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Activity of primate inferotemporal neurons related to a sought target in pair-association task

(visual cortex/long-term memory/visual imagery/paired associates/delayed matching to sample)

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ABSTRACT **Visual long-term memory in primates has been assessed by using the pair-association (PA) task, in which a subject retrieves and chooses the paired associate of a cue picture. Our previous studies on single neurons in the anterior inferotemporal (AIT) cortex suggested their roles in representing paired associates in the mind. To test the possibility that the delay activity of AIT neurons is related to a particular picture as a sought target, we devised the PA with color switch (PACS) task. In the PACS task, the necessity for memory retrieval and its initiation time were controlled by a color switch in the middle of the delay period. A control task, in which there is no color switch, corresponds to the conventional delayed matching-to-sample (DMS) task where the monkey chooses the same picture as a cue. We found that AIT neurons started to respond just after the color switch in the PACS task, when the cue-optimal picture's associate was presented as a cue. In contrast, they showed no response change in the DMS task. We confirmed that this effect is not due to the visual response to colors. Furthermore, when the cue-optimal picture was presented as a cue, these neurons showed suppression after the color switch in the PACS task. These results suggest that the activity of AIT neurons mediates gating mechanisms that preferentially pass information about a sought target, even when the sought target is retrieved from long-term memory.**

The anterior inferotemporal (AIT) cortex has been proposed to be the memory storehouse in object vision (1–4). Memory storage mechanisms have been examined with the pair-association (PA) task for monkeys, and the results have suggested that an associative mechanism is involved in the establishment of visual long-term memory (5, 6). Our previous neurophysiological studies showed that responses of single AIT neurons were tuned optimally to both paired associates learned in the PA task (6, 7). Moreover, the activity of AIT neurons may reflect retrieved information about paired associates, because we found pair-recall neurons in the AIT cortex, whose delay activity is closely coupled with the paired-associate retrieved through a cue stimulus (6). The purpose of the present experiment was to clarify that this pair-recall effect is related to a particular picture retrieved from long-term memory. We developed a novel task in which the necessity for memory retrieval and its initiation time were controlled by a color switch, independently of the cue stimulus presentation. By using this task, we examined whether delay responses of AIT neurons are affected by a change of target stimuli sought by the animal. We found significant effects of the color switch on the picture-selective delay activity such as enhancement and suppression, suggesting that these parallel mechanisms may be critically involved in the dynamics of AIT neurons.

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METHODS

Subjects. Two adult monkeys (*Macaca fuscata*; 8.0–9.5 kg) were used. Four head bolts and a cylindrical chamber for microelectrode recording were attached to the skull under aseptic conditions and general anaesthesia with Nembutal (30 mg/kg). The chamber was filled with sterile saline containing gentamycin. The monkey was given antibiotics and allowed sufficient rest for recovery after surgery. Training for head restraint was achieved gradually, and the monkey's operant behavior was used as evidence of the absence of discomfort. Recording sessions usually lasted 3 h, during which the animals consumed 400–500 ml of fruit juice. The care and use of the animals conformed with the current guidelines of the US National Institutes of Health and of The Primate Research Institute, Kyoto University, Japan.

Behavioral Tasks. The monkey was first trained in the PA task. In a trial of the PA task, the monkey was presented 1 of 24 pictures as a cue and was required to retrieve the paired associate of the cue picture from long-term memory and to choose it (6). After the monkey learned the PA task, it was trained in the PA with color switch (PACS) task (Fig. 1*A*). As a control task, the conventional delayed matching-to-sample (DMS) task was used (8). Single-unit recording was carried out while the monkey was performing the PACS task and the DMS task.

In the PACS task and the DMS task, 12 pairs of Fourier descriptors (9) were used as visual stimuli (G1 and C1 to G12 and C12), each pair containing a green picture [Commission International d'Eclairage (CIE) coordinates, $x = 0.27, y = 0.58$; luminance, 30.5 cd/m^2) and a cyan picture (CIE coordinates, $x = 0.21, y = 0.31$; luminance, 33.7 cd/m^2) (Fig. 1*B*). The forms of these stimuli and the pair combinations were the same as those used in the PA task (6). In the PA task, all of the stimuli were yellow pictures. The sequence of events in a trial of the PACS task or the DMS task was as follows (Fig. 1*A*). When the monkey started to keep pressing a lever in front of the video monitor, a gray square (luminance, 19.3 cd/m^2) was presented at the center of the screen for 1 s (warning). After the cue presentation of 1 of 24 pictures for 0.5 s, a square was presented during the delay period. The square's color was the same as the cue's color during the first part of the delay period (delay period 1) for 2 s in the PACS task or for 5 s in the DMS task. In the PACS task, the square's color changed into the color of the paired associate after delay period 1, signaling the initiation of retrieval, and the second part of the delay period (delay period 2) for 3 s started. Delay period 2 was not included in the DMS task. To balance the visual stimulus conditions in the two tasks, a gray square (luminance, 19.3 cd/m^2) was presented for 1 s during the third part of the delay period (delay period 3). After delay period 3, a choice of two stimuli was shown

Abbreviations: AIT, anterior inferotemporal; PA, pair association; PACS, PA with color switch; DMS, delayed matching to sample.

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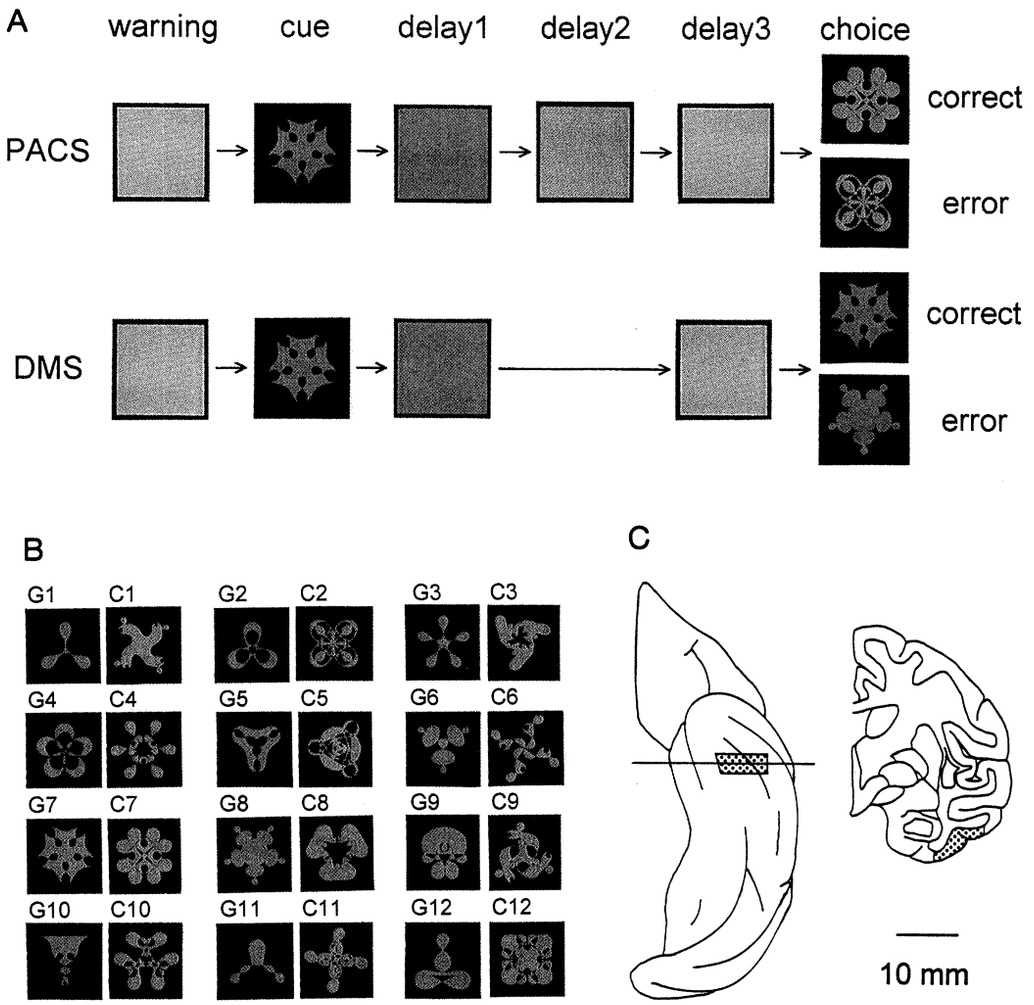

FIG. 1. PACS task and DMS task used to assess the delay activity of AIT neurons. (*A*) Sequence of events in a trial of the PACS task or the DMS task. Cue stimuli and squares were presented at the center of a video monitor. Choice stimuli were presented randomly in two of four positions on the video monitor. Warning, gray square (1 s in both tasks); cue, 1 of 24 pictures in *B* as a cue stimulus (0.5 s); delay period 1, square that has the same color as the cue picture (2 s in the PACS task; 5 s in the DMS task); delay period 2, square that has the same color as the paired associate of the cue picture (3 s in the PACS task); delay period 3, gray square (1 s in both tasks); choice, a choice of two stimuli (1.2 s in both tasks), the paired associate of the cue (correct) and one from a different pair (error) in the PACS task, or the same picture as the cue (correct) and one from a different pair (error) in the DMS task. (*B*) Twelve pairs of Fourier descriptors used as stimuli in both tasks. The first pair is picture G1 (green) and picture C1 (cyan), the second pair is G2 and C2, etc. (*C*) Locations of recorded AIT neurons. (*Left*) Ventral view (anterior at the top) of a monkey brain. (*Right*) Coronal cross-section (dorsal at the top) indicated by a horizontal line on the ventral view. The stippled area represents the range of recording sites.

randomly in two of four possible positions (arranged in two rows of two columns). The choice stimuli were the paired associate of the cue (correct) and a distractor (error) in the PACS task, while the choice stimuli were the same picture as the cue (correct) and a distractor (error) in the DMS task. The animal obtained a reward for touching the correct picture within 1.2 s. If the animal released the lever before the choice, that trial was aborted. In earlier experiments, we tested both tasks without delay period 3.

The response of a single neuron was first examined for its response selectivity in the PACS task. Trials with a green cue picture and those with a cyan cue picture were alternately tested in a block manner. When a neuron showed delay responses, we examined that neuron further in the DMS task. Trials in the PACS task and those in the DMS task were also alternately tested. The number of trials within each block was randomized between 12 and 30. The animal could not have known *a priori* which stimulus would need to be identified after several trials of each block. In the recording sessions after training, the performance of one monkey was 80–100% correct and the other's was 70–90% correct in both tasks. We did not find any differences in performance between the two tasks.

Recordings and Analyses. Extracellular discharges of single neurons were recorded in three hemispheres with a glass-insulated tungsten microelectrode. The electrode was inserted vertically into the target zone through the intact dura mater along a stainless steel guide tube, by means of a hydraulic microdrive manipulator. Standard chronic single-unit recording techniques were employed (10). The action potentials of single cells were amplified and passed through high-pass (50–200 Hz) and low-pass (5 kHz) filter circuits and were converted into digital pulses by a time–window discriminator. The isolation of each neuron was carefully monitored by using two sets of storage oscilloscopes and sound monitors. The eye position was monitored with a scleral search coil (11) in separate experiments. Horizontal and vertical eye positions were recorded every 80 ms while the monkey performed the PACS or DMS task. The spatial resolution of the eye-position monitoring system was $<0.1°$.

Mean discharge rate was calculated over 1 s of warning period as a baseline level. Cue and delay responses were

evaluated by calculating the mean discharge rate for each picture in each task. For the cue response, spike numbers were collected over 80–480 ms from the beginning of cue period. For the early delay response, spike numbers were collected over 1.5 s, starting 0.5 s after the onset of delay period 1. For the late delay response, the mean discharge rate was calculated over 1 s of delay period 3.

To analyze the effects of the task on delay period 1 and delay period 3 responses, we used an analysis of variance (ANOVA) in which the data formed a trifactorial, with tasks and periods as fixed factors and cells as random factors. In this ANOVA of a split-plot experiment, task × cell interactions were derived from main plot comparisons, and task × period interactions were derived from subplot comparisons. After confirming the significance of task × period interactions, we examined the effects of tasks and periods on delay responses further by using the two-tailed paired t test, in which paired samples were derived from the same cell.

For each cell in experiments using tasks without delay period 3, the effect of colors was examined by using cue responses obtained in both tasks over a 240- to 480-ms period from the beginning of cue period, in which there is behaviorally relevant information and the animals actually viewed the cue stimuli (0.3° right, 0.1° down and 1.6° left, 0.3° down from the center of the stimulus for the two animals, respectively, averaged over 288 trials). By using the Mann–Whitney test, we estimated whether one of the two colors elicited stronger cue responses than the other. For color-insensitive cells in experiments using tasks without delay period 3, spike numbers were collected over 1.5 s just before the presentation of choice stimuli during delay period 2 for late delay responses.

RESULTS

In this study, we used two memory tasks (Fig. 1*A*). The PACS task requires retrieval of a target stimulus from memory, whereas the DMS task does not require such a memory retrieval. The results are based on a total of 103 AIT neurons (70 cells from one animal and 33 cells from the other) that showed cue responses in both tasks. The recording area was localized in the inferotemporal gyrus and a part of the middle temporal gyrus, including both banks of the anterior middle temporal sulcus (Fig. 1*C*). The area was very similar to that shown in the previous report (6). Out of the 103 cells, 15 cells showing delay responses were held long enough to complete the PACS task and the DMS task. The effective pictures for eliciting responses from these 15 neurons covered the pictures in the set with no particular bias. When the paired associate of the cue-optimal picture was presented as a cue, 8 of the 15 neurons exhibited the highest activity during delay period 3 in the PACS task. In the PA task, we have reported (6) a similar type of cell (pair-recall neuron), in which the paired associate of the cue-optimal picture elicited the highest delay activity.

We found a clear task difference in delay responses when the best picture's associate was used as a cue. In this paper, we call the cue-optimal picture the best picture, irrespective of its delay response. Fig. 2 shows data from a single AIT neuron. One picture (G7) elicited the strongest response during cue period from this neuron in both the PACS task and the DMS task (Fig. 2 *A* and *E*). The paired associate (C7) of the best picture (G7) elicited little response during the delay period in the DMS task (Fig. 2*F*). In contrast, this neuron started to respond just after delay period 2 (d2) onset when the square's color changed from the cue's color (C7; cyan) to that of the paired associate (G7; green) in the PACS task (Fig. 2*B*). The picture-selective activation after the color switch in the PACS task is called here the "pair-recall" effect, according to the report (6). These results suggest that this delay discharge that is specific to the PACS task may be triggered by memory retrieval.

We noted another task difference in delay responses when the best picture (G7) was used as a cue (Fig. 2*A* and *E*). In the DMS task, this neuron exhibited sustained activation during the delay period (Fig. 2*E*). In contrast, the response of this neuron was suppressed after delay period 2 onset when the square's color changed from the cue's color (G7; green) to the associate's color (C7; cyan) in the PACS task (Fig. 2*A*). The picture-selective suppression after the color switch in the PACS task is called here the "pair-suppression" effect.

We also observed that the effects of pair recall (Fig. 2*B*) and pair suppression (Fig. 2*A*) continued from delay period 2 into delay period 3 in which the square's color was the same gray in both tasks. Therefore, these effects were not due to the square's color, as confirmed by the following observations. The pair-recall effect was observed in trials with cue C7 (Fig. 2*B*), but not in trials where other cyan pictures were used as a cue (Fig. 2*D*). Similarly, the pair-suppression effect was observed in trials with cue G7 (Fig. 2*A*), but not in trials where other green pictures were used as a cue (Fig. 2*C*). These results suggest that the pair-recall effect and the pair-suppression effect cannot be explained by the visual response to colors.

Fig. 3 summarizes the comparison between responses in the PACS task and the DMS task for the 15 neurons. For each neuron, we calculated average discharge rates in each of three periods: warning, delay period 1, and delay period 3. These averages were calculated across trials with the same cue picture in the same task. Fig. 3*A* shows the comparison between the two tasks when the paired associate of the best picture was used as a cue. The plotted points are the mean discharge rates for each neuron, and they are joined by lines for individual cells. An increased response from delay period 1 to delay period 3 was observed for 13 cells in the PACS task and for 5 cells in the DMS task. Fig. 3*B* shows the comparison between the two tasks when the best picture was used as a cue. The decrease of response from delay period 1 to delay period 3 was observed for all 15 cells in the PACS task and for 6 cells in the DMS task.

We examined the activity of these 15 neurons further by testing the overall significance of the pair-recall effect and the pair-suppression effect. From the average responses for each neuron (Fig. 3), we obtained grand means and standard errors across the 15 cells (Table 1). We analyzed the data of delay period 1 and delay period 3 responses with ANOVA of a split-plot experiment. To characterize the pair-recall effect, we collected trials whose cue picture was the best picture's associate. For the pair-suppression effect, we collected trials whose cue picture was the best picture. The effect of task on the delay response was significant for the pair-recall effect [$F(1, 14) = 19.8$; $P < 0.001$] and for the pair-suppression effect [$F(1, 14) = 24.5$; $P < 0.001$]. Furthermore, there was an interaction between task and period for the pair-recall effect [$F(1, 28) = 12.2$; $P < 0.005$] and for the pair-suppression effect [$F(1, 28) = 20.8$; $P < 0.001$].

For the pair-recall effect, we analyzed responses among periods in each task and responses between the tasks in each period. In both tasks, responses in delay period 1 remained equal to warning responses (see Table 1). These delay period 1 responses were thus task-independent. In delay period 3 of the PACS task, the responses were significantly stronger than those in delay period 1 ($t = 3.5$, $P < 0.005$; see Table 1), while the delay period 3 responses in the DMS task remained equal to the delay period 1 responses. The delay period 3 responses in the PACS task were significantly stronger than those in the DMS task ($t = 5.2$, $P < 0.001$). These results indicate that the pair-recall effect is triggered by the color switch.

For the pair-suppression effect, we performed the same analyses. In both tasks, responses in delay period 1 were significantly stronger than warning responses (PACS, $t = 6.6$, $P < 0.001$; DMS, $t = 3.5$, $P < 0.005$; see Table 1). The delay period 1 responses were not significantly different between the two tasks. In delay period 3, the responses were significantly

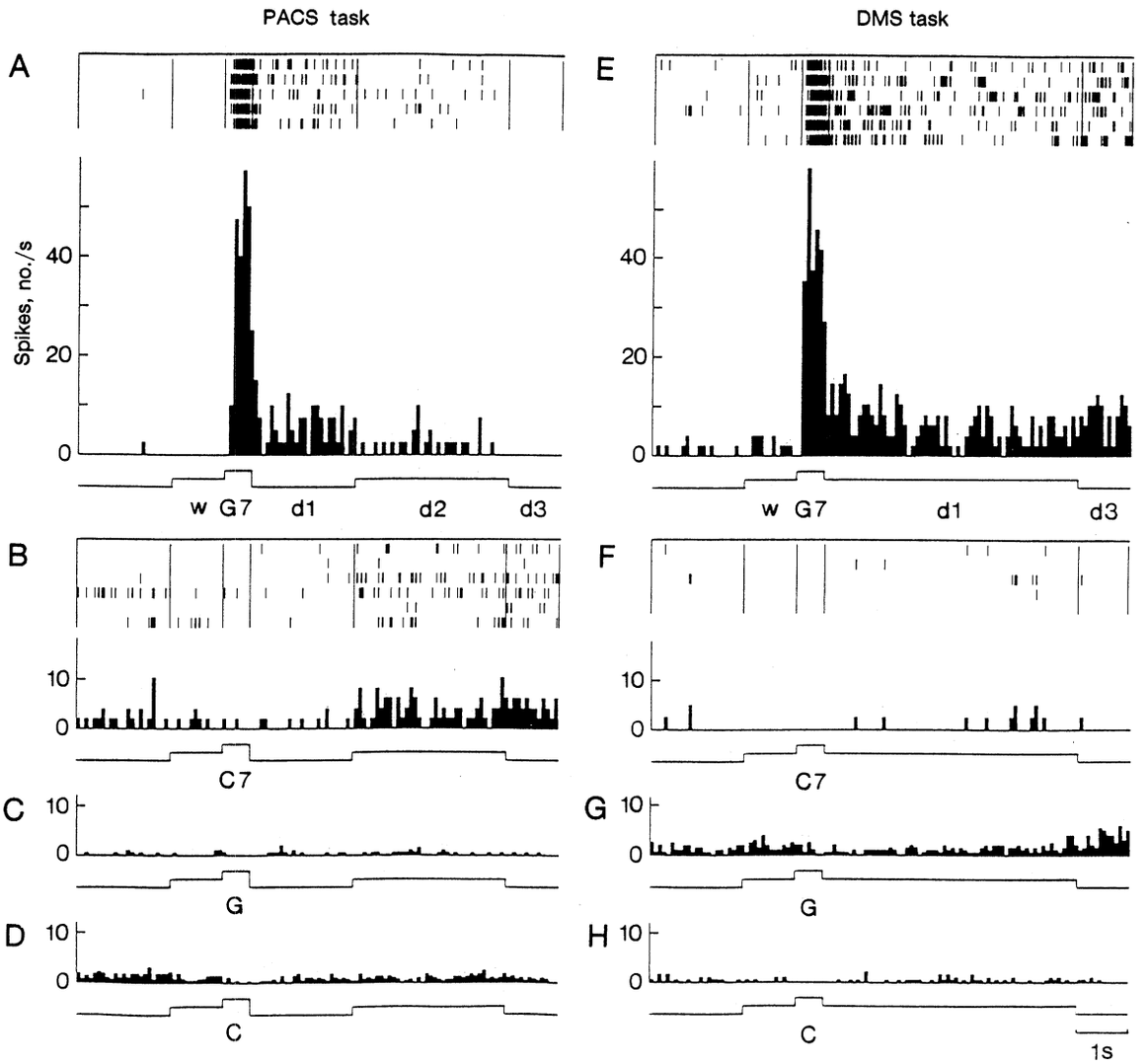

FIG. 2. Differential delay responses of a single AIT neuron in the PACS task and the DMS task. Rastergrams of neural discharges in each trial and spike density histograms are shown. These trials in each task were originally separated by intervening trials with other cue pictures and were sorted by off-line computation. Bin width, 80 ms. (*A–D*) Responses in the PACS task. (*E–H*) Responses in the DMS task. (*A* and *E*) Responses in trials with cue G7. (*B* and *F*) Responses in trials with cue C7. (*C* and *G*) Responses in trials where one picture (*G*) of G1–G12 except G7 was used as a cue. (*D* and *H*) Responses in trials where one picture (*C*) of C1–C12 except C7 was used as a cue. Picture G7 elicited the strongest cue response in both tasks (*A* and *E*). Note the suppressed response during delay period 2 (d2) and delay period 3 (d3) in the PACS task (*A*) but not in the DMS task (*E*). We called this phenomenon the pair-suppression effect. In trials with cue C7, little response was observed during cue period in both tasks (*B* and *F*). Note the enhanced response during delay period 2 and delay period 3 in the PACS task (*B*) but not in the DMS task (*F*). We called this phenomenon the pair-recall effect. In trials with cue G or C, no responses were observed in either task (*C, D, G,* and *H*), indicating that there was no significant color effect.

weaker than the delay period 1 responses only in the PACS task ($t = -7.4$, $P < 0.001$; see Table 1). The delay period 3 responses in the PACS task were significantly weaker than those in the DMS task ($t = -5.6$, $P < 0.001$). These results indicate that the pair-suppression effect is also triggered by the color switch.

In a separate experiment, we examined eye positions during delay period 3 in each task. There were no significant differences in either horizontal or vertical eye positions between trials of the PACS and DMS tasks for each animal (horizontal, $P > 0.1$ for the two animals; vertical, $P > 0.25$ and 0.75 for individual animals; t test, $n = 288$). The mean eye positions were 0.8° left and 2.2° up from the center of the stimulus in one monkey and 3.4° right and 4.4° down, in the other. The difference between neuronal responses in the PACS task and those in the DMS task cannot be explained by retinal factors related to differences in eye position.

Before the experiments using tasks with delay period 3, we tested single neuron responses in the PACS and the DMS tasks without delay period 3. In these earlier experiments, we successfully examined 16 cells that were responsive during the delay period, as well as the cue period, and insensitive to colors ($P > 0.05$; Mann–Whitney test). In these 16 cells, there was an interaction between task and period for the pair-recall effect [$F(1, 30) = 4.5$; $P < 0.05$] and for the pair-suppression effect [$F(1, 30) = 12.6$; $P < 0.005$]. For the pair-recall effect, late delay responses were significantly stronger than early delay responses in the PACS task ($t = 4.3$, $P < 0.001$), while late delay responses remained equal to early delay responses in the DMS task. For the pair-suppression effect, late delay responses were suppressed compared to early delay responses in the PACS task ($t = -2.5$, $P < 0.05$), and late delay responses were even stronger than early delay responses in the DMS task. These results of the experiments using tasks without delay period 3 confirmed the conclusion described above.

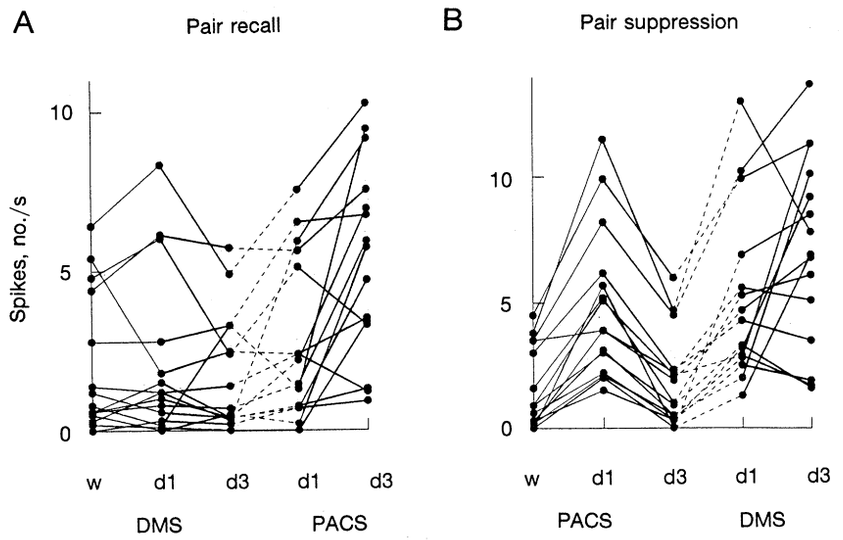

FIG. 3. Pair-recall and pair-suppression effects in the PACS task. (*A*) Discharge rates in trials where the best pictures' associates were used as a cue in the PACS task and the DMS task. (*B*) Discharge rates in trials where the best pictures were used as a cue in these two tasks. Each circle denotes the average firing rate for one of single AIT neurons recorded ($n = 15$). The activity during warning period (w) reflects a condition that provides no specific information about paired pictures. The average firing rates in each condition are joined by lines for each neuron. For most of the 15 cells in the PACS task, activities during delay period 3 (d3) were higher than those during delay period 1 (d1) for *A* (pair recall), whereas activities during delay period 3 were suppressed compared to those during delay period 1 for *B* (pair suppression).

DISCUSSION

We have reported (6) pair-recall neurons, whose delay activity is closely coupled with the paired associate that is not actually seen but retrieved through a cue stimulus. In the present study, it was possible to extend the previous observation on pair-recall neurons to other AIT neurons with delay responses. We have interpreted the pair-recall effect as a prospective code of a sought target that is generated by the conversion of a cue into its paired associate (4). We found that a single AIT neuron started to respond just after the color switch (Fig. 2*B*) and that it did not respond without the color switch (Fig. 2*F*), when the best picture's associate was presented as a cue. The pair-recall effect could be induced if the signal provided by the color switch changed a prospective code of an ineffective target into that of an effective target for that cell. While there was no such signal, the prospective code of an ineffective target would be maintained. Moreover, when the best picture was presented as a cue, the same neuron showed sustained activation while a prospective code of an effective target was maintained (Fig. 2*E*), and its response was suppressed after the signal for changing the prospective code into that of an ineffective target (Fig. 2*A*). This dual parallelism provides compelling evidence that supports the prospective code hypothesis. Although a retrospective code, which is a persistent representation of a cue stimulus itself, may be partially involved in the delay activity, it does not account for the pair-recall effect in the PACS task.

Whereas the sustained activation is a well-known phenomenon in the DMS task (4, 8, 12, 13), the pair-suppression effect in the PACS task is a novel phenomenon, to our knowledge, first reported in this study. This effect is not due to a simple decay of responses over time, because the delay response in the DMS task showed a gradual increase rather than attenuation (see Table 1). Furthermore, the pair-recall and pair-suppression effects cannot be explained by the visual response to colors for the following reasons. First, we confirmed the statistical significance of these effects in both of two separate studies, where the contribution of color factors was carefully excluded: In experiments with delay period 3, these effects (*i*) were analyzed during delay period 3, in which a gray square was presented; (*ii*) in experiments without delay period 3, only cells that did not show significant color preference were analyzed (see *Results*). Second, pair-recall and pair-suppression effects were observed in trials with a particular cue, but not in trials where other pictures with the same color were used as a cue. Typical examples are shown in Fig. 2 *A* and *C* and Fig. 2 *B* and *D*. Therefore, these PACS-task-dependent effects are related to form information rather than color information.

Haenny *et al.* (14) proposed that the activity of some V4 neurons in monkeys performing an orientation matching task is related to the orientation for which the animal is seeking. This proposal has been supported by the finding that individual V4 neurons show similar effects for samples of visual and tactile modality (15). Such a signal of the sought orientation

Table 1. Significant effects of pair recall and pair suppression in the PACS task

		Response, no. spikes per s				*t* value	
Cue picture	Task	Warning	Cue	Delay 1	Delay 3	Delay 1 vs. warning	Delay 3 vs. delay 1
Best picture's associate	PACS	2.4 ± 0.6	4.9 ± 1.8	2.8 ± 0.7	5.3 ± 0.8	1.9	3.5*
	DMS	2.0 ± 0.6	3.6 ± 1.5	2.1 ± 0.7	1.8 ± 0.5	0.4	−0.8
Best picture	PACS	1.6 ± 0.4	27.9 ± 4.5	4.9 ± 0.8	1.8 ± 0.5	6.6*	−7.4*
	DMS	3.0 ± 0.9	27.0 ± 3.5	5.2 ± 0.9	7.0 ± 1.0	3.5*	1.8

Data are the mean ± SEM.
*$P < 0.005$, two-tailed paired *t* test ($n = 15$; df = 14).

indicates a prospective code, although those studies addressed changes in responsivity to stimuli rather than delay activity. Recently, Motter (16) reported "pop out" phenomenon such that single V4 neurons started to respond to an oriented bar in the receptive field when the color of a fixation point changed into the color of the bar signaling attention to that stimulus. This attentional effect triggered by the color change might be similar to the pair-recall effect in our paradigm. It should be noted, however, that V4 neurons respond to bars that are physically present in the receptive field, whereas AIT neurons respond to pictures that are not physically present but retrieved from long-term memory. Thus the pair-recall effect may be interpreted as a result of one of the subprocesses involved in generating mental imagery of paired associates. We hypothesize that visual imagery is implemented by the interaction between memory retrieval and focal attention mechanisms (17). According to our scheme, visual imagery is generated by top-down activation of perceptual representations (18). This model is consistent with our present finding that the picture-selective responses in AIT neurons are controlled dynamically by the color switch in the PACS task as the color switch subserves a signal for changing prospective codes. Furthermore, the pair-suppression effect suggests gating mechanisms that preferentially pass information about a sought target, thereby suppressing the activity of neurons that respond to a cue stimulus and enhancing the activity of neurons that respond to its paired associate. The dynamics of AIT neurons for memory retrieval appears to result in the parallel operation of these two mechanisms—one being enhancement and the other being suppression.

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