Attention and Memory-Related Responses of Neurons in the Lateral Intraparietal Area During Spatial and Shape-Delayed Match-to-Sample Tasks

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Sereno, Anne B. and Silvia C. Amador. Attention and memory-related responses of neurons in the lateral intraparietal area during spatial and shape-delayed match-to-sample tasks. J Neurophysiol 95: 1078–1098, 2006. First published October 12, 2005; doi:10.1152/jn.00431.2005. When a monkey attends to, remembers, and looks toward targets, the activity of some neurons in the lateral intraparietal area (LIP) changes. We recorded from isolated neurons during both a spatial and a shape match-to-sample task to examine and characterize voluntary active processes in LIP. Many LIP neurons show spatially selective activity during the delay period that depends on the location of the sample, but for most cells, this activity does not differ between the two tasks. Although much past work in posterior parietal cortex has explained responses in this region in terms of active processes such as decision-making and motor planning, our findings suggest that much of that activity represents more passive processing. Nevertheless, we do see a significant minority of units that demonstrate instruction-dependent activity during the delay period, suggesting that these units could represent the neural correlates of voluntary or active processes. Separately, we found that during the presentation of the sample stimulus and test array, some units show stronger responses to the stimulus in the shape-matching task when the animal must attend to the shape of a stimulus. This elevated response to the sample during the shape task provides evidence for feature-based attention in LIP. Attention to shape is a property that has not previously been described in primate cortex.

INTRODUCTION

The discovery of specialized cortical visual areas that represent different stimulus properties (Cowey 1979; Felleman and Van Essen 1991; Maunsell and Newsome 1987) has helped establish the idea that many perceptual dimensions are processed independently. Many behavioral theories of attention (Cave and Wolfe 1990; Rossi and Paradiso 1995; Treisman and Gelade 1980) have also proposed functionally separate maps for different properties, and these ideas have been supported by physiological findings (Corbetta et al. 1991; Courtney et al. 1996; Goldman-Rakic 1988). The best-characterized segregation in sensory processing in cerebral cortex is that between a ventral stream that includes areas of temporal cortex and is involved in visual form analysis and object recognition (the “what” pathway) and a dorsal stream that includes areas of parietal cortex and is important for vision related to spatial relations and actions (the “where” or “how” pathway) (Baizer et al. 1991; Goode and Milner 1992; Maunsell and Newsome 1987).

This distinction between object and spatial properties has also been proposed as an important factor in understanding the mechanisms of short-term memory and is the basis for the idea that object and spatial memory are also segregated (Funahashi et al. 1990; Rao et al. 1997; Wilson et al. 1993). Posterior parietal cortex, and the lateral intraparietal area (LIP) in particular, has been extensively studied over the past two decades, defining its important role in spatial attention and spatial short-term memory (Andersen 1987; Bushnell et al. 1981; Colby 1991; Goldberg et al. 1994; Robinson et al. 1978). However, recent work has shown that responses of neurons in LIP are also sensitive to nonspatial attributes of stimuli (Gifford and Cohen 2005; Toth and Assad 2002), including reports demonstrating appreciable selectivity for two-dimensional (2D) (Sereno and Maunsell 1998) and 3D shapes (Sereno et al. 2002). In addition, many units in LIP show enhanced activity during periods when the animal must remember simple geometric 2D shapes (Sereno and Maunsell 1998).

It is not known whether activity related to remembering a location or remembering a shape is selectively engaged when the animal must actively remember that information (e.g., working memory) or if the activity occurs in a more passive or automatic way when such stimuli are viewed (e.g., spatial and object priming). This distinction between reflexive (passive, bottom-up) and voluntary (active, top-down) cognitive processing has been most clearly defined with respect to spatial attention and saccadic eye movements (e.g., Gaynard et al. 1998; Klein et al. 1992; Munoz 2002; Pierrot-Deseilligny et al. 1991; Sereno 1996). Much work has documented differences in behavior, physiology, and anatomy between these reflexive and voluntary processes (e.g., Briand et al. 1999; Connolly et al. 2002; Gaynard et al. 1999; Larrison-Faucher et al. 2004; Matsuda et al. 2004; Mort et al. 2003; Munoz 2002; Seldits et al. 2003; Sweeney et al. 1996). Specifically, with respect to spatial attention, both a nonpredictive peripheral cue and a centrally presented, predictive, symbolic arrow cue will result, for a certain interval of time, in subjects being able to better detect, identify, and discriminate stimuli at the cued location. The peripheral sudden onset cue reflexively draws attention, whereas the central symbolic cue causes a voluntary shift of attention and much work suggests that there are important differences in the behavior (e.g., time course), physiology, and structures that are critically involved in these two forms of spatially selective attention (e.g., Corbetta et al. 1993; Klein et al. 1992; Rafal et al. 1989; Rosen et al. 1999; Sereno et al.

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However, much previous work in neurophysiology has not distinguished between these processes. For example, in a memory-saccade paradigm, a peripheral cue indicates the location that is to be remembered. Hence, neural activity for this location could be related to automatic, reflexive processing of the cue (i.e., reflexive spatial attention, passive memory trace, automatic saccade programming) or to an active voluntary processing of the cue that indicates that 100% of the time the cued position is the position to be remembered (i.e., voluntary spatial attention, active working memory, voluntarily planned saccade programming). Despite the ambiguity, many studies suggest that the neural activity that results represents a voluntary process (e.g., Chafee and Goldman-Rakic 1998; Funahashi et al. 1990). In fact many different active processes have been proposed to account for the selective activation during the delay period including a working memory interpretation of delay period activity (Colby et al. 1996; Goldberg et al. 2002), an intentional interpretation of delay period activity (Andersen 1995; Snyder et al. 2000), as well as a decision or gain theoretic account of delay period activity (Platt and Glimcher 1999; Shadlen and Newsome 1996).

To examine and disambiguate voluntary processes in LIP, we use a modified delayed match-to-sample task that keeps task conditions identical and varies only what the animal must actively attend to and remember (i.e., either the sample shape in the shape-matching task or the sample location in the location-matching task). The animal is cued as to which task he will perform by a briefly presented central symbolic cue at fixation that precedes the trial. It is important to note that we do not eliminate passive processes (given we are using a peripheral sample); however, these passive processes should be identical across the two tasks. Hence, in the shape-matching task, in addition to the active process of attending to and remembering the sample shape, there will be passive shape and spatial processes that reflexively occur after presentation of a peripheral sample shape. Likewise, in the location-matching task, in addition to the active process of attending to and remembering the sample location, there will be the same passive shape and spatial processes that reflexively occur after presentation of a peripheral sample shape. Thus in a carefully controlled design, we test here whether tasks requiring active attention and memory for shape versus spatial location differentially modulate the activity of individual cells in area LIP.

**Methods**

**Animals, animal care, and surgical procedures**

Two rhesus monkeys (Macaca mulatta) were first implanted with a head post and scleral search coil in an aseptic surgery and then trained to perform two delayed match-to-sample tasks (DMTS) and a passive fixation task, obtaining a liquid reward for every correct trial. After completion of behavioral training, a recording chamber was implanted. The chambers were centered, 3–5 mm posterior and 10–12 mm lateral, over the right cerebral hemisphere. All experimental protocols were approved by the University of Texas and Baylor College of Medicine Animal Welfare Committees and were in accordance with the National Institutes of Health Guidelines.

**Stimulus shapes**

Sample and test stimuli were chosen from a subset of eight possible shapes (see Sereno and Maunsell 1998). Each shape was a simple 2D black-and-white geometric form. Each shape fit within the same-sized square region and had an equal number of white pixels.

**Behavioral tasks**

**DMTS tasks**

The two animals performed shape and location DMTS tasks that presented trials with identical sample stimuli and test arrays (see Fig. 1). Shape and location task trials were either randomly interleaved on a trial-to-trial basis or presented in nine trial blocks. In both tasks, the animal fixated a 0.1° spot in the center of the video display throughout each trial. Eye position was monitored using the scleral search-coil method. After a minimum of 400 ms of fixation, a 0.5° instruction cue was presented surrounding the fixation spot for a minimum of 250 ms. For the shape task, the cue was a set of four small colored circles positioned at the vertices of an imaginary square centered on the fixation point. This cue signaled to the animal that it needed to remember the shape of the sample. In the location task, the cue was a white square outline that flickered on and off indicating to the animal that it needed to remember the position of the sample. After the cue offset, the animal maintained fixation for another 500 ms. Then a sample stimulus was presented (for 200–400 ms) in one of three locations. For most units, the sample was immediately followed by a high-contrast full-screen pattern mask (duration 27 ms) and then a variable delay period (ranging from 600 to 2700 ms among the units recorded). Finally, three test shapes appeared together on the display, equidistant from the fixation spot. In the shape DMTS task, the animal was required to make an eye movement to the test shape that matched the sample shape for a juice reward. In the location DMTS task, the animal was required to make an eye movement to the test location that matched the sample location for a juice reward. The latency of the saccade was defined as the time after test onset at which point the eye left the fixation window (1° window, centered on the fixation spot). During recording from each unit, sample and test stimuli were a subset of three of eight possible shapes. For most of the units recorded, stimulus eccentricity was between 3.5 and 6.0° and stimulus size was between 0.4 and 0.8°. In general, when eccentricity of the stimuli was increased, the stimulus size was increased to ensure that the stimuli remained easily discriminable. Catch trials comprised ≈20% of trials. In catch trials in the shape DMTS task, the test array did not include the sample shape, which was replaced instead by one of the five other shapes. In catch trials in the location DMTS task, the test array did not include any stimulus in the correct target location. For both shape and

![FIG. 1. Schematic diagram of the location and shape-matching tasks. Each trial began when the animal fixated a spot in the center of the video display. A small cue centered on the fixation spot instructed the animal as to which task he was to perform. After the cue disappeared, a sample shape was presented and followed by a brief presentation of a full screen pattern mask. Finally, after a delay period, a test array of 3 shapes appeared. On trials in which the animal had been instructed to remember the location of the sample (location task), the animal was required to make an eye movement (indicated by an arrow during the test period) directly to the shape that appeared in the remembered sample location to obtain a juice reward. On trials in the shape-matching task, the animal was required to make an eye movement to the test shape that matched the sample shape to obtain a juice reward.](JNeurophysiol_%20Vol%2095%20_February%202006%20www.jn.org)
location task catch trials, the animal was rewarded for maintaining fixation on the central spot until it disappeared (after an additional 1.3–1.9 s).

PASSIVE FIXATION TASK. During the passive fixation task, the stimulus shape was positioned within the receptive field, in the same position that elicited the strongest response in the DMTS tasks. The stimulus for each trial was selected from the same set of eight shapes used in the DMTS tasks. In each trial, one randomly selected shape was presented four times before a central fixation spot was extinguished. Each presentation of the shape lasted for 250–300 ms and each fixation interval following the shape was 500–750 ms. The animals were required to maintain fixation within 0.5° of the central 0.1° spot in the center of the video display throughout the trial. The animals were rewarded for maintaining fixation on the central spot until it disappeared.

Recording procedures

Monkeys performed the matching tasks while the recording electrode was slowly advanced with a hydraulic micropositioner in search of neurons. We recorded any neuron that we could isolate well and that appeared stable. Once a neuron was well isolated, we presented a stimulus at varying locations (typically 8 locations equally spaced around the fixation spot) to determine the location in the receptive field that elicited the strongest response and then selected the three locations for the matching tasks. The three possible stimulus positions were configured so that at least one stimulus position fell within the receptive field in the location that elicited the strongest response at a given eccentricity. In addition, the three locations chosen were typically equally spaced (~120° apart). We then presented all shape stimuli at the preferred location and determined the three shapes for the matching tasks. For most units, the two shapes that elicited the strongest response and the one shape that elicited the weakest response were selected. For most units, data were then collected with the two matching task trials intermixed (either randomly or alternated in ~9 trial blocks). For a few units, data were collected for each matching task sequentially. As long as the isolation could be maintained, recordings were collected for 216 correct matching trials [or 12 trials per each of 9 sample conditions (3 shapes by 3 locations) for each of 2 matching tasks]. If the unit remained well isolated, we recorded responses during the passive fixation task for all eight shape stimuli (6 trials each).

We recorded at least five repetitions (median = 12) for each combination of sample shape and sample location from 122 isolated neurons in the lateral bank of the intraparietal sulcus in the right hemisphere of both animals. There were 85 units recorded from one animal and 37 recorded from the second animal. In addition, for 52 of these isolated neurons with spatially selective delay period activity, we recorded at least three trials (median = 6) for each sample shape in the passive fixation task. For the passive fixation task, there were 36 units recorded from one animal and 16 recorded from the second animal. Because there were no obvious differences between the two animals, the data have been combined.

Behavioral monitoring, eye position and spike sampling, and online data analysis were performed under computer control. Stimuli were presented on a 20-in computer monitor (75 Hz), positioned 57 cm from the animal. While animals performed the experimental tasks, action potentials were recorded extracellularly with either transdural Pt/Ir (1–2 MΩ) or tungsten microelectrodes (1–2 MΩ, Microprobe). Signals from the electrode were amplified, filtered, and transformed into pulses by a window discriminator. Spike times were recorded with 1-ms resolution.

Anatomical localization

We recorded from 122 isolated neurons in the lateral bank of the intraparietal sulcus of two animals. Histological reconstruction from one animal showed that 79 of the 85 units assigned to the lateral bank were within LIP defined as including a densely myelinated zone and a region extending 2 mm further dorsal (Andersen et al. 1990; Ungerleider and Mishkin 1982). The remaining six units were within another millimeter further dorsal, and because they were ≥4 mm below the surface and gave vigorous visual responses, we have included them in the current analysis. Histological reconstruction from the second animal is not available, but the physiological results from that animal were consistent.

Data analysis

For statistical analyses in the DMTS tasks, F tests were performed on the average rate of firing in four different trial intervals: for the sample period, starting 50 ms after the onset of the sample stimulus and ending with stimulus offset (200–400 ms durations across the population of recorded units); for the delay period, the last 600 ms of the delay period; for the test period, starting 50 ms after the onset of the test array and ending 150 ms after test array onset; and for the peri-eye movement (EM) period, starting 100 ms before the onset of the EM and ending 100 ms after the EM onset. For analyses of the sample and delay periods, trials were sorted based on the task instruction, sample shape, and sample location (see Fig. 2A). For analyses of the test and EM periods, trials were sorted based on the task instruction, target shape, and target location (see Fig. 2B). For analyses of shape effects, the average firing rate for each shape was collapsed across matching tasks and locations (see highlighted histograms in Figs. 4 and 5, broken down by task). For analyses of spatial effects, the average firing rate for each location was collapsed across matching tasks and shapes (see highlighted histograms in Fig. 3, broken down by task). For analyses of task instruction effects, the average firing rate for each matching task was collapsed across shapes and locations (see highlighted histograms in Fig. 6). Similar to the analyses of task

FIG. 2. Sorting of data for analyses. A: for analyses of sample and delay periods, data were sorted by the sample conditions (purple box). Specifically, data were sorted by the matching task instruction (shape task in red, location task in blue), sample shape (3 possible shapes), and sample location (3 possible locations). B: for analyses of test and eye movement periods, data were sorted by the test array and eye-movement conditions (green box). Specifically, data were sorted by the matching task instruction (shape task in red, location task in blue), target shape (for these trials, the square), and target location (for these trials, to the right of fixation).
instruction effects, for analyses of check and change effects, the average firing rate for each subset of task trials (see Fig. 16) was collapsed across target shapes and locations (see highlighted histograms in Fig. 15).

A task selectivity index (SI) for each unit was calculated using the average rate of firing during the appropriate time period during the shape and location tasks collapsed across shapes and locations: task SI = (shape task - location task)/(shape task + location task). A location SI was calculated using the average rate of firing during the appropriate time period in the location that elicited the best response and the location that elicited the weakest response collapsed across tasks and shapes: location SI = (best location - worst location)/(best location + worst location). A shape SI was calculated using the average rate of firing during the appropriate time period for the shape that elicited the best response and the shape that elicited the weakest response collapsed across tasks and locations: shape SI = (best shape - worst shape)/(best shape + worst shape).

For statistical analysis with the passive fixation task, the average rate of firing for the matching task, location, and shape that elicited the best response during a period 245–495 ms after the sample offset was compared with the average rate of firing during the passive fixation task following the presentation of the same stimulus presented in the same position (i.e., average rate of firing during the first interstimulus interval, from 245 to 495 ms after the first sample presentation of the trial). For all statistical tests, a criterion level of $P < 0.05$ was used for significance.

The delay population averaged spike density histograms (Fig. 8) are the averaged response of the 20 neurons with significant differences in task during the delay period. Separate histograms are shown for units with greater activity in the location task ($n = 12$) and those units with greater activity in the shape task ($n = 8$). For each unit, the pair of histograms representing the average response of that unit during the shape- and location-matching tasks for the location and shape that elicited the best response during the delay period was included in the respective population average histogram (shape task or location task). These population average spike density histograms, sampled at 1 kHz, were then convolved with a Gaussian of sigma 15 ms and the average spike train including the delay interval displayed. For the delay period analysis for task effects, described in the preceding text, the SE for each task was calculated for each unit. Error bars in the population histogram represent the SE calculated for the delay period for each unit and task averaged across the units included in the population histogram. The sample population averaged spike density histograms are the average response of the 24 neurons with significant differences in task during the sample period. Separate histograms are shown for units with greater activity in the shape task ($n = 15$) and those units with greater activity in the location task ($n = 9$). For each unit, the pair of histograms representing the average

![Figure 3](https://example.com/image3.png)

**FIG. 3.** Single unit with spatial selective delay activity. Each of the 18 histograms within the black outlined rectangle represents the average spike density histogram across 12 trials from 1 neuron in the 18 possible sample trial conditions (2 matching tasks, 3 locations, and 3 shapes). For each combination of sample shape and location trial type, shape-matching task histograms are in red (top), whereas location-matching task histograms are in blue (bottom). The average spike density histograms highlighted in the right margin are histograms averaged across the 3 shapes (i.e., each histogram averaged across 36 trials). The average spike density histograms in the bottom margin are averaged across the 3 locations (i.e., each histogram averaged across 36 trials). The pair of histograms in the lower right corner is averaged across both the 3 locations and the 3 shapes (hence, each histogram is an average of 108 trials). Each histogram shows the activity of the neuron during the presample fixation period (F), the minimum sample period across all trials (S, indicated by the horizontal bar below each histogram) aligned with sample onset, and the minimum delay period across all trials (D; see labels at bottom of figure) aligned with delay onset. The horizontal bar below the histogram represents both the minimum duration of the sample (green) and the duration of the mask (black, if present). The vertical shaded green region brackets a 600-ms period of the delay period before the test onset. The total duration of the histograms are indicated in the bottom right corner of the figure. For the averaged histograms, mean saccade latency and the number of trials it represents are indicated in the upper left hand corner of the histogram. The highlighted histograms in the right margin nicely illustrate a main effect of location. That is, this neuron was much more active during the sample presentation and during the delay period that followed when the sample appeared in location 1 (location effect during delay period, $P < 0.0001$; SI = 0.46). This spatially selective delay activity existed whether or not the animal was required to remember the location of the sample [task instruction effect during delay period, $P > 0.46$; selectivity index (SI) = –0.01].
response of that unit during the shape- and location-matching tasks for the location and shape that elicited the best response during the sample period was included in the respective population average histogram (shape or location task). These population average spike density histograms, sampled at 1 kHz, were then convolved with a Gaussian of sigma 15 ms and the average spike train including the sample interval displayed. For the sample period analysis for task effects described in the preceding text, the SE for each task was calculated for each unit. Error bars in the population histogram represent the SE calculated for the sample period for each unit and task averaged across the units included in the population histogram.

RESULTS

Spatial and shape-selective LIP properties

Most LIP units (80%, 97/122) responded to the sample stimuli and gave statistically significantly different responses depending on where the sample stimulus appeared (Fig. 3; see also Fig. 13). In addition, most units (71%, 87/122) also had a significant difference in activity during the delay period depending on whether the sample had appeared in the receptive field. As we have previously reported (Sereno and Maunsell 1998) and as illustrated in Fig. 4 (see also Fig. 14), many LIP units also showed a significant difference in activity depending on the sample shape either when it was presented at sample (41%, 50/122) or during the subsequent delay period (34%, 41/122), independent of the following EM.

EFFECT OF TASK INSTRUCTION DURING THE DELAY PERIOD. Most units did not show a significant difference in delay period activity between the two tasks (84%, 102/122). Even among units with significant spatially selective delay period activity (e.g., Fig. 3), this delay activity was typically as pronounced (i.e., no significant differences across task instruction) during the shape memory task (84%, 73/87). Figure 3 shows data recorded from one LIP neuron during the shape (top red rows) and location (bottom blue rows) matching tasks. Each histogram represents the average activity of the unit when each of three possible shapes was presented in one of the three different sample positions. When the sample appeared in location 1, there was an elevated level of activity during its presentation and the delay period that followed. No appreciable change in activity occurred when the sample appeared in other locations. This unit, like the majority of units with spatially-selective delay period activity, demonstrated a consistent level of spatially selective delay period activity whether or not the animal

FIG. 4. Single unit with shape-selective delay activity. Conventions are the same as in Fig. 3. The highlighted histograms in the bottom margin nicely illustrate a main effect of shape. That is, this neuron was much more active during the sample presentation and during the delay period that followed for the H-like shape (shape effect during delay period, *F* test, *P* < 0.0001; shape SI = 0.62). This neuron also showed a small but significant increase in delay activity when the animal was required to remember the location of the sample (task instruction effect during the delay, *P* < 0.043; task SI = −0.06). Note that this is the same neuron that was previously shown in Fig. 3B of Sereno and Maunsell (1998). In this figure, we show data from the 3 conditions (i.e., the first 3 red histograms in the top row) that were depicted in Fig. 3B of Sereno and Maunsell (1998), as well as the activity of the neuron for the other 15 trial conditions and the activity of the neuron averaged across these different shape and/or location conditions (14 histograms).
needed to remember the sample position. The same was true for units with shape-selective delay period activity: For most such units (e.g., Fig. 5), the shape-selective delay period activity was also present during the location-matching task (83%, 34/41 units with shape-selective delay).

As illustrated in Fig. 6 (see also, Fig. 4), some units (16%, 20/122) did show significantly different activity during the delay period depending on whether the animal had to remember the sample shape or location (see also, summary table in Fig. 7). The unit in Fig. 6 was much more active during the delay period when the animal was performing the location task and needed to remember the sample position (in location 1, 20 vs. 8 spikes/s, for location and shape task, respectively; task S.I. = −0.41). We calculated a task SI for each unit using the average rate of firing during the last 600 ms of the delay period during the shape and location tasks (see METHODS). Figure 8A shows the distribution of indices for the units recorded. Among the units with significant differences in delay period activity between the two tasks (units with significant task instruction effect during delay period indicated in dark gray in Fig. 8A), 12 were more active during the location task and 8 were more active during the shape task (see also summary table in Fig. 7).

The population histograms of the significant units in Fig. 8, B and C, show the average response of these units during the delay period. The population histogram of units with significantly greater responses during the delay in the location-matching task (Fig. 8B, n = 12) show units that demonstrate enhanced activity when the animal needed to remember the sample location.

Figure 9 shows a unit with significantly greater activity during the delay period for the shape task compared with the location task. This unit showed, in the LVF (i.e., contralateral visual field), a brief transient excitatory response to the sample followed by a suppressive response during the sample presentation and then, after a vigorous response to the full-field pattern mask, continued to show a suppressed response during the delay period in the contralateral locations with greater suppression occurring during the delay in the location-matching task (9.8 vs. 12.4 spike/s for location and shape task respectively averaged across shape in the contralateral location 1; task SI = 0.07). Hence for this unit, the enhanced activity during the delay period for the shape task is actually a reduced suppressive response in the contralateral visual field during the shape task or, in other words, enhanced suppressive response during the location task. This interpretation would suggest that the distribution of positive selectivity indices (Fig. 8A, red...
highlighted part of range) and the population histograms of significant units with significantly greater response during the shape task (Fig. 8C) is more difficult to interpret due to these units with suppressive responses in the contralateral visual field.

Spatial delay period activity in blocked conditions

Because the location and shape match-to-sample trials were randomly intermixed, it is possible that the spatially selective delay period activity existed during the shape task because the monkey elected to actively remember both the shape and position of each sample. We examined this possibility for nine neurons with spatially selective delay period activity by having the animal perform only the shape task for \( \geq 100 \) trials (12–22 min). The spatially selective delay period activity remained robust. Each of the neurons tested retained its significant delay selectivity when the shape task was performed alone. Five of these nine units were also recorded while the animal performed only the location task for \( \geq 100 \) trials. The mean ratio (best location/worst location) for the delay period activity of these units did not change whether the animal was performing the location task (3.40) or the shape task (3.34), \( P > .95 \) (t-test, 2-tailed). Six of these nine units were also recorded from while the animal performed the task with trials from the two matching tasks intermixed. For these units, the mean ratio (best location/worst location) for trials in the shape task also did not differ significantly depending on whether the animal was performing the shape task intermixed with the location task (2.60) or the shape task alone (2.88), \( P > .47 \) (t-test, 2-tailed).

Together these results suggest that changing the task conditions (e.g., shape task only) did not reduce the spatial selectivity of the units.

Spatial delay period activity in passive fixation task

To examine further whether the spatially-selective delay period activity in area LIP represents a purely passive memory, we also trained the animals on a fixation task that required no behavioral response. While the animal fixated, we presented the shapes from the matching tasks in the isolated neuron’s receptive field in the same position used during the matching tasks (see Experimental procedures). We compared the activity for each unit during the fixation period following the presentation of a given shape in this passive fixation condition with that during the delay period when the animal was required to remember the location of the sample (task instruction effect during delay period, \( F \) test, \( P < 0.0001 \); SI = –0.41).
significant spatially selective delay activity in the matching tasks, 20 (39%) had significantly greater activity in the delay period of the matching task compared with the first interstimulus period of the fixation task (Fig. 10). The failure of these units to show equivalent activation during the interstimulus interval of the fixation task shows that for some of the units with spatially selective delay period activity, this activity is not entirely passive or automatic.

EFFECT OF TASK INSTRUCTION DURING THE SAMPLE STIMULUS. In addition to differences in delay period activity between the two tasks, we also found significant differences in responses to the sample stimulus. As illustrated by the unit in Fig. 11A, a few units (24/122, 20%) had significant differences in activity to the sample stimulus depending on whether the animal needed to attend to and remember its shape or its location. We calculated a task SI for each unit using the average rate of firing during the sample presentation starting 50 ms after sample presentation during the shape and location tasks [SI = (shape – location)/(shape + location)]. Figure 8D shows the distribution of indices for all units recorded. Among the units with significant differences in sample period activity between the two tasks, 15 were more active during the shape task and 9 were more active during the location task (see also summary table in Fig. 7). The population histograms of the significant units show the average response of these units during the sample period. The population histogram of units with significantly greater responses in the shape-matching task compared with the first interstimulus period of the fixation task (Fig. 10). The failure of these units to show equivalent activation during the interstimulus interval of the fixation task shows that for some of the units with spatially selective delay period activity, this activity is not entirely passive or automatic.

FIG. 7. Summary table of units with significant task instruction effects across the four different trial intervals (sample, delay, test, and eye movement) for the whole population of recorded units (n = 122 units) and for the subset of units with ≥9 repetitions (n = 80 units). The purple box indicates trial periods where data were sorted by the sample conditions (as illustrated in Fig. 2). The green box indicates trial periods where data were sorted by the target and response conditions. For each set of units, the percentage and the number of units (in parenthesis) that showed significant task instruction effects are listed for each of the four trial periods. In the top right (in red) and bottom right (in blue) corners are the numbers of units with significantly greater response during the shape and the location tasks, respectively.

### TABLE 7

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<tr>
<th>TASK EFFECT</th>
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The unit shown in Fig. 11A was significantly more responsive during the sample period when the animal was performing the shape task and needed to attend to and remember the sample shape. Interestingly, most units with significantly greater activity in the location-matching task during the sample period showed suppressed responses in the contralateral visual field to the sample (6 of the 9 units). Consistent with units with increased responses to the sample presentation showing an enhanced response during the shape task, these units with suppressed responses showed a greater suppression of response during the shape task. This is similar to the pattern reported above for the delay period, where some of the units with significantly greater responses in the shape-matching task during the delay period were units with sustained suppressive responses in the contralateral visual field. Such units with suppressed responses in the contralateral visual field during the sample period suggest that the distribution of negative selectivity indices (Fig. 8D, blue highlighted part of range) and the population histogram of units with significantly greater response during the location task (Fig. 8E) is more difficult to interpret.

DIFFERENCES BETWEEN SAMPLE AND DELAY ACTIVITY. About 16–20% of units had a significant difference in activity between the two tasks during either the sample or delay periods. Only one unit showed significant task effects during both periods. Hence, it seems that these task effects occur in separate populations of units in LIP. Nevertheless, to see if there was a shift in the responses of LIP units between the sample and delay period such that the response during the sample was greater in the shape task, but during the delay, greater in the location task, we compared the task SIs across the sample and delay period, excluding only units with low firing rates (<3 spikes/s) during either period (n = 11). We found that for the sample of units we recorded in LIP, there was a significant shift in the SI between the sample and delay periods, P < 0.007, 1-tailed t-test (illustrated in Fig. 12 as a tendency for units to cluster below the diagonal line). Thus there was a significant shift of selectivity indices between the sample and delay periods that is consistent with more activity in the shape task during the sample and more activity in the location task during the delay period.

EFFECT OF TASK INSTRUCTION AFTER THE ONSET OF THE TEST ARRAY. For the preceding analyses of sample and delay periods, data were sorted by the sample (see Fig. 2A). To see if there were any task instruction-related differences in unit activity after the test array appeared, we sorted the data by task, target shape, and target location (Fig. 2B). First, as expected, most LIP units (80%, 98/122) gave a significant different response after the test array onset, depending on where the target appeared and hence to what location the
EM was directed (Fig. 13). In addition, after the test array onset many LIP units (44%, 54/122) also showed a significant difference in activity depending on the target shape (Fig. 14). Most importantly with respect to the effect of task instruction, after the test array onset, a few units showed a significant difference in activity during the test period (21%, 26/122; see unit in Fig. 11B) as well as many more units around the time of the EM (48%, 59/122; see unit in Fig. 15) depending on which task the animal was performing. During both the test and EM periods, slightly more units had significant differences with greater activity in the shape task (14/26 during test period and 30/59 around the EM; see summary table in Fig. 7). Hence in contrast to task differences during the preceding delay period, there were slightly more units with significant differences in activity during the test and EM period that had greater activity in the shape task. The two memory tasks require different cognitive processes after the test array appears. Hence, these differ-
ences in neuronal responses in LIP in the two tasks might reflect the different required cognitive processes.

**MODEL OF COGNITIVE PROCESSES REQUIRED AFTER TEST ONSET.** To examine if there were differences in the activity of LIP units during the EM period that reflected these different task requirements, the unit data were sorted by task, target shape, and target location as well as by whether the sample and test target were the same shape and in the same location (“pure” trials in Fig. 16). In all the trials, the presentation of the sample should have reflexively or exogenously brought spatial selective attention to the sample location (henceforth, labeled the attended location). During location task trials, after the test onset, the monkey could immediately execute the EM to the attended location (GO trials). These trials can be further divided into trials that presented the identical sample shape in the attended location (“pure” trials, one-third of all location task trials), and those trials in which a different shape than the sample shape appeared in the attended location (“non-pure” trials, two-thirds of all location task trials). In the shape task, on the other hand, when the test stimulus appeared, the monkey would first need to check the shape in the attended location (to see if it was the remembered shape) before executing the EM (CHECK-GO trials, one-third of all shape task trials). It is important to note that pure shape and pure location trials entailed the same stimulus configurations and the same EMs; however, the animal made the EM for different reasons (matching location vs. matching shape, for location and shape-matching tasks, respectively). In the non-pure trials in the shape task, the correct shape was always in a different location at test than in which it had appeared during the sample. Hence, after the test onset, the monkey would first need to check the shape in the attended location (to see if it was the remembered shape), then shift spatial attention and motor plan, and, finally execute the EM (CHECK-CHANGE-GO trials, two-thirds of all shape task trials).

To examine if there were behavioral (EM latency) and physiological changes in unit activity dependent on these conditions, we made comparisons across these conditions. Because we were looking at a subset of trials for each unit (i.e., 33 or 67% of all trials), we only included units that had more than nine repetitions for each sample shape and location and task (80 of 122 units). The pattern of findings for these 80 units was similar to what we have already reported in the preceding text for the entire population. Namely, 27% (22/80), 19% (15/80), and 59% (47/80), of this subset of units showed differential activity between tasks during the sample, delay, and EM periods, respectively (Fig. 7).

**Saccade latencies and error rates.** Despite a large 78-ms difference in EM latency between tasks \( P < 0.01; \) spatial task: 181 ± 3 (SE) ms; shape task: 259 ± 2 ms], there was no
significant difference in error rates (1.7%, $P > 0.23$; spatial task: 21.2 ± 1.0%; shape task: 22.9 ± 0.9%). To examine if behavioral evidence supported these different processes (GO, CHECK, and CHANGE), we examined EM latency and error rates in the different trial conditions (see Fig. 16). We found that EM latencies were fastest in the “pure” GO trials (188 ± 2 ms), 43 ms slower in the CHECK-GO trials (231 ± 2 ms, $P < 0.01$) and another 44 ms slower in the CHECK-CHANGE-GO trials (275 ± 2 ms, $P < 0.01$). Thus EMs were delayed by the need to attend to the target shape (CHECK) and further delayed by the need to shift attention and change EM plan (CHANGE). We also found that error rates were consistent with these findings: error rates were lowest in the pure GO trials (1.3 ± 0.2%), 2.4% greater errors in the CHECK-GO trials (3.7 ± 0.4% ms, $P < 0.01$), and another 25.7% greater errors in the CHECK-CHANGE-GO trials (29.4 ± 1.1% ms, $P < 0.01$). Reduced error rates were also found in the location task when the identical sample shape appeared in the attended location (pure trials, 1.3 ± 0.2%) as opposed to a different shape (non-pure trials, 27.9 ± 1.2%, $P < 0.01$). Unexpectedly, however, EM latencies were 9 ms slower in this same condition ($P < 0.01$). That is, latencies were slower when the identical sample shape appeared in the attended location (pure trials, 188 ± 2 ms) as opposed to when a different shape appeared (non-pure trials, 179 ± 3 ms, $P < 0.01$). This may be due to the fact that we find that ~70% of LIP units (62 of 94 units recorded) show a significantly reduced response to a repeated shape stimulus in their receptive field during a passive fixation task similar to the attenuated responses that have been reported previously in AIT (Miller and Desimone 1994; Miller et al. 1993 1991). Hence, it is possible that these attenuated visual responses are responsible for the slightly longer latencies.

Physiology of attention to feature (CHECK) in LIP. To investigate whether the differences in activity after the test onset could be due to this additional requirement to check the shape at the attended target location before making an EM, we compared stimulus configurations in the two tasks where the animal made the same EM to the same shape (i.e., pure location GO trials and pure shape CHECK-GO trials, Fig. 16). The only difference in these trials was whether the animal needed to attend to the shape before making the EM. Surprisingly, even with our reduced number of trials, some units during the test (12%, 12/80) and EM (6%, 5/80) periods had significant differences between these task conditions (see Fig. 17A). This unit showed an enhanced activity after the test array onset and at the time of the EM during the shape task when the animal needed to check the shape before making the EM, suggesting that, similar to what we have reported during the sample period, this enhanced activity in LIP is associated with attention to shape.

Physiology of attentional shift or change in motor plan (CHANGE) in LIP. To investigate whether the differences in activity after the test onset could be due to this additional requirement to shift attention and change the EM motor plan (i.e., CHANGE), we compared the CHECK-GO trials to the CHECK-CHANGE-GO trials from the shape task (Fig. 16). The difference between these two trial types is that in the non-pure shape trials, the target shape would have appeared in a different location at sample so that the animal would have been required to shift his attention and change his EM plan to the new location before making the identical EM to the identical shape.
FIG. 11. Task instruction effects during the sample, test, and eye movement periods. A: attention to shape during the sample period in LIP. Single unit with task selective sample activity showing greater activity in the sample period during the shape-matching task (red). Average spike density histograms for the neuron’s preferred location for 3 different sample shape presentations during shape (red)- and location (blue)-matching tasks. Each histogram was compiled from 12 trials and shows the activity of the neuron during the presample fixation period (F), the minimum sample period across all trials (indicated by the horizontal bar below each histogram) aligned with sample onset, and the minimum delay period across all trials (D) aligned with delay onset. The total duration of the histograms are indicated in the figure legend. The activity is aligned with the onset of the sample presentation (S, dashed line) and the sample time period for analysis is shaded in gray and bracketed by the solid vertical lines (starting 50 ms after the sample presentation and ending with the offset of the sample for the minimum sample duration). This neuron was more active during the sample presentation when the animal was performing the shape-matching task (task instruction effect during sample period, P < 0.0001; SI = 0.16). B: attention to shape during the test period in LIP. Single unit with task selective test activity showing greater activity in the test period during the shape-matching task (red). Average spike density histograms for the neuron’s preferred target location for 3 different test target shape presentations during shape (red)- and location (blue)-matching tasks. Schematic diagram above the histograms indicates the trial conditions and the target shape. Asterisks indicate the 2 other shapes that were presented in the other locations. Average spike density histograms from 1 neuron for its preferred target location (highlighted) with 3 different target shapes presented in the target location during the shape (red)- and location (blue)-matching tasks. Each histogram was compiled from 12 trials and shows the activity of the neuron during the last 500 ms of the delay period (D) before the test array onset (T) and 700 ms after the test array onset. The activity is aligned with the onset of the test array (dashed line) and the test time period for analysis is shaded gray and bracketed by the solid vertical lines (starting 50 ms after the test onset and ending 150 ms after the test onset). The green bar under each histogram represents the range of test array durations across all trials included in the histogram. The blue bar under each histogram represents the range of saccade onsets across all trials included in the histogram. The vertical bar below this blue bar indicates the mean saccade onset of these trials. This neuron was more active during the test presentation when the animal was performing the shape-matching task (task instruction effect during test period, P < 0.0002; SI = 0.18).

A few units showed significant differences in activity between these two conditions during the test period (11%, 9/80) and around the time of the EM (17%, 13/80). Figure 17B shows a unit that showed a significantly enhanced activity around the EM during the shape task when the animal needed to shift its attention and change its EM plan.

DISCUSSION

As expected, most neurons in LIP showed spatially selective sensory (80%) and delay period (71%) activity. However, many neurons in parietal cortex that represent remembered locations were active irrespective of whether the animal remembered shape or location. Our findings suggest that many neurons in this region contribute to a more reflexive or automatic process. Nevertheless, in agreement with previous studies, we do find that the delay period activity of some units in LIP reflects a more active process. Specifically, we show for the first time, under highly controlled conditions the following: 1) neurophysiological evidence that the delay period activity of some neurons in LIP represents what the animal is actively attending, remembering, planning, or deciding; and 2) neurophysiological evidence that the responses of some neurons in LIP are modulated when the animal attends to shape providing the first neurophysiological evidence for shape-selective attentional mechanisms in visual cortex.

Much delay period activity is not specific for the to-be-remembered event

Current work suggests that one of the functions of parietal cortex is to contribute to a salience map (Goldberg et al. 2002;
Gottlieb et al. 1998). Salience accrues not only from reflexive or intrinsic properties of the stimuli (e.g., abrupt onsets) but also from voluntary or task-related properties (e.g., behavioral relevance: Kusunoki et al. 2000). This study attempts to tease apart the influence of voluntary processes on neuronal responses in LIP. The lack of pronounced differences between the spatially selective delay period activity for the two attention tasks for most units in LIP calls into question the standard interpretation of the delay period activity in LIP as representing primarily active processes such as active attention (Colby et al. 1996; Goldberg et al. 1990), mnemonic (Funahashi et al. 1989), motor-preparatory (Gnadt and Andersen 1988), or decision-related responses (Platt and Glimcher 1999), as these studies did not control for the effects of passive attentional, mnemonic, and motor-preparatory signals that automatically arise with a peripheral onset stimulus. The present study controls for passive or reflexive activations. Hence any differences we report can be attributed to active processes.

It appears that even when the animal need remember only the sample shape, its position is represented in visual cortex. One possible explanation is that location is a special case compared with other stimulus attributes (Kwak and Egeth 1992; Nissen 1985; Tsal and Lavie 1993). That is, attending to any attribute of a stimulus, such as its shape or color, necessarily entails directing attention to its location. However, we also found shape-selective delay activity in many of those units that was not affected by what task the animal was performing. Of the total of 122 units, only 17% (7/41) of the shape-selective units and 16% (14/87) of the spatially selective units showed a significant difference depending on the task instruction.

In the location task, after the sample is presented, the animal knows unequivocally which position to attend, remember, and plan an eye movement to, for a reward 100% of the time. This is not true in the shape task, and this difference is reflected in the saccade latencies. In the shape task, on one-third of the trials, the sample shape appears at test onset in the same location. Even though these trials are identical to a portion of location task trials, the animal initiates a saccade 43 ms later. Hence although the behavior of the animal is strikingly different, no differences appear in the delay period activity of many LIP units. Although parietal cortex has been the focus of much work on behavioral relevance (Colby et al. 1996) or decision-related variables (Platt and Glimcher 1999; Roitman and Shadlen 2002; Snyder et al. 1997), the present findings suggest that active task-dependent signals comprise only a part of the delay period activity that is present in most LIP units. LIP projects strongly to frontal regions where perhaps there is greater discrimination between tasks during the delay period and hence a more robust neural correlate for these active processes (cf. Goldberg and Segraves 1987). Interestingly, recent fMRI findings are supportive of such a view and suggest that within the frontoparietal networks that control saccade generation, the human frontal eye fields, but not the intraparietal sulci, are critically involved in coding both the readiness and intention to perform a particular movement (Connolly et al. 2002).

What then does the delay period activity in the majority of LIP units (e.g., 71% for spatial delay effects) signify? We argue here that much of these effects represent a more passive or reflexive trace of the sample. For decades, various researchers have distinguished between a reflexive and voluntary form of spatial selective attention (e.g., see Klein et al. 1992; Seidlis...
et al. 2003). Similar distinctions have been argued to exist with respect to memory processes (Moscovitch 1995; Rugg et al. 1998; Squire 1987) and saccades (Briand et al. 1999; Guittion et al. 1985; Pierrot-Deseilligny et al. 1991). When a peripheral stimulus is presented, attention is automatically and exogenously drawn to the location of the stimulus, a passive memory trace is formed, and a reflexive or “default” eye movement plan is generated (see e.g., Rafal et al. 1989; Rizzolatti et al. 1994). Our data suggest that some of the ubiquitous delay period activity in LIP primarily represents such passive traces. Hence even in the shape task when the animal knows that the sample location is not likely to be the saccade goal, the animal still has shorter saccade latencies (44 ms) if the matching shape happens to appear in the sample location.

However, this spatial delay activity does not seem to reflect a wholly reflexive process as presentation of the sample shape while an animal is only passively fixating results in a reduced magnitude of the spatially-selective delay activity in 39% of the units compared with the spatially selective delay activity in the matching tasks. This percentage of active task-related neurons is similar to some previous studies demonstrating behavioral modulation of neuronal responses in ~40% of parietal neurons (e.g., Bushnell et al. 1981; Platt and Glimcher 1999). Nevertheless, in our study, the data from our more controlled comparison between the matching tasks suggest that much of these active modulations are not specific to the to-be-remembered event. Hence some of these active modulations in our study perhaps reflect the cognitive processes of alerting or vigilance that are required in the matching task compared with passive fixation (Posner and Dehaene 1994).

Neural correlates of voluntary motor plans in LIP

Nevertheless it is essential to recognize that the task-related differences we do report during the sample and delay period, even if found in only some neurons, are significant and also very important. The existence of these active task-dependent signals is in agreement with previous studies. In particular, during the delay period, the animal knows where to plan the upcoming saccade in the location-matching task but not the shape-matching task, hence an increased activity in the location-matching task during the delay period would be consistent with previous studies. In particular, during the delay period, the animal knows where to plan the upcoming saccade in the location-matching task but not the shape-matching task, hence an increased activity in the location-matching task during the delay period would be consistent with the idea that this activity represents a voluntary attentional or motor planning signal (Colby and Goldberg 1999; Snyder et al. 1997). Furthermore, the task-related differences we report
demonstrate that the animals are not actively performing both tasks.

Neural correlates of attention to shape in LIP

In addition to the units that demonstrated active task-dependent responses during the delay period, there was a similar percentage of largely nonoverlapping units that demonstrated active task-dependent responses during the sample period (Fig. 11A). During the sample, test, and EM periods, activity tended to be stronger while the animal was performing the shape task, whereas during the delay periods, activity tended to be stronger while the animal was performing the location task. We suggest that enhanced activity to the sample stimulus in the shape task represents a physiological signature for attention to shape in LIP.

Previous work (Platt and Glimcher 1999) has suggested that LIP neurons are insensitive to changes in the behavioral relevance of a stimulus unless it is the target of a saccade. In the location task, the sample stimulus indicated the target location of the upcoming saccade. In contrast, in the shape task, the sample location was not likely to be the target location of the upcoming saccade. Nevertheless, we found that some neurons in LIP showed enhanced activity for the sample in the shape task. Unlike enhancement for a stimulus in a location that will be the target of an upcoming saccade, there is a stronger response for a stimulus in the same location that only occasionally is the target location of an upcoming saccade (see also, Bisley and Goldberg 2003).

The explanation that enhanced activity to the sample stimulus in the shape task represents a physiological correlate for attention to shape is simple and parsimonious. For both tasks, the onset of the sample automatically results in spatial attention to this position. Furthermore this onset is salient for both tasks; the animal needs to spatially attend to this onset to remember either the sample’s position or shape. Hence both passive and active spatial attention effects during the sample do not differ between tasks and hence would not be obvious during the sample period. However, only in the shape task does the animal need to attend to the sample shape to perform the task. Shape is irrelevant in the location task. During the delay period, the active task-dependent traces are dominated by enhanced activity for the remembered spatial location. Finally, when the test
array is presented in the location task, this is a go signal to execute the planned eye movement. In the shape task, the animal needs to attend to the shapes (CHECK) before making the proper eye movement. Immediately after test onset, some units show enhanced activity during the shape task (Figs. 11B and 15). This is true for some units even in the subset of trials that are identical in the location and shape tasks, in which the animal makes the same saccade to the same stimulus (Fig. 17A). For this reason, the present study differs somewhat from other recent studies that also show that the activity of LIP neurons is dynamic and changes as a task progresses (e.g., Cohen et al. 2002; Platt and Glimcher 1999; Sabes et al. 2002; Shadlen and Newsome 2001). Namely, in the present study, activity differences persist later in the trial even when the animal is encoding the same movement plan, due, presumably, to the fact that different processes are required for the ultimate coding of the same eye movement.

Effects of training and task effects

An alternative explanation for the lack of differences in neuronal response between the two tasks for many units is that the animals actively attended to and remembered both the sample shape and location on every trial due to the animal’s training history. That is, Grunewald et al. (1999) have shown that after training animals on an auditory-saccade task training, 12% of neurons in LIP become active de novo for auditory stimuli in a passive fixation task. They suggest that once the animals have learned that these stimuli are important for oculomotor behavior that some units in LIP become active for these auditory stimuli in a passive fixation task. As Grunewald et al. (1999) suggest, it is possible that training unmasks connections that existed all along but were silent. Further, although not suggested by the authors, it is possible that these units are active for other behaviorally relevant auditory stimuli, but not the bandlimited white noise stimuli that were presented (Gifford and Cohen 2005). Hence, the change in responsiveness may reflect a change in tuning of the auditory cells to include this normally ethologically insignificant sound (cf. Linden et al. 1999). Such an increase of task relevant stimulus responses has been shown before in visual areas (Kobatake et al. 1998). Interestingly, Grunewald et al. (1999) only found changes in auditory stimulus responses and not visual. It is possible that this difference may be a difference between areas. Alternatively, it may be that these effects were reduced in the
It remains possible that the animals are actively doing something different for the two tasks (because passive conditions are kept identical). Nevertheless, it remains to be seen how much of this training effect is a change in active, “top-down” processes but passive processes, as all the recordings in Kobatake et al. (1998) were done in anesthetized animals before and after training. Hence, it remains to be seen how much of this training effect is a passive process and how much involves active processes. In the present study, we examine and characterize active processes. It is possible in the present study that the animal would choose a strategy of actively attending to and remembering both the sample shape and location on every trial. It is unlikely the animal chose such a strategy due to the difficulty of the tasks and the cost of such a strategy both in time and accuracy.

There is no evidence in the present study that would suggest that the animal waited until the test array to decide which task to perform and figure out what (sample shape or location) was the relevant remembered event needed for the decision: the average saccade latency in the location task to the test array was 182 ms. In fact, in the present study, due to differences in the animals’ behavior (i.e., different EM responses depending on task, and difference in RT between task conditions), we are able to state unequivocally that the animals are actively doing something different for the two tasks (because passive conditions are kept identical). Nevertheless, it remains possible that at least on some trials that the animals could choose to actively remember both the sample shape and sample location.

Linden et al. (1999) examined the effects of task on single-unit responses in LIP and report that the spatially tuned responses during the delay period are stronger during a memory saccade task than during the delay of a fixation task for both auditory and visual stimuli. However, they also note that response differentials in the delay period of fixation trials are significantly correlated with response differentials in the delay period of memory-saccade trials and suggest that auditory and visual stimuli may evoke “default” attentional or movement plans that activate area LIP during the delay period of the fixation task, even though the fixation task does not require either an eye movement or a redirection of attention. Such a view has also been postulated by others (Bracewell et al. 1996; Snyder et al. 1997, 1998). The present study tries to differentiate between these default (or reflexive) attentional or movement plans and the more active voluntary attentional or movement plans. It is possible that there may be a relationship between these processes. That is, perhaps some units that are involved in reflexive spatial attention may also be involved in voluntary spatial attention as opposed to these processes occurring in independent or separate populations of units. The differences we report between the passive fixation task and the match-to-sample task represent active processes. In addition, the more carefully controlled comparisons between the two matching tasks and the differences we report for these comparisons also represent active processes that are specific for the to-be-remembered event. We see a number of units in LIP that carry these active attentional and movement signals.

In sum, the existence of some neurons with differences between the two matching tasks during the delay period supports the idea that the animals did not actively attend to and remember shape and location equally when performing the two tasks. Further, we also report that some LIP neurons show differential responses to the same sample stimulus depending on which task the animal is performing. These findings suggest that the animals, even early in the trial at the presentation of the sample, are differentiating between the two tasks. Finally, and

![Model of cognitive processes required in the matching tasks.](image-url)
perhaps most directly, average saccade latencies for identical trials in the two tasks (i.e., identical both in stimuli at sample and test and with identical response) were 43 ms longer (and 2.4% more errors) on shape-matching trials than on location-matching trials. Taken together, these observations show that the animals indeed adopt different behavioral sets between tasks but that much of the spatially-selective delay period activity in area LIP is independent of what the animal voluntarily attends to and remembers, and some of this activity represents reflexive shape and spatial processes.

Task difficulty

An alternative explanation for the enhanced activity to the sample stimulus in the shape task could be a difference in task difficulty (i.e., the shape task is a more difficult task). Although there are longer latencies in the shape-matching task (259 ms) than the location-matching task (181 ms), there were no differences in error rate (22.9 vs. 21.2%, respectively). For an argument that differences in task difficulty could explain the present findings, a number of...
specific ad hoc assumptions need to be made. First, it would have to be explained how increased task difficulty during the shape-matching task was limited in time (dominating during the sample or after test presentation), even though the animal is cued to this particular task at the start of the trial. Further, task difficulty during the shape-matching task would need to come and go very rapidly during the trial (present at sample, gone at delay, present after test onset). Hence, if task difficulty is defined as being present only when the animal needed to attend to and discriminate shapes, it is not clear how this differs from an explanation that suggests a neural correlate for attention to shape. Recent work has shown changes in the onset of attentional modulation in V4 neurons across time (Ghose and Maunsell 2002). These attentional effects occurred in a task that drastically altered the temporal occurrence of the attended event. In the present tasks, the timing of the stimuli are somewhat variable, but identical across both tasks. The important difference between the shape and location tasks is not in the timing of the to-be-attended event but rather in the fact that, in the shape task, when the sample appears, the animal needs to attend to and remember its shape.

In addition, if latency is to be considered our measure of task difficulty and the monkey is 43 ms slower to initiate an EM on the “pure” shape task trials than the pure location task trials, one might argue that the increased activity during the sample period is due to this increased task difficulty. However, the monkey is also 44 ms slower (a nearly equal amount) to initiate an EM on the “non-pure” shape trials compared with the pure shape trials. Even though there is an increased task difficulty on these non-pure trials, there is no accompanying increased activity during the sample period due to this increased task difficulty. So one would need to postulate multiple forms of task difficulty, and these different kinds express themselves on different trial types at different time periods. One might argue that these different task difficulties represent the different cognitive processes that are required. Task difficulty is an important variable; but there is no simple account that could explain the present findings. Future work will need to examine the effects of task difficulty independently of other variables such as attention to shape or change in attentional and motor plans.

In sum, in a carefully controlled design, we find that much delay period activity in LIP represents a passive or reflexive process. However, we do find some neurons that represent active or voluntary spatial signals (e.g., attention, memory, motor-preparatory). During the sample and after the onset of the test array, some neurons in LIP demonstrate active signals that could represent a neural correlate for attention to shape, a property not previously described in visual cortex. Interestingly, the percentage of units in LIP showing task instruction effects at sample is similar to what we have reported in AIT for units recorded in the same monkeys performing the same matching tasks (Sereno et al. 1997). Recent studies have demonstrated nonspatial processing in the dorsal pathway (Gifford and Cohen 2005; Sereno and Maunsell 1998; Sereno et al. 2002; Toth and Assad 2002; see also Cohen et al. 2004). It remains to be seen what, if any, differences there are in shape effects these two cortical areas that are considered late stages in two different cortical processing streams.

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