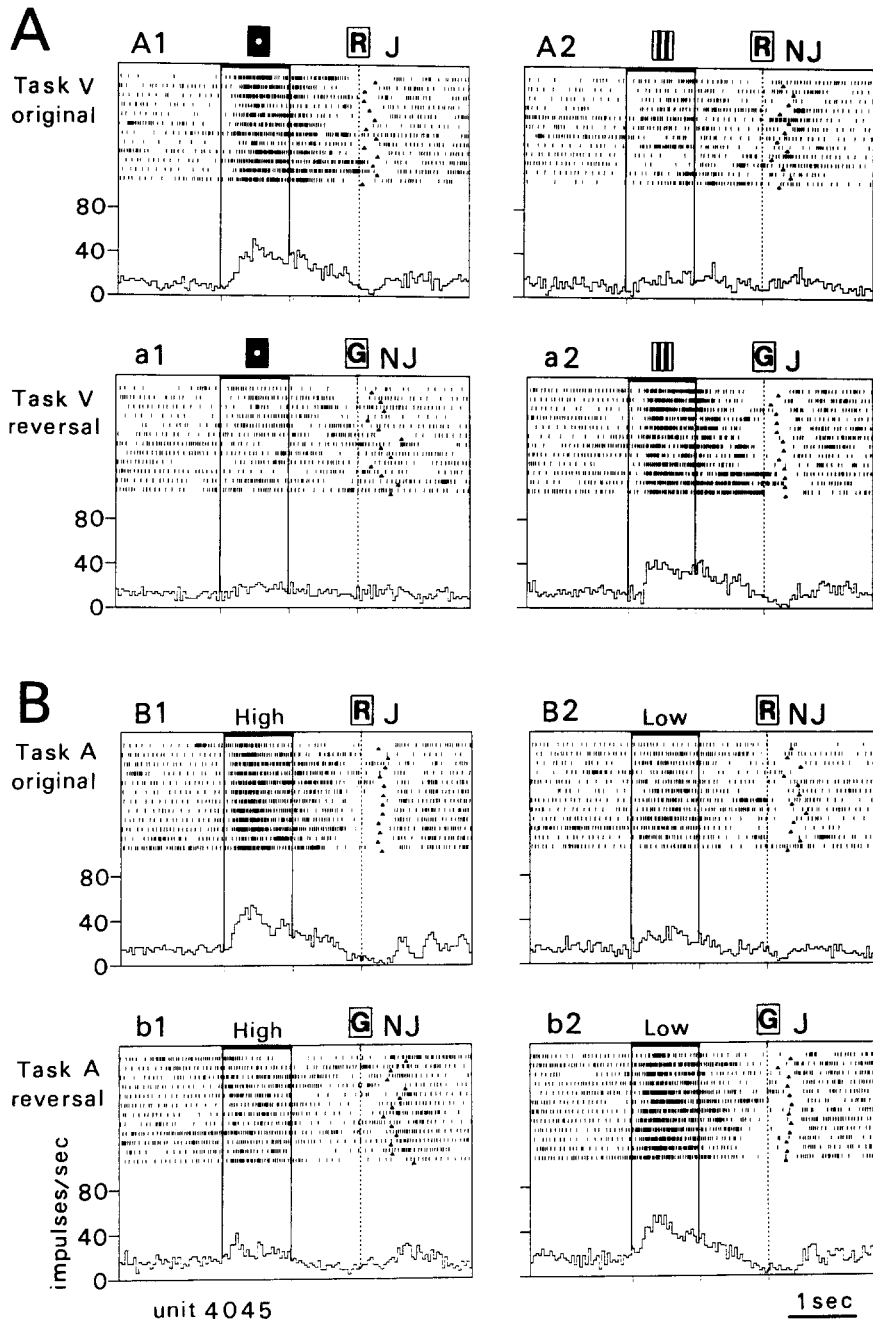
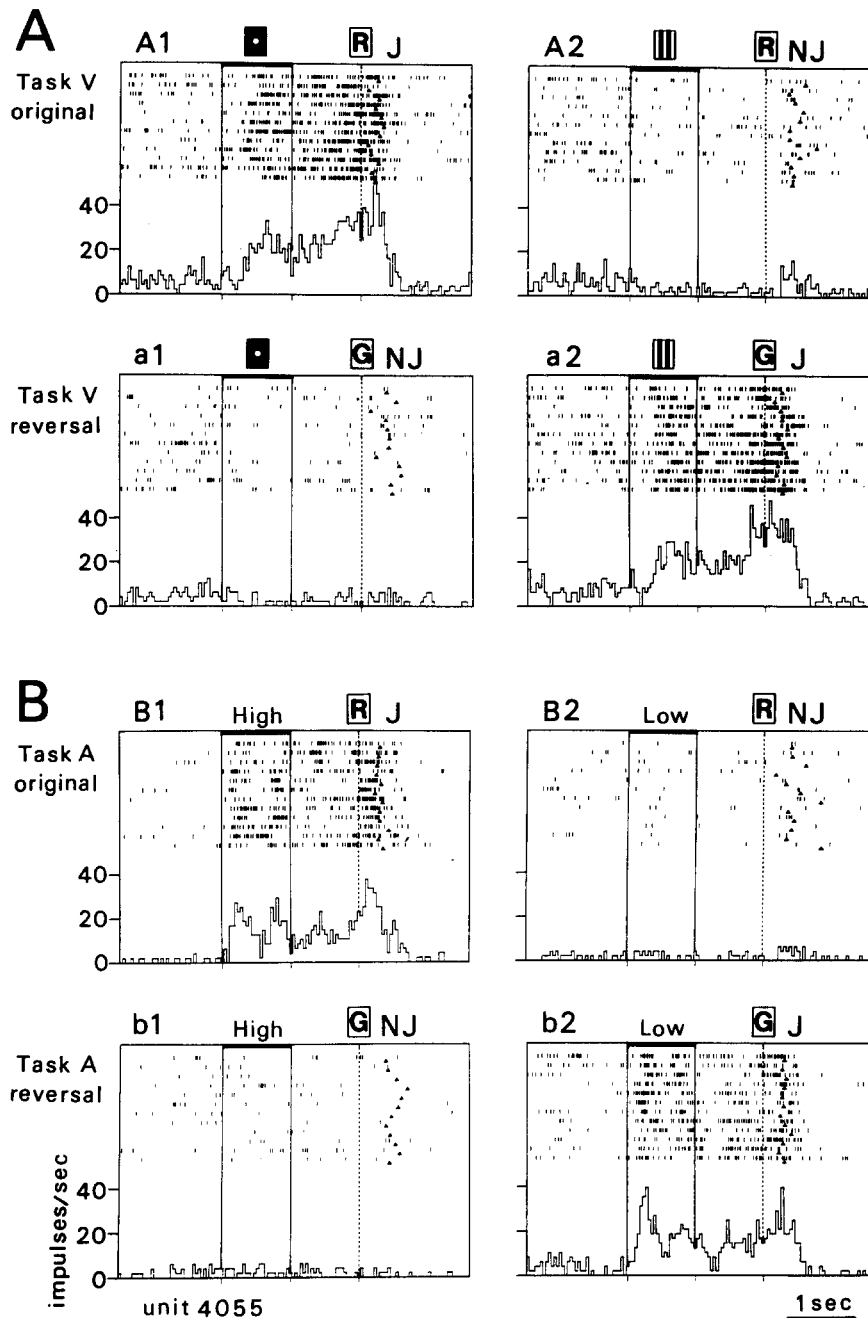


Fig. 4. An example of the activity of a *VM-AM* unit recorded in the PM area. Conventions are the same as in Fig. 2

differential and nondifferential) units in the 4 subareas of the frontal cortex. Locations of penetrations of bimodal units are presented in Fig. 10. It should be noted that the description concerning the distribution and proportion of each type of bimodal units is only tentative because of the sampling bias in unit recording; in this experiment, (1) only those units were recorded which showed clear task-related activity changes; (2) unit recording was done more intensively in the vicinity of those units which showed *clear* cue-related activity changes; (3) PM units were recorded only from a restricted (lower part of the post-arcuate) area of one hemisphere of one monkey whose cylinder was situated more posteriorly than had been intended. How-

ever, since all the cue-related differential units found were equally examined, the proportion of each type of units among them may be less biased.

The proportion of bimodal (both differential and nondifferential) units among cue-related units in the principalis (PS) and inferior convexity (IC) areas was about 35% and was not different between these two areas whereas the proportion of bimodal *differential* units was larger (about 65%) in the arcuate (AS) area. In the PM area, the proportion of bimodal (both differential and nondifferential) units was the largest. Table 4 indicates that the numbers of *VM-AN* units and *VM-AM* units increase from anterior to posterior in the frontal cortex. Visually



**Fig. 5.** Another example of the activity of a *VM-AM* unit recorded in the PM area. Conventions are the same as in Fig. 2

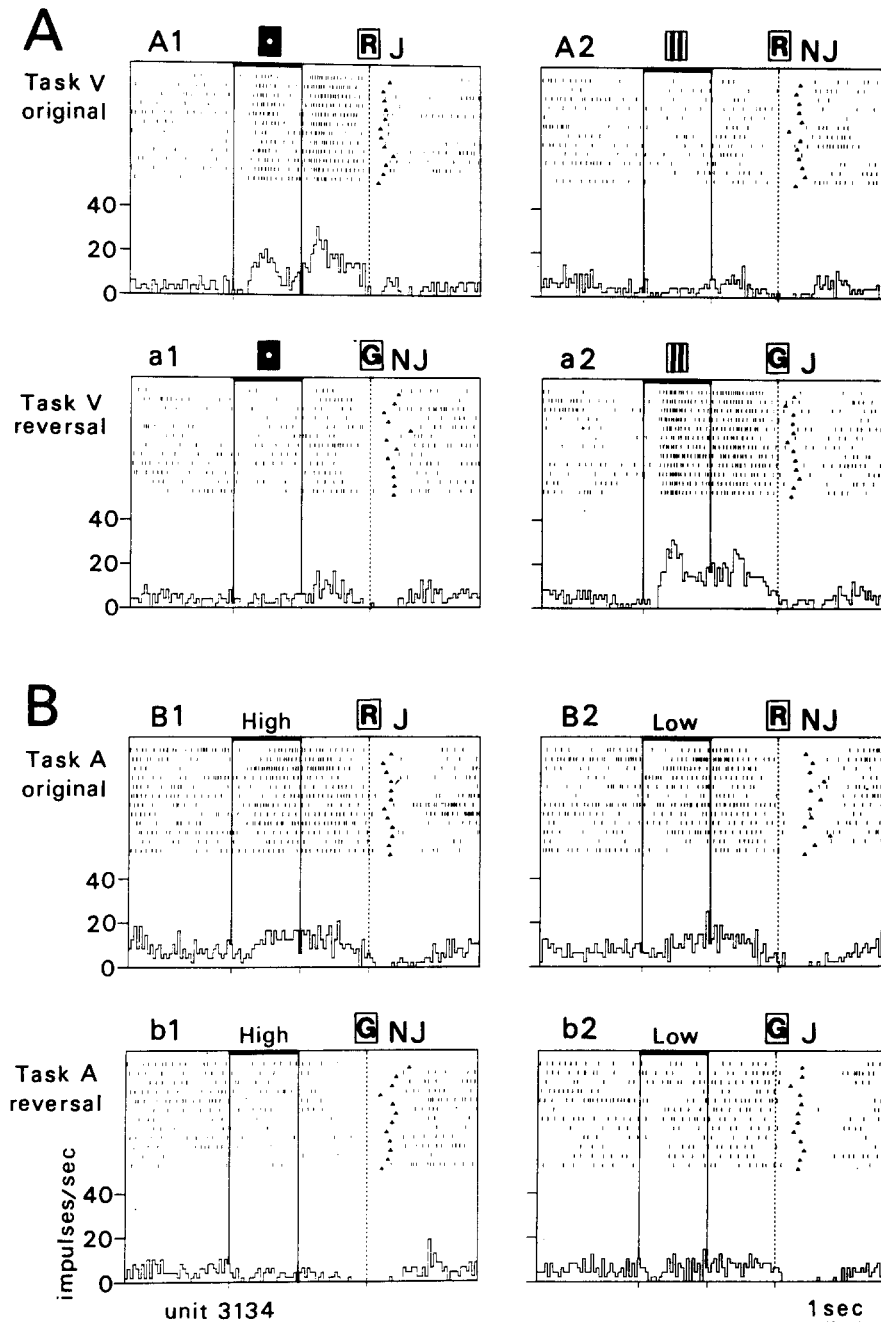
responsive Type P units were found almost exclusively in the PS and IC areas while most of auditory responsive Type P units were found in the IC and AS areas. Concerning Type MP activity, *VMP-AO* units were found predominantly in the PS and IC areas and *VMP-AN* units were found only in the AS area (visual) while *VN-AMP* units were found only in the IC and AS areas (auditory). Units which showed Type MP activity on both tasks (*VMP-AMP* units) were found only in the IC and AS areas. Units which showed different types of differential activity between the two modalities of tasks were mainly found along the arcuate sulcus and in the IC area (Fig. 10E).

## Discussion

### *Proportion of bimodal units in the frontal cortex*

The first aim of the present experiment was to verify the convergence of visual and auditory inputs in single units of the frontal (PFC and PM) cortex. Many frontal units were found to be responsive to both visual and auditory cues. The proportion of bimodal units among stimulus-related units in the frontal cortex differs among different studies; from zero (Azuma and Suzuki 1984) to 73% (Vaadia et al. 1986). Such differences may be caused by differences in the animal's preparation, in the task situation, in the area





**Fig. 6.** An example of the activity of a principalis VMP-AMP unit. Conventions are the same as in Fig. 2

explored or in the stimuli presented to the animal. The relatively lower proportion of auditory responsive units in the present experiment may be caused by the employment of a pure tone as a cue on Task A. Such stimuli do not activate as many frontal units as do natural vocalizations (Wollberg and Sela 1980), and they may not be as discriminative as the visual pattern stimuli used in the present experiment.

Each group of cue-related units were unevenly distributed in the 4 frontal subareas (Tables 4 and 5). It appears that there is a gradient in the proportion of bimodal units from anterior to posterior within the frontal

cortex, although the sampling bias in unit recording must be taken into consideration.

#### *Cue-related differential activity on visual and auditory tasks*

No Type P unit was found in the PM area in either Task V or Task A. The results are in accordance with those of a previous study using a Go/No-go discrimination task (Watanabe 1986) and suggest that the PM area is not involved in coding the physical properties of the cue. No VP-AP unit was found in the present experiment. This

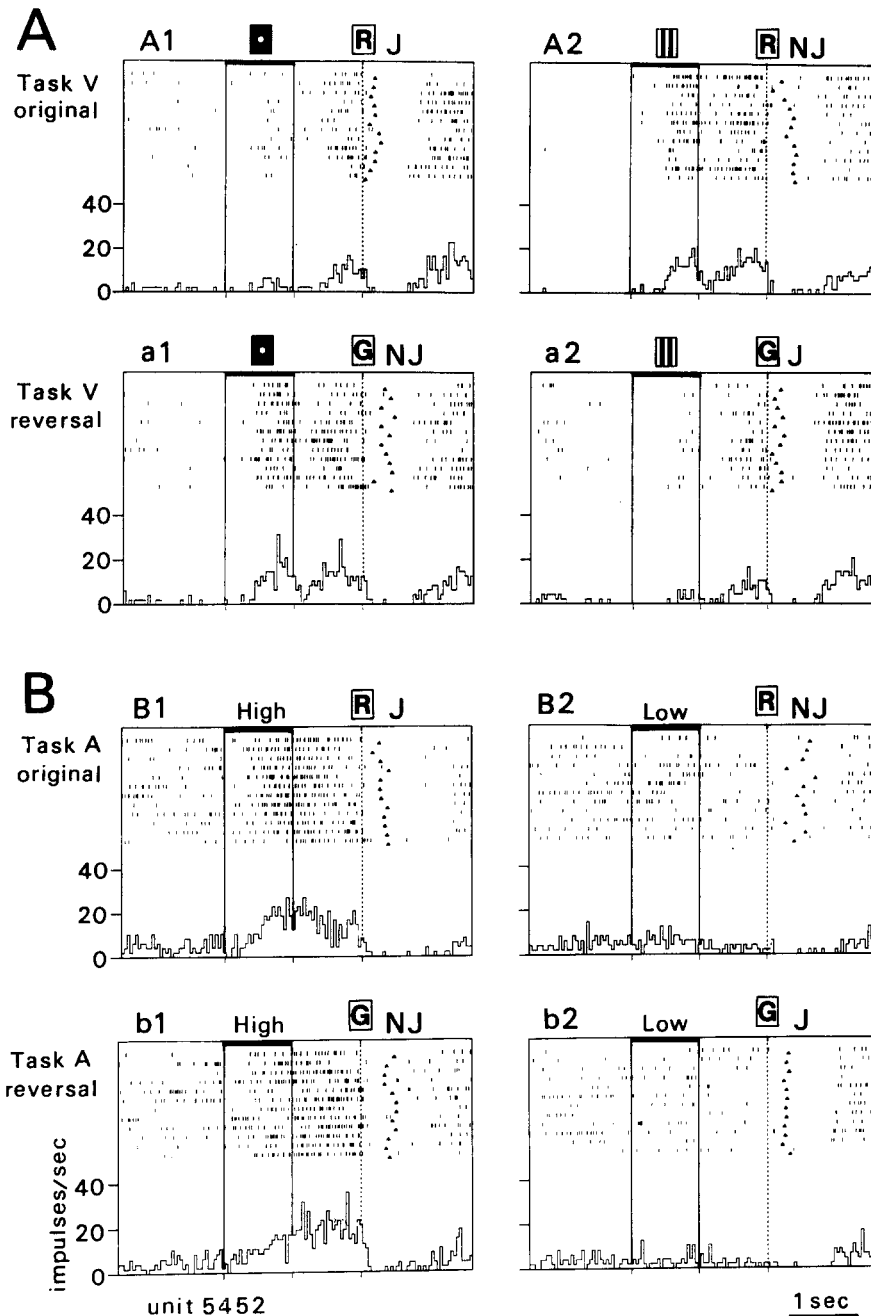


Fig. 7. An example of the activity of a *VM-AP* unit recorded in the IC area. Conventions are the same as in Fig. 2

may indicate that there may be no *bimodal* frontal units involved in coding the physical properties of both modalities of stimuli. However, if I had used visual and auditory stimuli different from those used in the present experiment, with some common properties (intensity or interruption-frequency), there is a possibility that *VP-AP* units might be found in the frontal cortex.

It has been suggested that Type P units receive information concerning the physical properties of the cue from the posterior association cortices. Type MP units may get information from Type P units and may be involved in the intermediate stage of information processing for extracting the meaning of the cue (Watanabe

1986), possibly getting information from the limbic system. Judging from the distribution of each group of units (Table 4), it seems that the initial information processing for extracting the meaning of the stimulus (Type P and Type MP activity) is done in modality specific regions, mainly in the PS and IC areas for the visual cue and almost exclusively in the IC and AS areas for the auditory cue.

Units which showed Type M activity only on Task V were found in the three PFC subareas and PM area while those which showed Type M activity only on Task A were found exclusively in AS and PM areas. The number of *VM-AM* units, whose activity reflected the meaning of both modalities of cues, became larger from anterior to

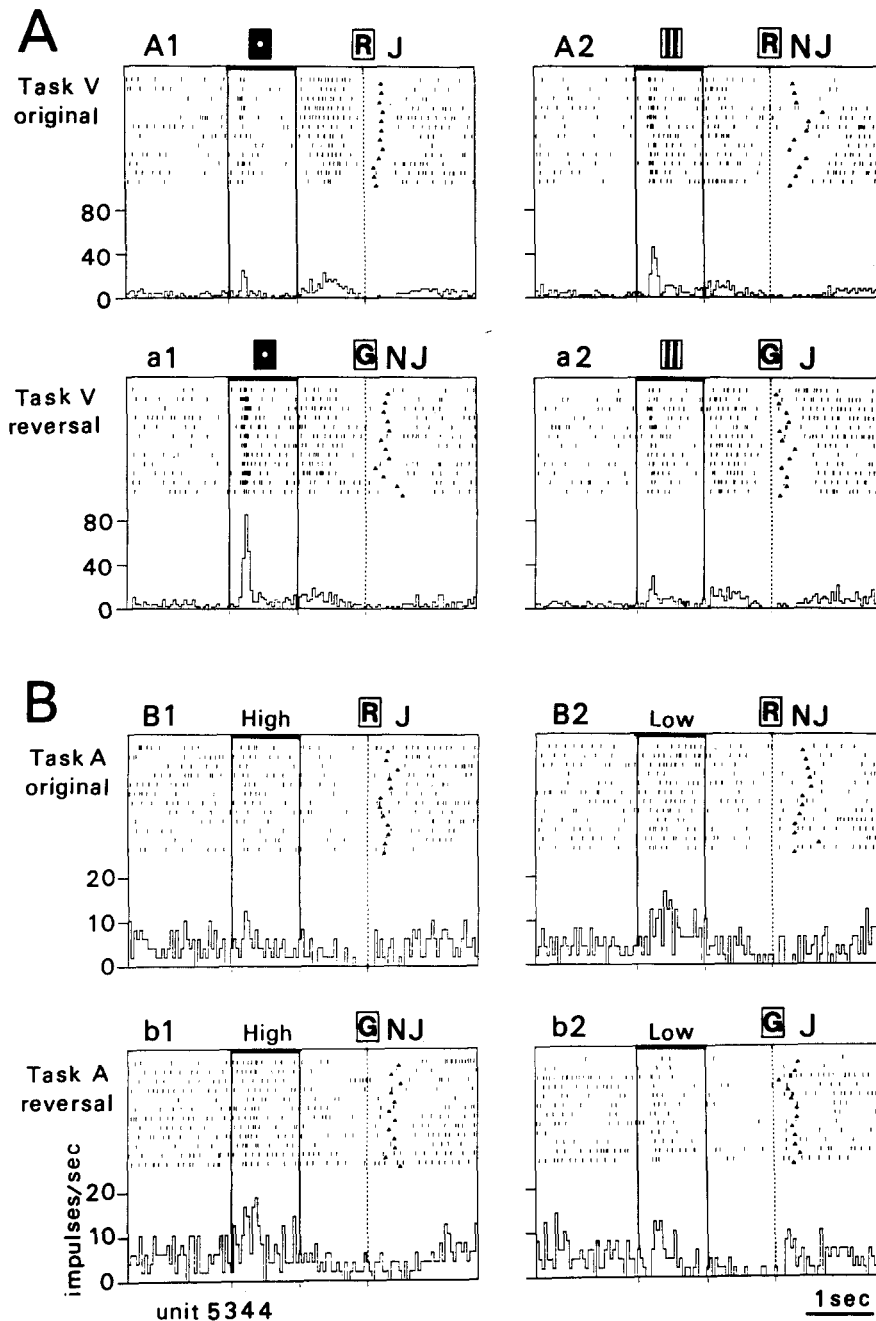


Fig. 8. An example of the activity of an arcuate VMP-AM unit. Conventions are the same as in Fig. 2

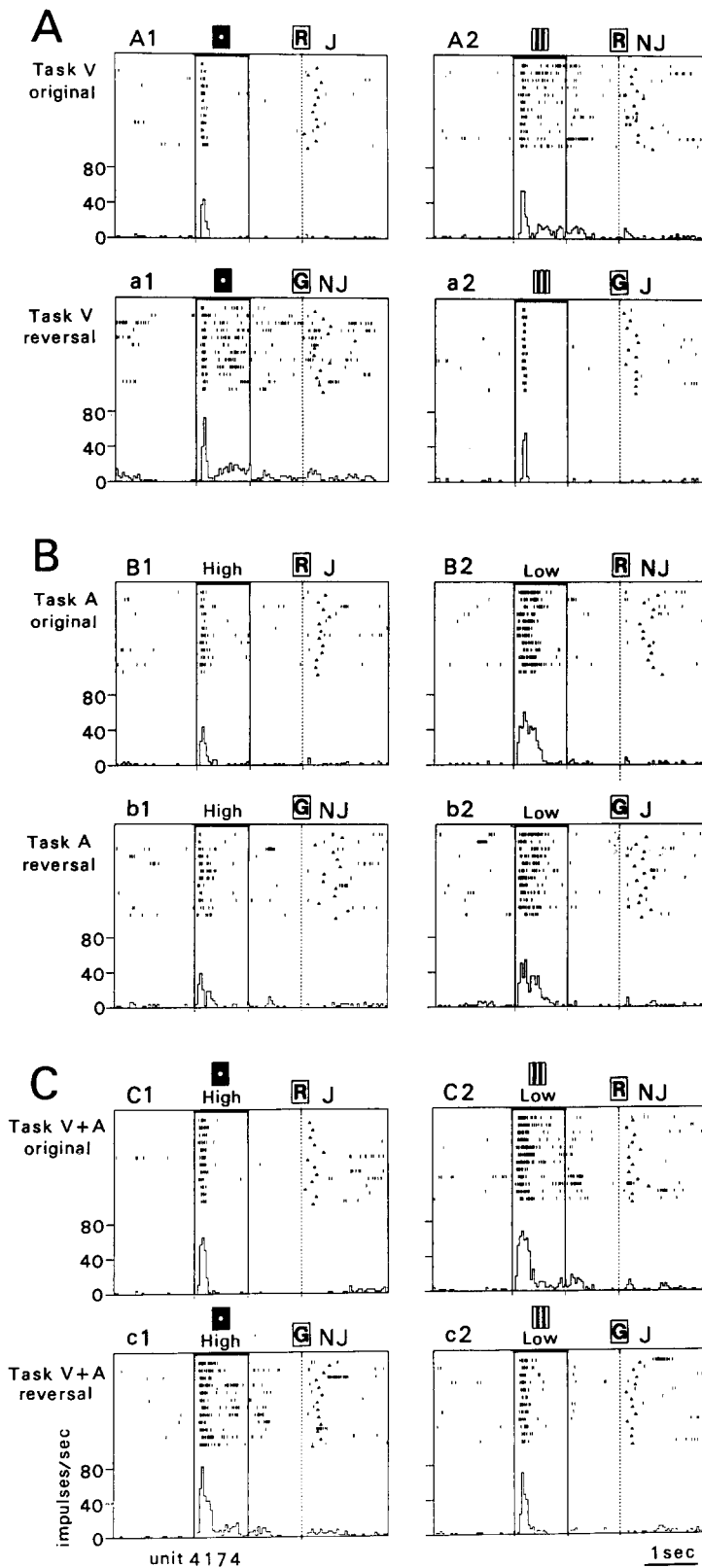
posterior in the frontal cortex. The distribution of each type of cue-related differential units suggests a flow of information from anterior to posterior regions of the frontal cortex for extracting the meaning of the stimulus.

#### Crossmodal coding of the associative significance of the cue

About 28.6% ( $n=50$ ) of cue-related differential units (VM-AM units) coded the meaning of the cue across visual and auditory modalities. As is shown in Tables 4 and 5, 22 of them (44%) were found in the PM area. A possible explanation of the high incidence of VM-AM

units in PM cortex might be that their activity is associated with preparatory consummatory movements made in anticipation of the juice reward (Rizzolatti et al. 1981). However it should be noted that this would itself presuppose learning of the significance of the cues; and that the differential activity was as often related to NJ as to J trials (see Watanabe 1990). Furthermore, some units showed Type M activity for only the visual or the auditory task, ruling out a possible motor-preparatory role.

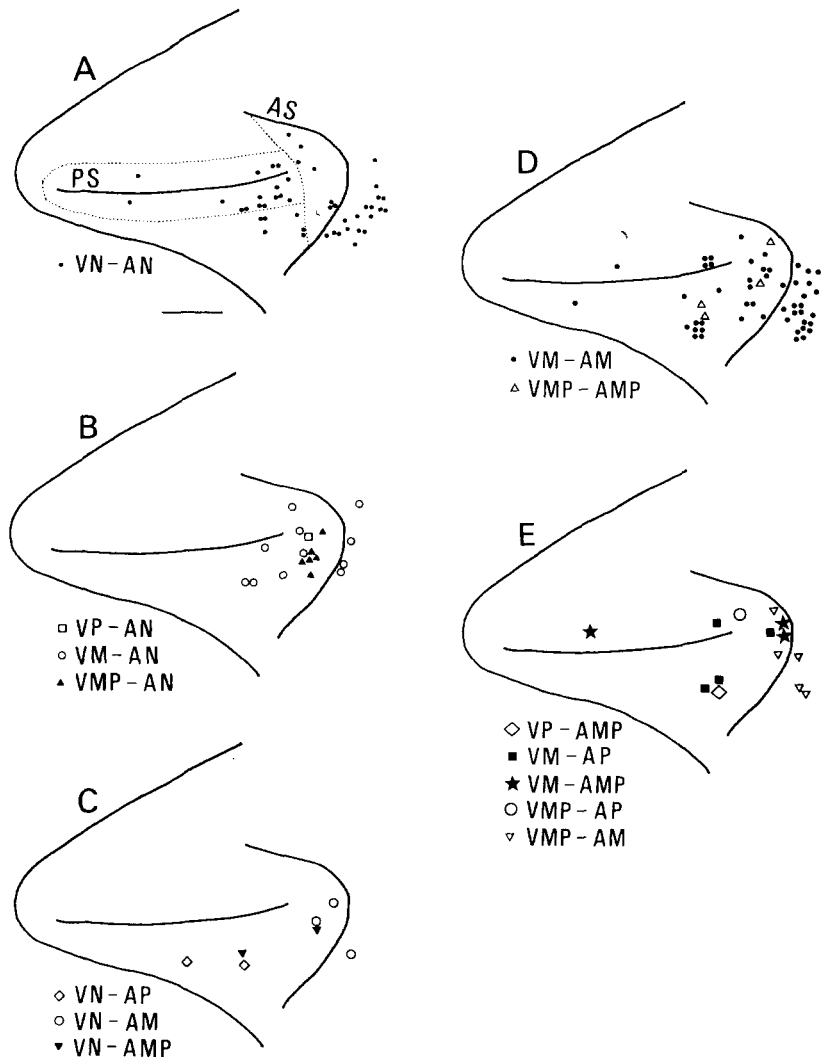
Among the 289 cue-related units examined, 106 (36.7%) had VM properties (showed Type M activity on Task V) while 61 (21.1%) had AM properties (showed Type M activity on Task A). Thus, it could be estimated



**Fig. 9A–C.** An example of the activity of a *VM-AP* unit recorded in the principalis area on Task V (A), on Task A (B) and on Task V+A (C). In C the activity of the unit is shown when visual and auditory cues which had the same associative significance were simultaneously presented. On each black horizontal bar which indicates the cue period, are shown the two kinds of stimuli which were actually presented. The upper two displays are for original trials (C1 and C2) and the lower displays are for reversal trials (c1 and c2). Other conventions are the same as in Fig. 2

that one could expect to find *VM-AM* units, by chance, with the probability of 7.7% ( $0.367 \times 0.211 = 0.077$ ). The observed proportion of *VM-AM* units ( $n = 50$ ) was 17.3%, which is much higher than expected by chance. This may

indicate that the frontal cortex plays important roles in the *crossmodal* coding of the associative significance of the stimulus. However, even among *VM-AM* units, 42% ( $n = 21$ ) showed pre-cue base-line activity, and/or stimulus



**Fig. 10A–E.** Locations of penetrations of bimodal units. **A** Units which showed nondifferential activity changes to both visual and auditory cues (*VN-AN* units); **B** Units which showed cue-related differential activity on Task V and showed nondifferential activity changes on Task A (*VP-AN* unit, *VM-AN* units and *VMP-AN* units); **C** Units which showed cue-related differential activity on Task A and showed nondifferential activity changes on Task V (*VN-AP* units, *VN-AM* units and *VN-AMP* units); **D** Units which showed the same type of cue-related differential activity on both Task V and Task A (*VM-AM* units and *VMP-AMP* units); **E** Units which showed different type of cue-related differential activity between Task V and Task A (*VP-AMP* unit, *VM-AP* units, *VM-AMP* units, *VMP-AP* unit and *VMP-AM* units). Dotted line in **A** indicates approximate boundary of the principalis, arcuate and inferior convexity areas, following the study by Rosenkilde (1979). The inferior convexity area begins at an imaginary line ca. 4 mm below and parallel to the principal sulcus, and extends around the edge of the hemisphere to the lateral orbital sulcus (which does not appear on this figure), posteriorly being bounded by the arcuate sulcus (AS) and the lateral fissure (not shown in this figure). PM area is situated posterior to the arcuate sulcus (AS) and anterior to the primary motor (M1) area (which does not appear on this figure). Scale bar in **A** indicates 5 mm. Abbreviations: PS, principal sulcus; AS, arcuate sulcus

triggered response that differed between visual and auditory tasks, as in Fig. 5. In these units, coding of the meaning of the stimulus may be done in different ways between visual and auditory tasks. Alternatively, they may not be actively involved in the *crossmodal* coding of the meaning of the stimulus, but may simply get information concerning the meaning of the stimulus from modality-specific Type M units. On the other hand, the remaining 58% of *VM-AM* units (which constitute 9.8% of cue-related units) ( $n=29$ ) with similar cue-related activity changes between Task V and Task A, seem more likely to be involved in the *crossmodal* coding of the associative significance of the stimulus.

#### *Convergence of different modalities of sensory inputs in the frontal cortex*

Chavis and Pandya (1976) have shown that the lower part of the AS area (area 45 of Walker (1940)) and a part of the IC area (lower part of area 46 of Walker (1940)) receive convergent inputs from the sensory (visual and auditory) association areas. In the present experiment, bimodal units

were found not only in the IC and AS areas but also in the PS and PM areas where the convergence of visual and auditory inputs has not been previously reported. Polymodal responsiveness of frontal units is considered to be caused not only by the direct input from the posterior sensory association cortices, but also by the input from the STS which is itself polysensory, and by inputs from several areas of the limbic system (Amaral and Price 1984; Jacobson and Trojanowski 1977; Goldman-Rakic et al. 1984) which also receive polysensory inputs. Furthermore, interconnections within the PFC (Jacobson and Trojanowski 1977; Pandya and Barnes 1987) and between the PFC and PM (Jones and Powell 1970; Pandya and Kuypers 1969) may also play important roles in the bimodal responsiveness of frontal units.

#### *Characteristics of the frontal unit activity*

In the present experiment, 72% of cue-related differential units behaved in completely different ways between the two modalities of tasks. Ito (1982) also reported PFC and PM units which responded in different ways (e.g., increase

**Table 4.** Distribution of cue-related units in the four frontal subareas. In this table, PS indicates principalis area, IC indicates inferior convexity area, AS indicates arcuate area and PM indicates pre-motor area

(Type)	(Area)				Sum
	PS	IC	AS	PM	
VO-AN	0	0	2	5	7
VO-AP	0	2	1	0	3
VO-AM	0	0	2	1	3
VO-AMP					0
VN-AO	29	10	11	10	60
VN-AN	16	6	7	18	47
VN-AP	0	2	0	0	2
VN-AM	0	0	2	1	3
VN-AMP	0	1	1	0	2
VP-AO	3	6	0	0	9
VP-AN	0	0	1	0	1
VP-AP					0
VP-AM					0
VP-AMP	0	1	0	0	1
VM-AO	10	15	12	1	38
VM-AN	1	3	3	4	11
VM-AP	1	2	1	0	4
VM-AM	8	8	12	22	50
VM-AMP	1	0	2	0	3
VMP-AO	10	13	3	3	29
VMP-AN	0	0	6	0	6
VMP-AP	0	0	1	0	1
VMP-AM	0	0	2	3	5
VMP-AMP	0	2	2	0	4
(Sum)	79	71	71	68	289

versus decrease of firing rate) to visual and auditory cues. Quite recently, Vaadia et al. (1989) proposed that PFC units could participate in more than one process since individual units behaved quite differently when the modality of the cue was changed in the spatial localization task. These results indicate that a certain frontal unit could have completely different roles depending on the task situation. It seems that many frontal units have potentialities to play several different kinds of roles, and the same frontal unit can belong to two or more neuronal networks, each of which is related to completely different functional roles.

The PM area of the frontal cortex has been considered to be involved in 'motor planning' (Weinrich et al. 1984) or 'motor organization' (Rizzolatti and Gentilucci 1988). However, from the present study as well as from that on the Go/No-go discrimination task (Watanabe 1986), PM appears to have some cognitive functional roles, which might be related to information processing of a higher order, such as the coding of the meaning of the stimulus.

#### *Associative and behavioral significance and the modality of the cue*

This experiment has shown the existence of bimodal frontal units which show crossmodal or modality specific differential activity in relation to the associative signifi-

**Table 5.** A Numbers of bimodal units in the frontal subareas. "V" indicates visually responsive and "A" indicates auditory responsive

	(Differential)		(Nondifferential)	
	Bimodal	Unimodal	Bimodal	Unimodal
PS	11	$\begin{matrix} \text{V} & 23 \\ \text{A} & 0 \end{matrix}$	16	$\begin{matrix} \text{V} & 29 \\ \text{A} & 0 \end{matrix}$
IC	19	$\begin{matrix} \text{V} & 34 \\ \text{A} & 2 \end{matrix}$	6	$\begin{matrix} \text{V} & 10 \\ \text{A} & 0 \end{matrix}$
AS	33	$\begin{matrix} \text{V} & 15 \\ \text{A} & 3 \end{matrix}$	7	$\begin{matrix} \text{V} & 11 \\ \text{A} & 2 \end{matrix}$
PM	30	$\begin{matrix} \text{V} & 4 \\ \text{A} & 1 \end{matrix}$	18	$\begin{matrix} \text{V} & 10 \\ \text{A} & 5 \end{matrix}$

#### **B** Proportion of bimodal units in the 4 frontal subareas

	(Differential)	(Nondifferential)	(Total)
PS	11/34 (32.4%)	16/45 (35.6%)	27/79 (34.2%)
IC	19/55 (34.5%)	6/16 (37.5%)	25/71 (35.2%)
AS	33/51 (64.7%)	7/20 (35.0%)	40/71 (56.3%)
PM	30/35 (85.7%)	18/33 (54.5%)	48/68 (70.6%)

cance of the stimulus. In relation to the behavioral significance of the stimulus, a certain number of PM units have been found to show crossmodal or modality specific responses to triggering stimuli with the same behavioral significance in 3 sense modalities (Kurata and Tanji 1986). During a spatial localization task (Vaadia et al. 1986), and in our recent experiment on a Go/No-go discrimination with eye fixation (Niki et al. 1990), PFC and PM units have been found to code the behavioral significance of the stimuli either with modality specificity or across visual and auditory modalities.

Further study is needed to investigate the activity of polysensory units in the PFC, PM and STS in relation to coding the associative and behavioral significance of stimuli in all of the three main modalities.

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