Published in final edited form as:
J Vis. ; 10(1): 12.1–1216. doi:10.1167/10.1.12.

Effects of task and coordinate frame of attention in area 7a of the primate posterior parietal cortex

Justin B. Rawley and
Department of Neurobiology and Anatomy, Wake Forest University School of Medicine, Winston-Salem, NC, USA

Christos Constantinidis
Department of Neurobiology and Anatomy, Wake Forest University School of Medicine, Winston-Salem, NC, USA

Abstract

The activity of neurons in the primate posterior parietal cortex reflects the location of visual stimuli relative to the eye, body, and world, and is modulated by selective attention and task rules. It is not known however how these effects interact with each other. To address this question, we recorded neuronal activity from area 7a of monkeys trained to perform two variants of a delayed match-to-sample task. The monkeys attended a spatial location defined in either spatiotopic (world-centered) or retinotopic (eye-centered) coordinates. We found neuronal responses to be remarkably plastic depending on the task. In contrast to previous studies using the simple version of the delayed match-to-sample task, we discovered that after training in a task where the locus of attention shifted during the trial, neural responses were typically enhanced for a match stimulus. Our results further revealed that responses were mostly enhanced for stimuli matching in spatiotopic coordinates, although the proportion of neurons modulated by either coordinate frame was influenced by the behavioral task executed.

Keywords

neurophysiology; intraparietal sulcus; neglect; attention; saccade; training

Introduction

The posterior parietal cortex of humans and other primates plays a critical role in representing visual–spatial relationships andmediating spatial attention (Constantinidis, 2006; Goldberg, Bisley, Powell, & Gottlieb, 2006). One of the most striking conditions that follows posterior parietal damage, typically of the right hemisphere in humans, is neglect (Mesulam, 1999). Neglect patients are unable to perceive sensory stimuli on the side contralateral to the lesion (egocentric neglect) and/or to process the contralateral side of objects even if they appear in their ipsilateral field of view (allocentric neglect). Neurophysiological studies in primates have revealed that posterior parietal neurons are powerfully modulated by selective attention, including bottom-up and top-down processes (Bisley & Goldberg, 2003; Buschman & Miller, 2007; Constantinidis & Steinmetz, 2001a; Gottlieb, Kusunoki, & Goldberg, 1998). They are also modulated by the angle of gaze (position of the eyes in the orbit or rotation of the head),

Corresponding author: Christos Constantinidis, cconstan@wfubmc.edu, Department of Neurobiology and Anatomy, Wake Forest University School of Medicine, Medical Center Blvd., Winston-Salem, NC 27157-1010, USA.

Commercial relationships: none.

which allows the neural population to represent information about the position of the stimulus in multiple coordinate frames, e.g., relative to the eyes, head, or body (Andersen, Essick, & Siegel, 1985; Pouget & Snyder, 2000; Snyder, Grieve, Brotchie, & Andersen, 1998).

How these factors interact with each other has not been determined until now. In order to investigate this question, we recorded activity from neurons in posterior parietal area 7a. Area 7a comprises the end stage of the dorsal visual pathway (Felleman & Van Essen, 1991), placing it in a key position to process information about location and spatial relationships of stimuli in the visual field and feed information to frontal lobe areas. Although the homology of human and monkey parietal areas is not entirely clear, area 7a appears to be most similar to human areas 39/40, which include the temporal-parietal junction (TPJ) in humans (Buckner, Andrews-Hanna, & Schacter, 2008; Vincent et al., 2007). This region of the human parietal cortex is often referred to as the "ventral attention system" and has specifically been implicated in allocentric neglect (Corbetta, Patel, & Shulman, 2008; Hillis et al., 2005; Karnath, Ferber, & Himmelbach, 2001; Medina et al., 2009). Understanding how neurons represent the locus of attention in this area is essential for uncovering the nature of perceptual deficits in neglect.

Previous neurophysiological studies in area 7a have demonstrated robust effects of directed attention (Constantinidis & Steinmetz, 2001a, 2001b, 2005; Raffi & Siegel, 2005; Steinmetz, Connor, Constantinidis, & McLaughlin, 1994; Steinmetz & Constantinidis, 1995). In the present experiment, we adapted a behavioral paradigm that has been used extensively in the study of attentional effects in area 7a: a spatial version of a delayed match-to-sample task. In this task, neurons respond significantly differently to the same stimulus depending on whether it is a match (appears at an attended location) or not. We exploited this property in order to test how neuronal responses are modulated when visual stimuli appear at either the same retinal coordinates (retinotopic frame) or the same coordinates on the screen (spatiotopic frame).

Materials and methods

Two male macaque monkeys (*Macaca mulatta*) weighing between 5 and 8 kg were trained in the behavioral tasks described below. Neurophysiological recordings from single, isolated neurons were made in area 7a of the posterior parietal cortex. All experiments were performed in accordance with guidelines set forth by the National Institutes of Health, reviewed and approved by the Institutional Animal Care and Use Committee of the Wake Forest University.

Behavioral task

Subjects were seated in a purpose-built primate chair with their heads fixed while they viewed stimuli displayed on a monitor 60 cm in front of them. The monkeys performed variants of a spatial, delayed match-to-sample task. During each trial they were required to remember the location of the first stimulus presented briefly on the screen as a cue. They would then report when they saw a stimulus reappear at the same location as the cue, thus constituting a match. They were required to ignore any intervening nonmatch stimuli that appeared at other locations (Figure 1A). The animals had to pull a behavioral control lever to start each trial and release this lever to signal a match stimulus. A pseudo-random number of zero, one, or two nonmatch stimuli could be presented before the match.

The monkeys were required to perform this task while maintaining gaze of a 0.2° fixation point, which appeared prior to the presentation of the cue. Eye position was monitored online with an infrared eye tracking system (model RK-716, ISCAN, Burlington, MA) and trials were terminated if eye position deviated from a predetermined window, typically of 2° size. Eye data were sampled, digitized, and recorded at 240 Hz.

Stimuli consisted of 1.5° red or green squares. Stimuli of the same color were always used to test each neuron and the color of the stimulus had no significance for this experiment. Stimulus locations were constrained to a 5 × 5 grid centered in the monitor of equally spaced 10° increments (Figures 1D and 1E). The interval between the cue and the following stimulus was always 1 s; all other stimuli were separated by 500-ms delay periods. Subjects were required to wait during the full presentation of the match, and after the match disappeared they had 500 ms to release the lever in order to receive a liquid reward. Early lever release constituted an error and aborted the trial. Subjects did not receive a reward on error trials, but instead heard one of two feedback tones indicating the type of error (incorrectly timed lever release, or gaze deviation from the fixation window).

In the basic version of the task the fixation point remained fixed throughout the trial, hence the cue and match stimuli appeared at the exact same locations (Figure 1A). We refer to stimuli appearing in this task as “fixed match” and “fixed nonmatch” stimuli. All stimuli appeared at locations in a 10° grid (Figure 1D; same as inner 3 × 3 grid in Figure 1E). Nine randomly interleaved trial types showed the cue/match stimulus in each of the nine grid positions to determine the locations in which neurons responded optimally to stimulus appearance. The number of intervening nonmatch stimuli between the cue and match varied pseudo-randomly to prevent monkeys from associating a particular location with a specific number of nonmatch stimuli.

Two other variants of the task were used. In the first variant (Figure 1B) subjects were trained to report appearance of a match stimulus at the same location *on the screen* relative to the cue. We refer to this paradigm as the “Screen Match Task”. In this task, the fixation point sometimes appeared at an eccentric location (10° peripheral to the center in one of the cardinal directions). In these trials, 500 ms after the cue presentation, the fixation point moved to the center of the screen. Subjects were required to shift their gaze within 450 ms to acquire the new, central fixation point. Appearance of a subsequent stimulus now constituted a match only if it appeared at the same location as the original cue, in screen coordinates.

The animals were subsequently retrained over a period of several months in a variant of the task in which they had to report appearance of a match stimulus at the same *retinal position* relative the cue (Figure 1C). We refer to this task as the “Retinal Match Task”. For example, if the fixation point moved by 10° to the left, the monkey needed to release the lever after a stimulus presentation 10° to the left of the cue on the screen (retinocentric coordinates). The stimulus that constitutes a match in the context of each task and requires a lever release is referred to as a “behavioral match”. Recordings were initially performed using the Screen Match task. A second set of recordings was performed a few months later, while the monkeys performed the Retinal Match task.

During recording sessions, the monkeys first performed the basic task (Figure 1A), which allowed us to determine whether neurons responded to the visual stimuli and to locate their receptive fields. We then tested neurons with either the screen or retinal match paradigm, placing the stimuli of interest at the neuron’s receptive field and its diametric location.

The Screen Match and Retinal Match sets consisted of trials representing 10 conditions (see Auxiliary Figure 1), the first five of which always displayed the second stimulus (first stimulus after the cue) in the neuron’s receptive field and the other five at the diametric location, out of the receptive field. In these trial types the second stimulus could be: (1) match with no movement of the fixation point (fixed match), (2) match in retinal coordinates (retinal match), (3) match in screen coordinates (screen match), (4) nonmatch with no movement of the fixation point (fixed nonmatch), (5) nonmatch with moving fixation. The difference between the Screen Match and Retinal Match versions of the task is that in the Screen Match task, the test stimulus

in trial type 3 is the behavioral match to which the animal needs to respond with a lever release, whereas in trial type 2, the second stimulus is a behavioral nonmatch and the animal must wait for an additional stimulus to appear in the original screen location of the cue (Figures 1B and 1C). Because the fixation point is always in the center of the screen before the onset of the second stimulus, the latter always falls within the central 3 × 3 grid. In this manner, the neuron's response to a stimulus in the receptive field could be measured under different operant conditions in which the stimulus dictated action or was to be ignored. Trials were randomly interleaved in blocks containing each possible trial type. Typically ten correct trials of each trial type were collected during neurophysiological recordings.

A software system that was developed in the laboratory using Matlab (Mathworks, Natick, MA) and psychophysics toolbox (Brainard, 1997) controlled the visual stimulus display, synchronized behavioral and physiological data, and verified the lever and eye position online during trial execution (Meyer & Constantinidis, 2005).

Training

Monkeys were trained to perform the task in the following sequence. They were initially shown a 0.5° fixation target in the center of the screen, on which they had to fixate while they held back the behavioral control lever. Once the fixation target was extinguished, subjects had to release the lever within a predetermined reaction time to receive a reward. Both the fixation target presentation duration and the reaction time could be set by the operator. Target presentation duration was gradually increased while reaction time incrementally decreased to 500 ms. Upon mastering the fundamental components of fixating, using the lever to start the trial, and releasing the lever for reward, the additional element of behavioral stimuli was added. The animal was next presented with trials involving immediate match presentations, in which the cue and match stimulus was repeated after a 1-s interval. The subject was initially shown the match in only one location and was rewarded for releasing the lever after the second stimulus disappeared. Gradually, more locations and intervening nonmatch stimuli were included until the animal could perform the basic version of the match-to-sample task (Figure 1A). Subjects were then trained to do the Screen Match variant of the task (Figure 1B) and all physiological data for this part of the study were recorded over a period of several months. Animals were finally retrained on the Retinal Match version of the task (Figure 1C) and the second data set was collected.

Surgery and recording

Once the subjects could perform the Screen Match task, an anatomical MRI was acquired to determine the stereotaxic coordinates of posterior parietal area 7a (Figure 2). A 20-mm diameter craniotomy was then made over the region and a recording cylinder was implanted over it. Extracellular recordings were made using up to four electrodes spaced 0.2–1.5 mm apart. The geometric center of the cylinders placed in three hemispheres was 8 mm posterior to the interaural line and 13 mm lateral to the midline. Placement of the cylinders was somewhat constrained by the head-post and anchoring screws in our head implant system; recordings were collected primarily from the medial part of the cylinders. Each of the four electrodes could be advanced independently into the cortex using an electronic microdrive system (EPS microdrive, Alpha-Omega Engineering, Nazareth, Israel). Electrodes moved within stainless steel guide tubes that were placed onto the dura with a mechanically driven microdrive (FHC, Bowdoin, ME). The electrode/guide tube position was fixed laterally by a grid system (Crist Instruments, Hagerstown, MD). A second grid with holes offset from center by 0.5 mm was also used to increase the number of available areas to sample. Two types of electrodes were used: epoxylite-coated tungsten with a diameter of 125 μm and an impedance of 4MΩ measured at 1 kHz (FHC, Bowdoin, ME); and glass-coated tungsten electrodes, with a diameter of 250 μm and an impedance of 1 MΩ at 1 kHz (Alpha-Omega Engineering, Nazareth, Israel).

Up to four electrodes were housed within single guide tube, segregated by spacers that kept them electrically insulated from one another and insured independent movement (four-electrode, single guide tube manifold, FHC, Bowdoin, ME). Recordings with one or two electrodes were performed in some sessions, with each electrode housed within its own guide tube (single electrode and single guide tube or two-electrode, two-guide-tube manifold, FHC, Bowdoin, ME). Signals isolated by each electrode were amplified, band-pass filtered between 500 Hz and 10 kHz, then sampled at 40 kHz, and digitized (APM data acquisition system, FHC, Bowdoin, ME). A 1.75-ms sample was captured around each action potential and was stored for offline analysis.

Data analysis

We implemented the automated clustering algorithm KlustaKwik (Harris, Henze, Csicsvari, Hirase, & Buzsaki, 2000) in Matlab to separate recorded waveforms into signals from individual neurons. Groupings were made on the basis of predefined user features such as the peak, valley, and first principle component of each waveform. Spike trains were constructed for each neuron using the timestamps of the peak of each waveform associated with the neuron, and then average firing rates were computed for each task epoch. First, visually responsive neurons were identified by comparing discharge rate during the interval of stimulus presentation in any task to the baseline firing rate recorded within the 500 ms preceding the cue. Those neurons that showed significant rate elevation during the presentation of any stimulus (paired *t*-test, $p < 0.05$) were included in the analysis. To ensure that neuronal responses remained stable during the data set analyzed we identified recordings in which a significant effect of trial presentation sequence was evident in the baseline firing rate (ANOVA, $p < 0.05$), e.g., due to a neuron disappearing or appearing during a run, as we were collecting data from multiple electrodes. Data from these sessions were truncated so that analysis was performed on a range of trials with stable firing rate. A spike density function was then obtained by convolving the spike trains with a Gaussian kernel function of 10 ms standard deviation, producing a smoothed and continuous function. All further analysis was performed on firing rates computed based on these spike density functions. Average responses during the interval of stimulus presentation were used for all comparisons.

To test if a neuron's response to visual stimulation in the receptive field varied depending on task condition, a one-way ANOVA test was performed comparing firing rates during the presentation of the second stimulus. Comparisons always involved presentation of identical stimulus in the receptive field, under the same angle of gaze, differing only in terms of the significance of the stimulus in the task depending on the preceding, cue stimulus. Neurons with significant effects (ANOVA test, $p < 0.05$) were considered to be modulated by the match or nonmatch status of a stimulus. We refer to these neurons as "Task Selective".

Population responses in both tasks were evaluated using Peri-Stimulus Time Histograms (PSTHs) constructed from the mean firing rates of multiple neurons. PSTHs span the epochs before the presentation of the fixation through the delay after the second stimulus. We compared responses to match and nonmatch stimuli in trials where the fixation point did not move as well as during trials in which there was a fixation jump. These comparisons were evaluated in both Retinal and Screen Match variants of the task. Linear regression analyses were performed to test the relationship between the firing rates of neurons in various task conditions.

Results

Database

We analyzed neuronal activity from area 7a of the posterior parietal cortex of two monkeys trained to perform a spatial delayed match-to-sample task. In the basic task, the monkeys were required to maintain fixation on the center of the screen, observe and remember the position of a cue stimulus, ignore intervening stimuli appearing at different locations, and release a lever after a stimulus appearing at the same location as the cue (Figure 1A). We used two additional variants of this task to probe the influence of coordinate frame of attention on the responses of parietal neurons. The first variant contained trials in which the location of the fixation target shifted on the screen after the presentation of the cue and subjects had to respond when a stimulus appeared at a location that matched the position of the cue in screen coordinates (Figure 1B). The second task also contained trials in which the fixation target moved. In this task subjects had to report when a stimulus matched the cue in terms of its position on the retina, which might now correspond to a different location on the screen (Figure 1C). We refer to these tasks as "Screen Match" and "Retinal Match," respectively. Trials with moving fixation point were randomly interleaved with trials that required no change in gaze angle, in both tasks (Auxiliary Figure 1).

Recordings were performed in posterior parietal area 7a, on the crown of the gyrus bounded by the intraparietal and superior temporal sulci (Figure 2). A total of 72 visually responsive neurons was tested in their receptive field with the Screen Match task (46 and 26 from each of the two monkeys, respectively). Another 138 neurons were recorded with the Retinal Match task (89 and 49, respectively). Monkeys were initially trained to execute the Screen Match task (as well as the basic task) and neurophysiological data were collected. The same animals were subsequently retrained on the Retinal Match task (while they continued to perform the basic task) and a second round of recording was conducted.

Behavioral performance

We computed the monkeys' performance in the task by calculating the percentage of correct responses, after excluding eye errors due to breaks in fixation. During the sessions in which area 7a neurons were recorded in the Screen Match task, the monkeys performed 83% correct trials (90% and 74% for our two animals, respectively). The error rate of the second monkey was inflated by timing errors involving premature lever releases before the offset of the match stimulus; such errors were observed in all tasks and types of trials, including those where the fixation point did not move. After retraining in the Retinal Task, the average performance in sessions where area 7a neurons were recorded was 78% (84% and 70%, respectively). The slightly increased error rate in the Retinal Task was stable during the time period of recordings and represented asymptotic performance: no significant effect of session number on performance was seen in this task (regression analysis, $p > 0.2$ for both monkeys), and performance in the first half sessions was essentially identical to the last half (84% vs. 83% correct for the first monkey and 71% vs. 69% for the second one).

Screen match task

Our analysis of neural responses sought to determine whether neurons in area 7a responded differently to stimulus presentations, depending on the location and coordinate frame of the match. Previous studies demonstrated significant differences in neuronal firing rates between stimulus conditions; these most prominently described reduced responsiveness to a stimulus that constitutes a match to a previously cued location, as compared to the same stimulus when it appeared as a nonmatch (Steinmetz et al., 1994). We similarly identified neurons whose responses to identical stimulus presentations in the receptive field were significantly modulated, depending on whether the stimulus constituted a match or nonmatch stimulus in

the task. This relationship was further examined under the conditions in which the match was defined in screen and in retinal coordinates. A total of 35 out of 72 neurons tested displayed significant modulation to these stimulus conditions (ANOVA, $p < 0.05$). We refer to these neurons as "Task Selective". We were surprised to discover that the majority of Task-Selective neurons in our experiment (21/35) exhibited a stronger response to a stimulus appearing as a fixed match (with no movement of the fixation point) than the same stimulus appearing as a fixed nonmatch. Responses from a representative neuron are shown in Figure 3. This neuron responded more strongly to a match stimulus (Figure 3A) than to the identical stimulus appearing as a nonmatch (Figure 3B). When we examined this neuron's responses to a stimulus appearing at the same screen position as the cue (Figure 3C) we determined that the neuron responded better to this screen match stimulus compared to a stimulus appearing at the same retinal coordinates as the cue (Figure 3D). This response was specifically related to the stimulus presentation rather than nonspecific factors like the release of the lever that followed a match presentation because no responses were elicited after presentation of a match stimulus out of the receptive field (Figure 3E). This result was representative of our sample (Figure 4, left). Specifically, 17/21 (81%) of Task-Selective neurons with higher responses for a fixed match stimulus also responded best for a Screen Match (which was a behavioral match stimulus requiring a lever release) over a Retinal Match stimulus.

The population Peri-Stimulus Time Histogram in Figure 5 demonstrates that the majority of neurons responding preferentially to a fixed match also preferred a screen match over a retinal match (Figures 5A and 5B). The mean firing rate during the presentation of the screen match stimulus was significantly higher than the response to the retinal match for this population of neurons (*t*-test, $p < 0.05$). This analysis also revealed that activity following cue presentation in the receptive field was sustained during the delay period, while the monkey presumably remembered and attended the cued location (Figures 5A and 5B). However persistent activity during the delay period was a property present only in a minority of neurons. Only 7/21 Task-Selective neurons exhibited persistent activity in the last half second of the delay period following the cue presentation that was significantly elevated relative to the baseline (paired *t*-test, $p < 0.05$ corrected for multiple comparisons). The majority of neurons did not exhibit sustained activity after the cue presentation, yet appearance of a fixed match or screen match produced an elevated response over a fixed nonmatch or retinal match stimulus for those neurons.

To determine if a neuron's preference for a screen vs. retinal match could be determined from its preference for a fixed match vs. fixed nonmatch, we examined the difference in firing rate for these two pairs of conditions (Figure 6, left). A regression analysis revealed that there was a significant relationship between the two measures ($p < 0.005$). In other words, the difference in firing rate between fixed match and fixed nonmatch stimuli could predict the difference in responses to a screen match vs. a retinal match, on a neuron-by-neuron basis. The correlation coefficient between the two variables was $r = 0.50$ and the slope of the regression curve was $\alpha = 0.56$. Seventeen of 35 points in Figure 6 (left) fell in the upper right quadrant, confirming that responses were higher for both the fixed match stimulus and the screen match stimulus, which in this task constituted the behaviorally relevant match.

Neuronal preference for a fixed match over a nonmatch stimulus remained unchanged even when intervening stimuli appeared between the cue and the match. Mean discharge rates to a fixed match stimulus appearing immediately after the cue and after two intervening stimuli were significantly correlated ($r = 0.85$, $p < 0.005$). A significant relationship between the difference of match minus a nonmatch response was also present ($r = 0.69$, $p < 0.005$), when the stimulus appeared immediately after the cue and after two intervening stimuli (Figure 7, left). Overall, our findings from experiments in the Screen Match task indicate that individual

neurons had a set magnitude of response for stimuli that signified a behavioral match vs. a nonmatch and this relationship was reliable across task conditions.

To ensure that the preference for match stimuli across the population of neurons was not dependent on factors related to the behavioral response (as we demonstrated for the sample neuron in Figure 3E) we compared responses to a fixed match stimulus vs. a fixed nonmatch stimulus appearing out of the receptive field. Neurons that exhibited higher firing rate for a fixed match stimulus over a nonmatch stimulus in the receptive field showed no significant difference for stimuli presented out of the receptive field, although these stimuli required the same stereotypical lever release for the match, or withholding of release for the nonmatch; in fact the opposite trend was present (9.1 sp/s for nonmatch vs. 5.9 sp/s for match stimulus; paired *t*-test, $p > 0.05$).

We similarly tested whether elevated neuronal responses to the screen match stimulus might be somehow inflated due to the effect of the eye movement prior to the appearance of the stimulus. This seemed unlikely since, unlike LIP, area 7a neurons are only weakly modulated by eye movements (Blatt, Andersen, & Stoner, 1990). Furthermore the eye movement in the screen match condition was directed away from the neurons' receptive field so as to bring the stimulus into the receptive field for the first time, after the cue presentation (see Figure 3C). Nonetheless, we compared responses to stimulus conditions involving nonmatch stimuli appearing in the receptive field with and without an intervening eye movement in the same direction as in the screen match condition. The average responses to the two conditions were virtually identical (7.6 sp/s vs. 7.7 sp/s) and not significantly different from each other (paired *t*-test, $p > 0.05$).

These results indicate that the preference we observed for match stimuli was related specifically to their location and the significance of the stimuli in the context of the task rather than the behavioral response or the effects of the eye movements. This finding could mean that neurons in area 7a of the posterior parietal cortex represent match stimuli in screen coordinates. However, it could also reflect that the behavioral paradigm required the monkey to respond to a stimulus matching the cue in screen coordinates. In order to distinguish between these two possibilities, we tested the same two monkeys in a task that now required them to respond to a stimulus that constituted a match in retinal coordinates. We also sought to determine whether increased responsiveness to the match was specifically dependent on the screen match paradigm, in contrast to the decreased responses to the match stimulus observed in previous studies (Constantinidis & Steinmetz, 2001b; Steinmetz & Constantinidis, 1995).

Retinal match task

After retraining the same animals, we recorded from a total of 139 neurons in the Retinal Match task in area 7a, revisiting some of the same cortical sites sampled prior to training. Of those neurons, 46 responded differentially to an identical stimulus in their receptive field, depending on the preceding cue (ANOVA, $p < 0.05$). The percentage of neurons displaying task modulation in the Retinal Match task was significantly lower than in the Screen Match task (χ^2-test, $p < 0.05$).

Figure 8 depicts the responses of a neuron tested with the Retinal Match task. As in the sample neuron recorded in the Screen Match task, we saw enhanced responses to the fixed match over nonmatch (Figure 8A). Across the population of neurons, 28/46 (61%) exhibited a stronger response to a fixed match than a fixed nonmatch stimulus. This result essentially replicated our findings from the Screen Match task and stood in contrast with the previous studies mentioned above, where the typical effect was overwhelming suppression of match responses. An overall preference for the fixed match stimulus was observed in both of our monkeys: 63% and 52% of Task-Selective neurons responded better to the fixed match over the fixed nonmatch

stimulus, respectively (pooled across both tasks). As we did for the previous data set, we compared responses to the fixed match stimulus when it appeared immediately after the cue and when it appeared after two intervening stimuli. Responses were again strongly correlated ($r = 0.82$, $p < 0.005$). The difference in firing rate between fixed match and nonmatch stimuli was also significantly correlated (Figure 7, right) for stimuli appearing immediately after the cue vs. stimuli appearing after two intervening stimuli ($r = 0.76$, $p < 0.005$). These results confirmed that after training in the Retinal Match task, area 7a neurons still had an overall preference for a fixed match over a nonmatch stimulus, and that this preference was reliable, regardless of intervening stimulation.

When we compared the retinal match vs. screen match conditions, we now saw mixed responses in the Retinal Match task (Figure 4). Among neurons that responded best to the fixed match, approximately equal numbers of neurons also responded best to the screen match or the retinal match (12 vs. 16 neurons, respectively). This result deviated from what we observed in the Screen Match, which was skewed toward the screen match. The difference between the distributions observed in the two tasks was statistically significant (χ^2-test, $p < 0.05$). By examining results on a neuron-by-neuron basis, we found that the difference between the match and nonmatch stimuli was still positively correlated ($r = 0.32$) with the difference between the retinal and screen match stimuli (Figure 6). For a majority (24/46) of neurons, the sign of firing rate difference of fixed match minus fixed nonmatch was in the same direction as the firing rate difference of screen match minus retinal match (points in Quadrants I and III of Figure 6, right). However the effect was marginally significant ($p = 0.03$, and became nonsignificant with the removal of an outlier) and the slope of the regression was less steep. This result indicates that the preference of area 7a neurons for a fixed match over a nonmatch did not reverse in favor of a retinal match stimulus, even though the retinal match stimulus constituted a behavioral match and required a lever release. Neurons were now more evenly distributed in their overall preference for a screen or retinal match (around the horizontal axis). This mixed response to the two conditions was also evident in the population PSTH (Figure 5D). Among neurons with higher fixed match over fixed nonmatch responses, there was no overall significant difference between the retinal match and the screen match, although stronger responses to the retinal match would be expected if increased firing rate signified the behavioral match. The same was true for neurons with higher fixed nonmatch over fixed match responses (PSTH not shown).

Since behavioral performance in the Retinal Match task was slightly lower than the Screen Match task, we sought to ensure that enhancement of responses to the screen match stimulus was not the result of the monkeys' confusion in the task and habitual responses toward the screen match, as if it still were a behavioral match. In order to exclude this possibility, we selected a subset of sessions from the Screen and Retinal Match tasks that were closest in behavioral performance; we excluded the sessions with the highest performance rate from the Screen Match task and lowest performance rate from the Retinal Match task, and then paired each Screen Match session with the Retinal Match session that was closest in performance with it. Average performance was 81.1% in the Screen Match and 81.2% in the Retinal Match for this subset of sessions. We then repeated the regression analysis in Figure 6 for the 23 neurons recorded in the Screen Task and 20 neurons recorded in the Retinal Task in the performance-matched sessions. This analysis confirmed that the difference between fixed match and nonmatch was positively correlated with the difference between retinal and screen match, in both the Screen Match and Retinal Match tasks. Furthermore, the slope of the regression remained steeper for the Screen Match ($\alpha = 0.76$) than the Retinal Match task ($\alpha = 0.58$). This result revealed that match enhancement was still encoded in screen coordinates in the Retinal Match task and that this effect was not an artifact of difference in performance. Overall, our findings show that the effect of attended location on neural activity was somewhat plastic

depending on the task requirements; however, task effects in screen coordinates remained dominant in area 7a.

Discussion

We have recorded neuronal activity in area 7a of the Posterior Parietal Cortex while monkeys performed two variants of a spatial, delayed match-to-sample task. Previous studies have shown that neural responses to a visual stimulus are modulated depending on whether it appears at an attended or unattended location (and constitutes a match or nonmatch). In our study, most neurons responded best to a stimulus appearing at an attended location. We exploited this phenomenon to determine whether match enhancement is represented in retinotopic or spatiotopic coordinates. Our results revealed that modulation in spatiotopic coordinates was dominant, although the relative proportion of neurons was affected by training and task demands.

Match vs. nonmatch responses

A preference for the match stimulus was observed among the neurons in our sample, across both tasks (60% in the Screen Match task, 61% in the Retinal Match) and in both monkeys (63% and 52%, respectively). Responses to match and nonmatch stimuli were reliable in our task, with consistent preference for the match regardless of whether additional stimuli intervened between cue and match (Figure 7). These results stand in stark contrast with previous studies that indicated an overwhelming reduction of match over nonmatch responses in area 7a. Steinmetz et al. (1994) reported that among neurons significantly modulated by the task in three monkeys, 92% showed a decreased response to the match, and only 8% of neurons showing an increased response. A second study in two different monkeys with a task that involved multiple-stimulus displays indicated that 95% exhibited decreased and 5% exhibited increased match responses (Constantinidis & Steinmetz, 2001b). Recordings in these previous studies were performed in virtually identical cortical regions as the present one (see Figure 1C in Constantinidis & Steinmetz, 2001a and Figure 2). Similarly, overall decreased responses to a stimulus appearing at an attended location were observed in posterior parietal area LIP, in the context of other behavioral tasks (Powell & Goldberg, 2000;Robinson, Bowman, & Kertzman, 1995).

A possible explanation for this discrepancy comes from experiments in the inferior temporal (IT) cortex. Neuronal responses in a delayed match-to-sample task that required monkeys to remember the features of stimuli revealed decreased responses to match over nonmatch stimuli for almost all IT neurons that showed significant task modulation (Miller, Li, & Desimone, 1991, 1993). Differences in firing rate between match and nonmatch stimuli were modest but consistent, and replicable in the context of other behavioral paradigms as well (Woloszyn & Sheinberg, 2009). When the same animals trained in the delayed match-to-sample task were tested with stimulus sequences that included repeated nonmatch stimuli (A-B-B-A sequences), IT responses for the repeated nonmatch were also diminished compared to the initial nonmatch stimulus (Miller & Desimone, 1994). Monkeys tested in the A-B-B-A paradigm initially responded incorrectly to the second nonmatch presentation (they treated it as a match) and required extensive retraining in order to perform the task correctly. At the end of this retraining period, preference to a match over a nonmatch stimulus had reversed, with enhanced responses observed in most IT neurons (Miller & Desimone, 1994). Our results are similar to that effect. Our monkeys were first trained in the Screen Match task, in which they were required to perform an eye movement and ignore a stimulus that appeared at the same retinal location as the cue. This requirement to ignore stimuli appearing at a repeated location on the retina seems like a possible cause of the appearance of enhanced match responses.

The earlier area 7a studies interpreted the diminished responses to match stimuli as indicative of a signal serving to redirect visual attention (Steinmetz & Constantinidis, 1995). Stimuli appearing within the focus of attention were presumed to require no further focusing of attentional resources by the posterior parietal cortex. However, later studies in area LIP of the posterior parietal cortex suggest a more complex picture. Modulation (increase or decrease) of responses of LIP neurons was reported depending on task rule and type of motor response required (Snyder, Batista, & Andersen, 1997; Stoet & Snyder, 2004). Therefore modulation of neuronal responses appears to carry information for multiple factors and with variable sign. In this context, the effects of attention itself may be plastic and change sign depending on task, or attention may be only one of multiple factors reflected in the responses of individual neurons. Our current experiments cannot distinguish between these alternatives but indicate that significant changes in neuronal responses are observed in area 7a depending on the task the monkey has been trained to perform.

The percentage of neurons demonstrating significantly different responses to a stimulus depending on whether it is a match or nonmatch also appears to be contingent on the animals' training history and the task performed. Two earlier studies (Constantinidis & Steinmetz, 2001b; Steinmetz et al., 1994) reported that 55% and 60% of recorded neurons responded differently to match and nonmatch stimuli, in monkeys trained with the basic delayed match-to-sample task (Figure 1A). When we trained monkeys to perform the Screen Match Task in addition to the basic task (Figures 1A and 1B), we observed a relatively lower percentage of neurons modulating their responses depending on the match or nonmatch status of the stimulus (49%). This percentage became further significantly lower (χ^2-test, $p < 0.05$) after the same monkeys were additionally trained to perform the Retinal Match task (33%). These results raise the possibility that responses to particular stimulus conditions become less uniform among area 7a neurons as task demands become progressively more complex. It may also be the case that as additional factors influence neuronal responses with different signs of modulation (increase or decrease), their interaction is cancelled out in some neurons. Other recent studies in our laboratory have also shown that the responses of area 7a neurons to visual stimuli that capture attention differ depending on what task the animals have been trained to perform (Constantinidis & Steinmetz, 2005).

Coordinate reference frames

Regardless of the sign of the difference between match and nonmatch responses, the preference for one or the other allowed us to determine whether neurons are modulated by stimuli appearing at the same screen or retinal location. All of our comparisons involved presentation of the identical stimulus in the receptive field, under the same angle of gaze, differing only in terms of the significance of the stimulus in the task depending on the cue. During execution of the Screen Match task, a large majority of neurons with preference for the fixed match stimulus (81%) also responded best for a stimulus that appeared at the same screen coordinates as the cue. A significant correlation was present between the difference of fixed match vs. nonmatch responses and the difference of screen vs. retinal match responses (Figure 6). Hence, neurons that responded differentially to a stimulus depending on whether it appeared at the cued location or not exhibited the same modulation for stimuli appearing at a matching location in a screen-centered reference frame. To test whether this modulation in screen coordinates was simply a consequence of the task that required a response to the screen match stimulus, we retrained the same animals in the Retinal Match task. A positive correlation was still present between the difference of fixed match minus nonmatch and screen match minus retinal match responses (Figure 6B). This finding indicates that overall, neuronal responses continued to be modulated by the locus of stimuli in screen coordinates.

Our conclusions regarding the dominance of a screen-centered frame of reference are in agreement with other recent studies in area 7a. One series of experiments in particular demonstrated that area 7a neurons represent spatial locations in object-centered coordinates, in the context of object construction tasks (Chafee, Averbeck, & Crowe, 2007; Crowe, Averbeck, Chafee, & Georgopoulos, 2005).

An important caveat for the interpretation of the frame of reference is that the monkey's head was fixed during the experiments. In that sense, task modulation might be in head- or body-centered coordinates rather than allocentric (world) coordinates. Previous experiments have shown that stimulus location in area 7a is at least partially encoded in world-centered coordinates, unlike responses in neighboring area LIP, where position signals are represented predominantly in body-centered coordinates (Snyder et al., 1998). It remains to be seen whether attentional modulation shows a similar dichotomy as well.

Eye movements and motor responses

Our paradigm relied on an eye movement to shift the frame of reference in each trial and the observed differences across stimulus conditions might, in principle, be related to the eye movement, or to a receptive field movement that precedes the actual eye movement (Duhamel, Colby, & Goldberg, 1992). This is unlikely for several reasons. In contrast to area LIP, neurons in area 7a are weakly modulated by eyemovements (Blatt et al., 1990) and all responses we examined were obtained after the offset of the saccade; stimuli were displayed only after the monkeys had already completed their saccade and had maintained fixation at the new target for at least 50 ms (typically ~200 ms). Area 7a neurons may still have post-saccadic responses; however, eye movements in our experiment were directed out of the receptive field, so as to bring a stimulus into the receptive field after the saccade (see Figure 3 and Figure 8). Indeed, comparison of responses to nonmatch stimuli presented after an intervening saccade or not revealed no significant difference for our population of neurons that otherwise discriminated between match conditions.

The behavioral task relied on a lever release to signal the appearance of a match. To ensure that this motor response did not account for differences we observed between conditions, we tested whether area 7a neurons responded to the lever release itself by examining responses to match stimuli out of the receptive field (Figure 3E). Across the population of neurons we observed very little activity that could be accounted for by the motor response. Still, it is possible that motor readiness, alertness, or an efferent motor signal specifically facilitated visual responses in the receptive field. Although we cannot exclude this possibility for some of the neurons, the overall effects we observed cannot be fully explained by this possibility, either. First, the sign of the difference between match and nonmatch responses differed between the current study and the earlier studies in area 7a, although they required essentially the identical movement. This argues against a general enhancing effect of visual responses by motor factors. Second, when we trained the monkeys in the Retinal Match task, the difference of screen match minus retinal match response was in the same direction as the fixed match minus fixed nonmatch response, for the majority of neurons (points in Quadrants I and III of Figure 6, right). This was the case even though the screen match no longer required a lever release. These results indicate that task contingencies rather than motor responses are the dominant factor in determining neuronal responses to a stimulus.

Working memory

The behavioral tasks we used unquestionably had a working memory component. The animals needed to maintain the spatial location of the cue in memory and persistent discharges were observed in the population of neurons during the delay period following the presentation of the cue (Figures 3A and 3C). However persistent responses were observed only in a minority

of neurons that exhibited modulation to match and nonmatch stimuli. Many more neurons with no activity during the delay interval responded differentially to identical stimuli depending on whether they constituted a match or nonmatch (as were our sample neurons in Figure 3 and Figure 8). Other neurons with persistent responses during the delay period did not exhibit significant modulation to match and nonmatch stimuli. For these reasons, persistent activity appeared to be independent of the match/nonmatch effects that we describe here.

Implications for neglect

Our results provide insights on the consequences of parietal lesions and the nature of neglect. We show that area 7a neurons are modulated by matching stimuli primarily in screen-centered coordinates. Such a signal may be necessary for directing attention to a part of an object, regardless of its position on the retina. Conversely, loss of such a signal due to parietal injury may be responsible for the inability to shift attention to a part of an object, even when the entire object appears in the same side as the lesion (Pouget & Sejnowski, 2001). This is the hallmark of allocentric neglect, a condition that has been specifically associated with injury of the Temporal-Parietal Junction (Hillis et al., 2005; Karnath et al., 2001; Medina et al., 2009). This area is part of the human “ventral attention system” (Corbetta et al., 2008; Corbetta & Shulman, 2002). Recent anatomical work investigating the default network in humans and monkeys has suggested that monkey area 7a is homologous to this region, in agreement with anatomical and physiological homologies (Buckner et al., 2008; Vincent et al., 2007). As discussed above, our experimental design did not distinguish between an object-centered coordinate frame and a coordinate frame that remains anchored to the body. However, symptoms attributed to allocentric neglect are not typically distinguished with a reference to a body-centered coordinate frame, either.

We do not wish to suggest that representation of an attended stimulus in screen-centered coordinates is a general property of all areas of the visual cortex. As alluded to earlier, damage to other parts of the right parietal lobe can produce egocentric neglect, with loss of sensitivity to stimuli appearing in the left hemifield of vision (Hillis et al., 2005). One recent psychophysical study concluded that reaction times of humans after an eye movement are fastest when attention is directed to a location matching a cue in retinotopic rather than spatiotopic coordinates (Golomb, Chun, & Mazer, 2008). Our results speak specifically to area 7a, which represents the end stage of the dorsal visual stream (Felleman & Van Essen, 1991) and exhibits long response latencies. It is entirely consistent with our findings that behavior is initially guided by retinotopic attentional effects, and effects in spatiotopic coordinates emerge later in time. In fact, a recent study suggested that such a transformation takes place within area 7a itself (Crowe, Averbeck, & Chafee, 2008). That study utilized an object completion task and reported that early neuronal responses to a visual display in area 7a reflected the retinotopic coordinates while later responses represented object-centered coordinates. Our own experimental design did not address the time course of coordinate transformation but indicated that the modulation of overall neuronal responses in screen-centered coordinates is dominant overall.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We wish to thank Rob West and Keith Roberts for technical contributions to the experiments; Travis Meyer for essential help in implementing the computer system for behavioral control; and Emilio Salinas, Ramnarayan Ramachandran, and Terry Stanford for their comments on a previous version of this manuscript.

This work was supported in part by NIH Grant R01-EY016773 and a grant from the Whitehall Foundation to C.C.

References

Andersen RA, Essick GK, Siegel RM. Encoding of spatial location by posterior parietal neurons. Science 1985;230:456–458. [PubMed: 4048942]

Bisley JW, Goldberg ME. Neuronal activity in the lateral intraparietal area and spatial attention. Science 2003;299:81–86. [PubMed: 12511644]

Blatt GJ, Andersen RA, Stoner GR. Visual receptive field organization and corticocortical connections of the lateral intraparietal area (area LIP) in the macaque. Journal of Comparative Neurology 1990;299:421–445. [PubMed: 2243159]

Brainard DH. The psychophysics toolbox. Spatial Vision 1997;10:433–436. [PubMed: 9176952]

Buckner RL, Andrews-Hanna JR, Schacter DL. The brain's default network: Anatomy, function, and relevance to disease. Annals of the New York Academy of Sciences 2008;1124:1–38. [PubMed: 18400922]

Buschman TJ, Miller EK. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. Science 2007;315:1860–1862. [PubMed: 17395832]

Chafee MV, Averbeck BB, Crowe DA. Representing spatial relationships in posterior parietal cortex: Single neurons code object-referenced position. Cerebral Cortex 2007;17:2914–2932. [PubMed: 17389630]

Constantinidis C. Posterior parietal mechanisms of visual attention. Reviews in the Neuroscience 2006;17:415–427.

Constantinidis C, Steinmetz MA. Neuronal responses in area 7a to multiple stimulus displays: I. Neurons encode the location of the salient stimulus. Cerebral Cortex 2001a;11:581–591. [PubMed: 11415960]

Constantinidis C, Steinmetz MA. Neuronal responses in area 7a to multiple stimulus displays: II. Responses are suppressed at the cued location. Cerebral Cortex 2001b;11:592–597. [PubMed: 11415961]

Constantinidis C, Steinmetz MA. Posterior parietal cortex automatically encodes the location of salient stimuli. Journal of Neuroscience 2005;25:233–238. [PubMed: 15634786]

Corbetta M, Patel G, Shulman GL. The reorienting system of the human brain: From environment to theory of mind. Neuron 2008;58:306–324. [PubMed: 18466742]

Corbetta M, Shulman GL. Control of goal-directed and stimulus-driven attention in the brain. Nature Reviews Neuroscience 2002;3:201–215.

Crowe DA, Averbeck BB, Chafee MV. Neural ensemble decoding reveals a correlate of viewer- to object-centered spatial transformation in monkey parietal cortex. Journal of Neuroscience 2008;28:5218–5228. [PubMed: 18480278]

Crowe DA, Averbeck BB, Chafee MV, Georgopoulos AP. Dynamics of parietal neural activity during spatial cognitive processing. Neuron 2005;47:885–891. [PubMed: 16157282]

Duhamel JR, Colby CL, Goldberg ME. The updating of the representation of visual space in parietal cortex by intended eye movements. Science 1992;255:90–92. [PubMed: 1553535]

Felleman DJ, Van Essen DC. Distributed hierarchical processing in the primate cerebral cortex. Cerebral Cortex 1991;1:1–47. [PubMed: 1822724]

Goldberg ME, Bisley JW, Powell KD, Gottlieb J. Saccades, salience and attention: The role of the lateral intraparietal area in visual behavior. Progress Brain Research 2006;155:157–175.

Golomb JD, Chun MM, Mazer JA. The native coordinate system of spatial attention is retinotopic. Journal of Neuroscience 2008;28:10654–10662. [PubMed: 18923041]

Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. Nature 1998;391:481–484. [PubMed: 9461214]

Harris KD, Henze DA, Csicsvari J, Hirase H, Buzsaki G. Accuracy of tetrode spike separation as determined by simultaneous intracellular and extracellular measurements. Journal of Neurophysiology 2000;84:401–414. [PubMed: 10899214]

Hillis AE, Newhart M, Heidler J, Barker PB, Herskovits EH, Degaonkar M. Anatomy of spatial attention: Insights from perfusion imaging and hemispatial neglect in acute stroke. Journal of Neuroscience 2005;25:3161–3167. [PubMed: 15788773]

Karnath H-O, Ferber S, Himmelbach M. Spatial awareness is a function of the temporal not the posterior parietal lobe. Nature 2001;411:950–953. [PubMed: 11418859]

Medina J, Kannan V, Pawlak M, Kleinman JT, Newhart M, Davis C, et al. Neural substrates of visuospatial processing in distinct reference frames: Evidence from unilateral spatial neglect. Journal of Cognitive Neuroscience 2009;21:2073–2084. [PubMed: 19016599]

Mesulam MM. Spatial attention and neglect: Parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. Philosophical Transactions of the Royal Society of London B: Biological Sciences 1999;354:1325–1346.

Meyer T, Constantinidis C. A software solution for the control of visual behavioral experimentation. Journal of Neuroscience Methods 2005;142:27–34. [PubMed: 15652614]

Miller EK, Desimone R. Parallel neuronal mechanisms for short-term memory. Science 1994;263:520–522. [PubMed: 8290960]

Miller EK, Li L, Desimone R. A neural mechanism for working and recognition memory in inferior temporal cortex. Science 1991;254:1377–1379. [PubMed: 1962197]

Miller EK, Li L, Desimone R. Activity of neurons in anterior inferior temporal cortex during a short-term memory task. Journal of Neuroscience 1993;13:1460–1478. [PubMed: 8463829]

Pouget A, Sejnowski TJ. Simulating a lesion in a basis function model of spatial representations: Comparison with hemineglect. Psychology Reviews 2001;108:653–673.

Pouget A, Snyder LH. Computational approaches to sensorimotor transformations. Nature Neuroscience 2000;3:1192–1198.

Powell KD, Goldberg ME. Response of neurons in the lateral intraparietal area to a distractor flashed during the delay period of a memory-guided saccade. Journal of Neurophysiology 2000;84:301–310. [PubMed: 10899205]

Raffi M, Siegel RM. Functional architecture of spatial attention in the parietal cortex of the behaving monkey. Journal of Neuroscience 2005;25:5171–5186. [PubMed: 15917457]

Robinson DL, Bowman EM, Kertzman C. Covert orienting of attention in macaques. II. Contributions of parietal cortex. Journal of Neurophysiology 1995;74:698–712. [PubMed: 7472375]

Snyder LH, Batista AP, Andersen RA. Coding of intention in the posterior parietal cortex. Nature 1997;386:167–170. [PubMed: 9062187]

Snyder LH, Grieve KL, Brotchie P, Andersen RA. Separate body- and world-referenced representations of visual space in parietal cortex. Nature 1998;394:887–891. [PubMed: 9732870]

Steinmetz MA, Connor CE, Constantinidis C, McLaughlin JR. Covert attention suppresses neuronal responses in area 7a of the posterior parietal cortex. Journal of Neurophysiology 1994;72:1020–1023. [PubMed: 7983507]

Steinmetz MA, Constantinidis C. Neurophysiological evidence for a role of posterior parietal cortex in redirecting visual attention. Cerebral Cortex 1995;5:448–456. [PubMed: 8547791]

Stoet G, Snyder LH. Single neurons in posterior parietal cortex of monkeys encode cognitive set. Neuron 2004;42:1003–1012. [PubMed: 15207244]

Vincent JL, Patel GH, Fox MD, Snyder AZ, Baker JT, Van Essen DC, et al. Intrinsic functional architecture in the anaesthetized monkey brain. Nature 2007;447:83–86. [PubMed: 17476267]

Woloszyn L, Sheinberg DL. Neural dynamics in inferior temporal cortex during a visual working memory task. Journal of Neuroscience 2009;29:5494–5507. [PubMed: 19403817]

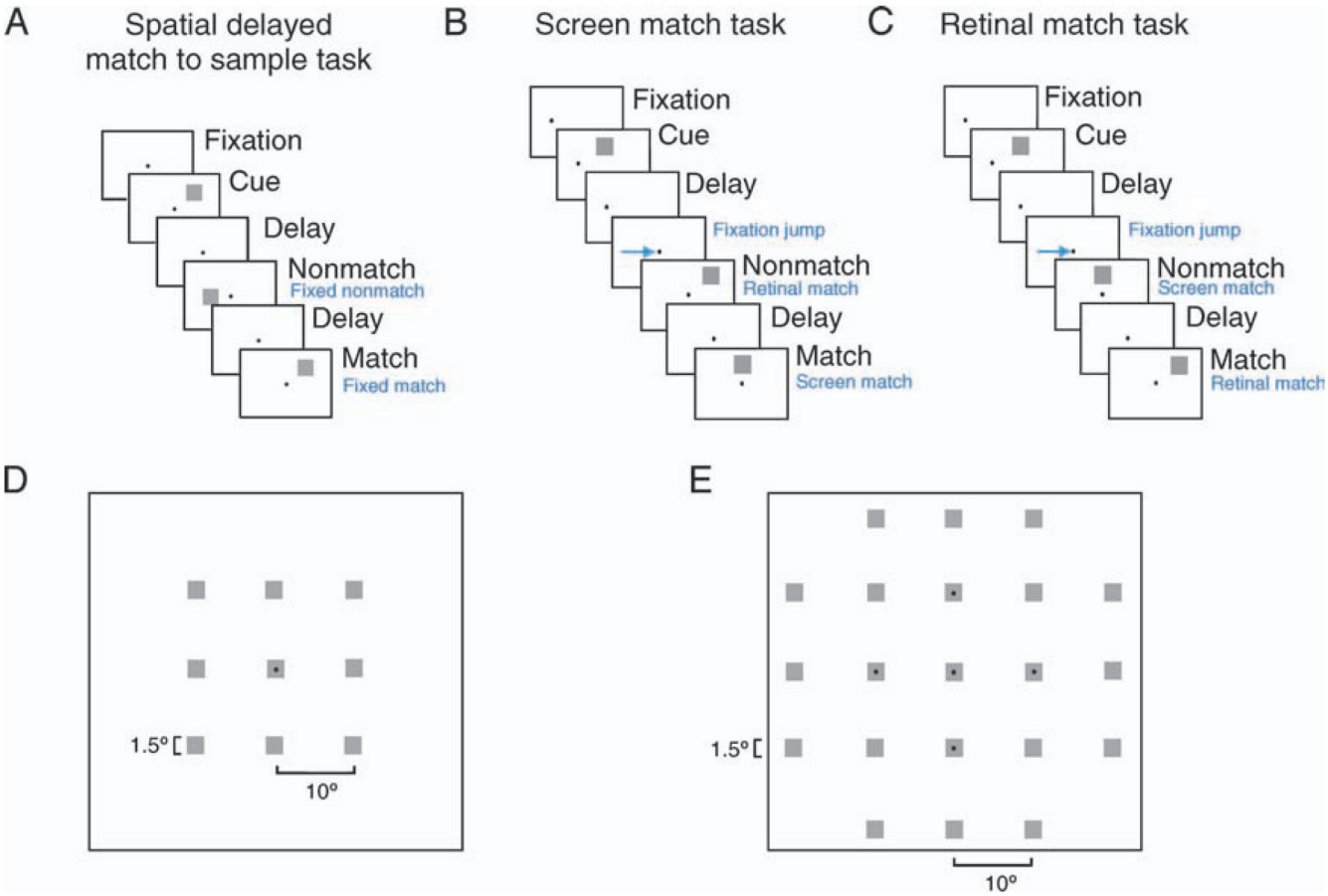

Figure 1.

Schematic diagrams of the behavioral tasks. (A) Sample trial in the spatial, delayed match-to-sample task (basic task). Frames represent successive stimulus presentations. The monkeys were required to pull back a lever in order to initiate a trial, to ignore a pseudorandom number of nonmatch stimulus presentations appearing at different locations, and to release the lever after the offset of a match stimulus. (B) Sample trial from the Screen Match task. The fixation point moved after the presentation of the cue and the monkey was required to remember the location of the cue in screen coordinates and to release a lever when a subsequent stimulus appeared at the same screen location. (C) Sample trial from the Retinal Match task. The monkey was required to remember the location of the cue in retinal coordinates (relative to the fixation point) and to release a lever after a match stimulus appeared at the same retinal location. (D) Possible positions where the fixation target (black dot) and stimuli (gray squares) could appear on the screen, in the basic task. (E) Possible locations of the fixation target (black dots) and stimuli (gray squares) in the Screen and Retinal Match tasks.

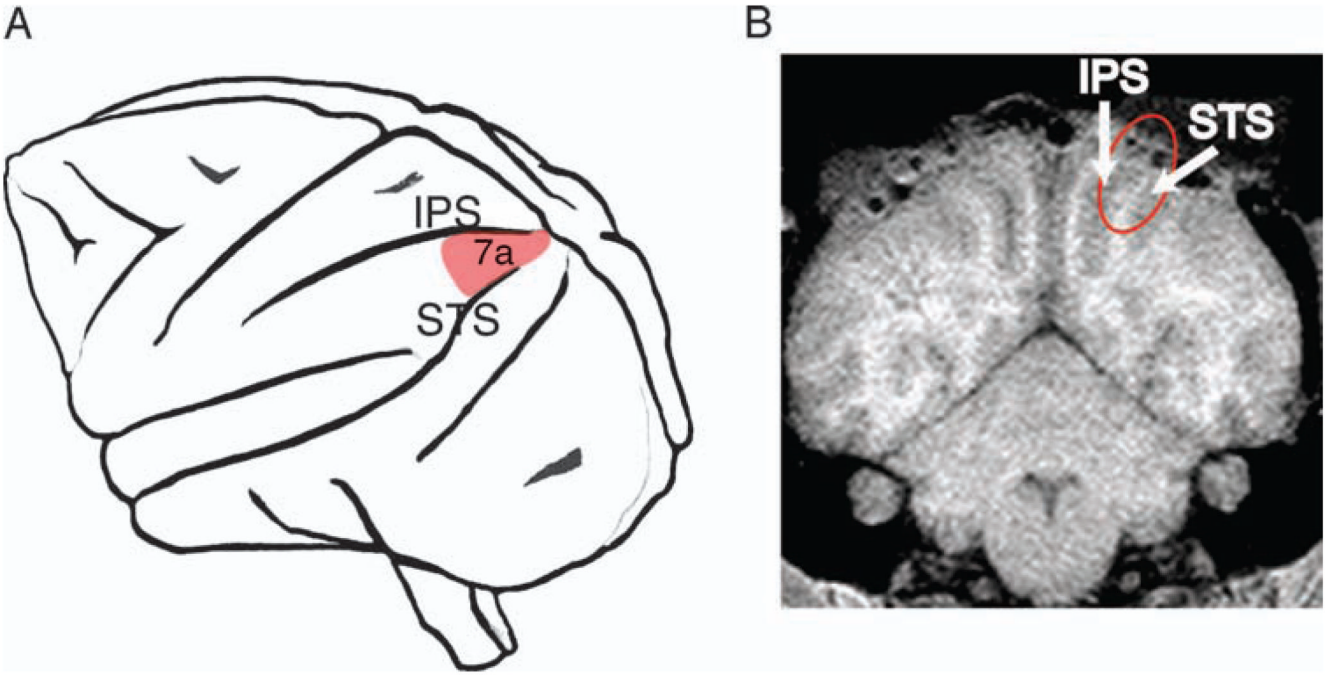

Figure 2.
Recording locations. (A) Schematic diagram illustrating the area where recordings were performed in area 7a of the monkey brain. IPS: intraparietal sulcus, STS: superior temporal sulcus. (B) Anatomical MRI from one subject. Recordings were performed from the crown of the gyrus posterior to the intraparietal sulcus.

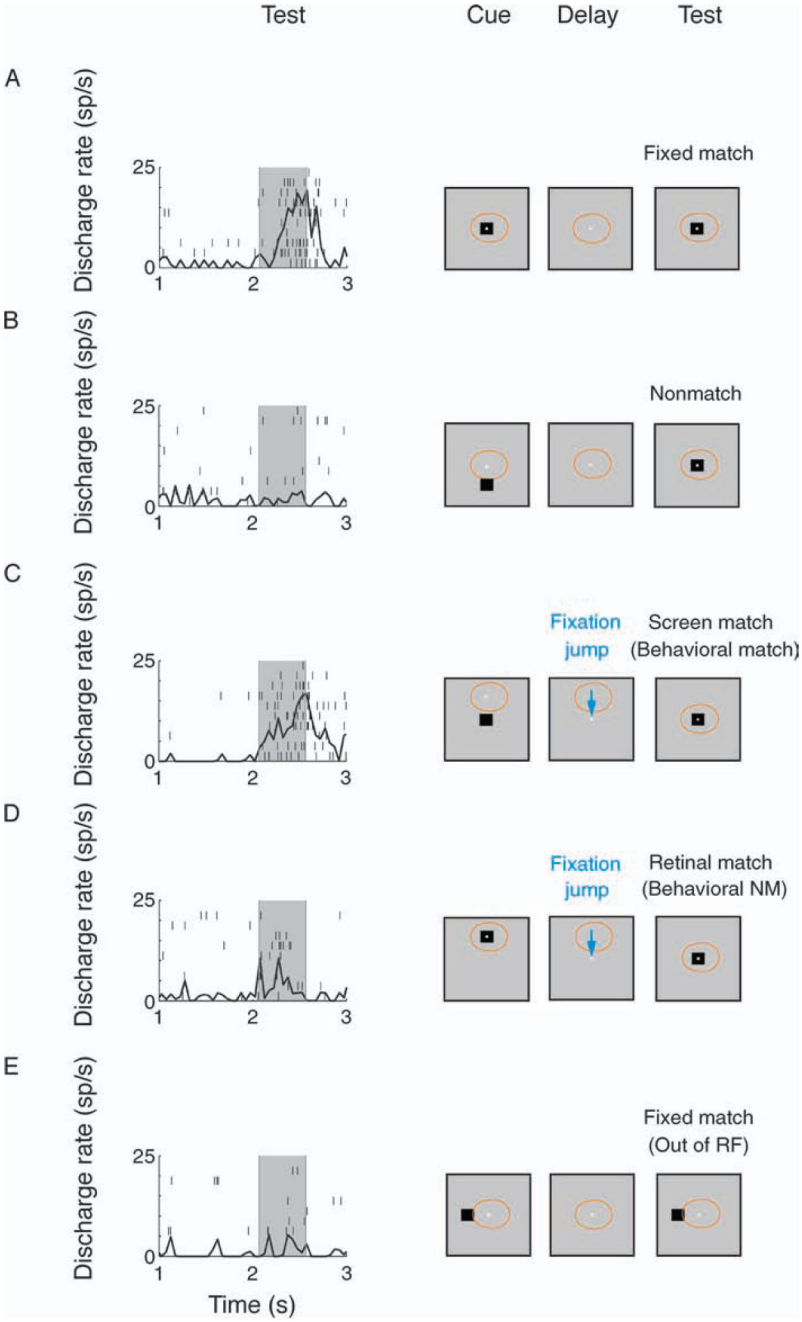

Figure 3.

Sample neuron in Screen Match Task. Histograms and rasters are shown for one area 7a neuron recorded while the subject performed the Screen Match task. The second stimulus is shown in each condition. Note that the stimulus is identical in (A)–(D) and appears inside the neuron's receptive field and under gaze directed to the center of the screen. Trials from all stimulus types were randomly interleaved, including trials where the second stimulus appeared out of the receptive field (not shown). (A) This neuron responded strongly to the Fixed Match stimulus, appearing in the same location as the cue when the fixation point remained stationary in the center of the screen. (B) The Fixed Nonmatch stimulus elicited virtually no response. (C) Strong response to the Screen Match stimulus which was a behavioral match in this task. (D)

A retinal match stimulus elicited a poor response. (E) No response was observed for presentation of a match stimulus out of the receptive field, providing evidence that the preference of the neuron for a behavioral match was not due to nonspecific factors such as the preparation for a lever release or anticipation of reward.

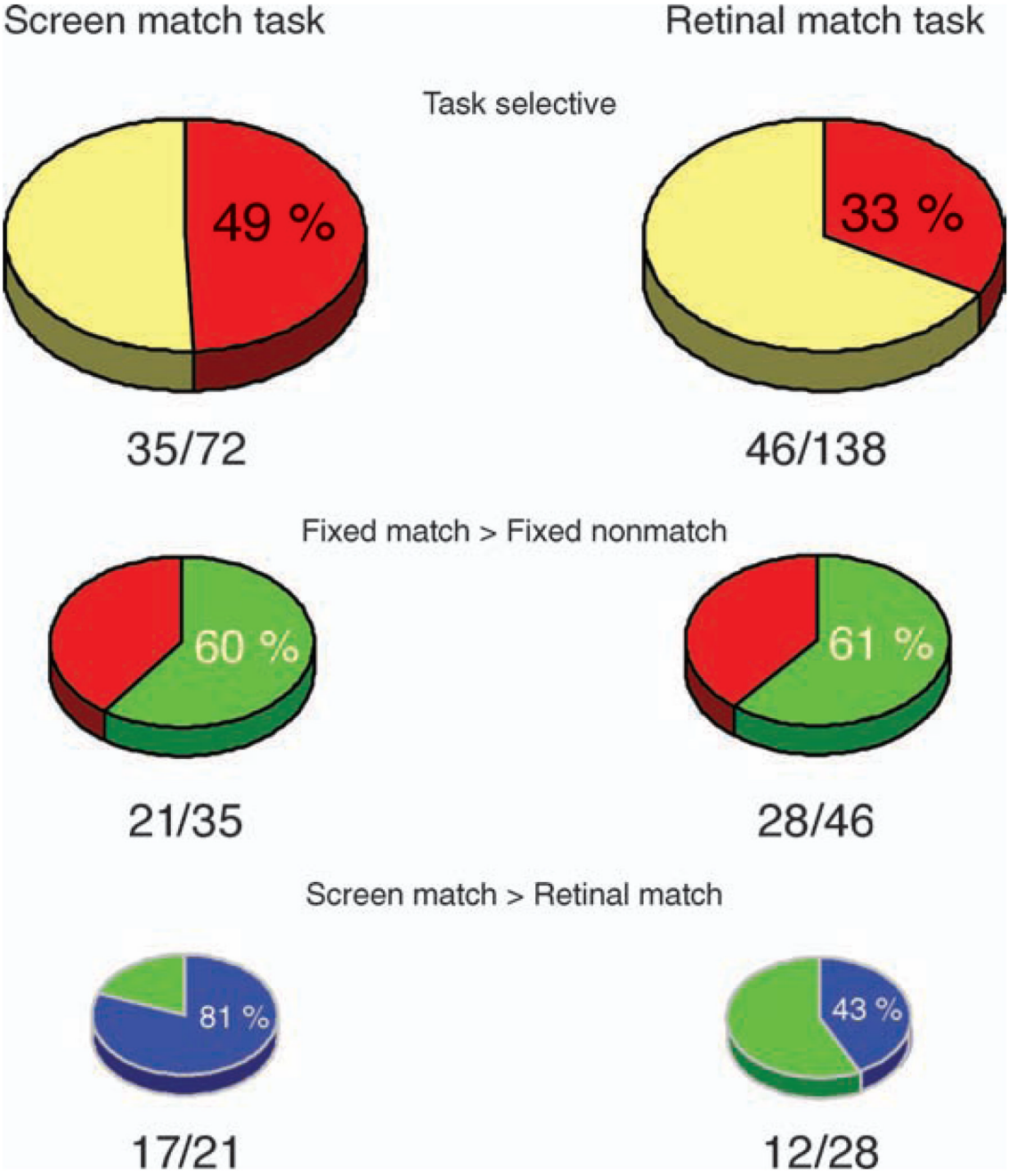

Figure 4.
Neuron preferences in the tasks. (Top) Number and percentage of neurons showing significantly different responses to the same stimulus when it appeared as a match or nonmatch stimulus in the task (Task-Selective neurons). (Middle) Percentage of neurons from the previous group that responded best to a fixed match over a fixed nonmatch stimulus. (Bottom) Percentage of neurons from the previous group that responded best to a screen match over a retinal match stimulus.

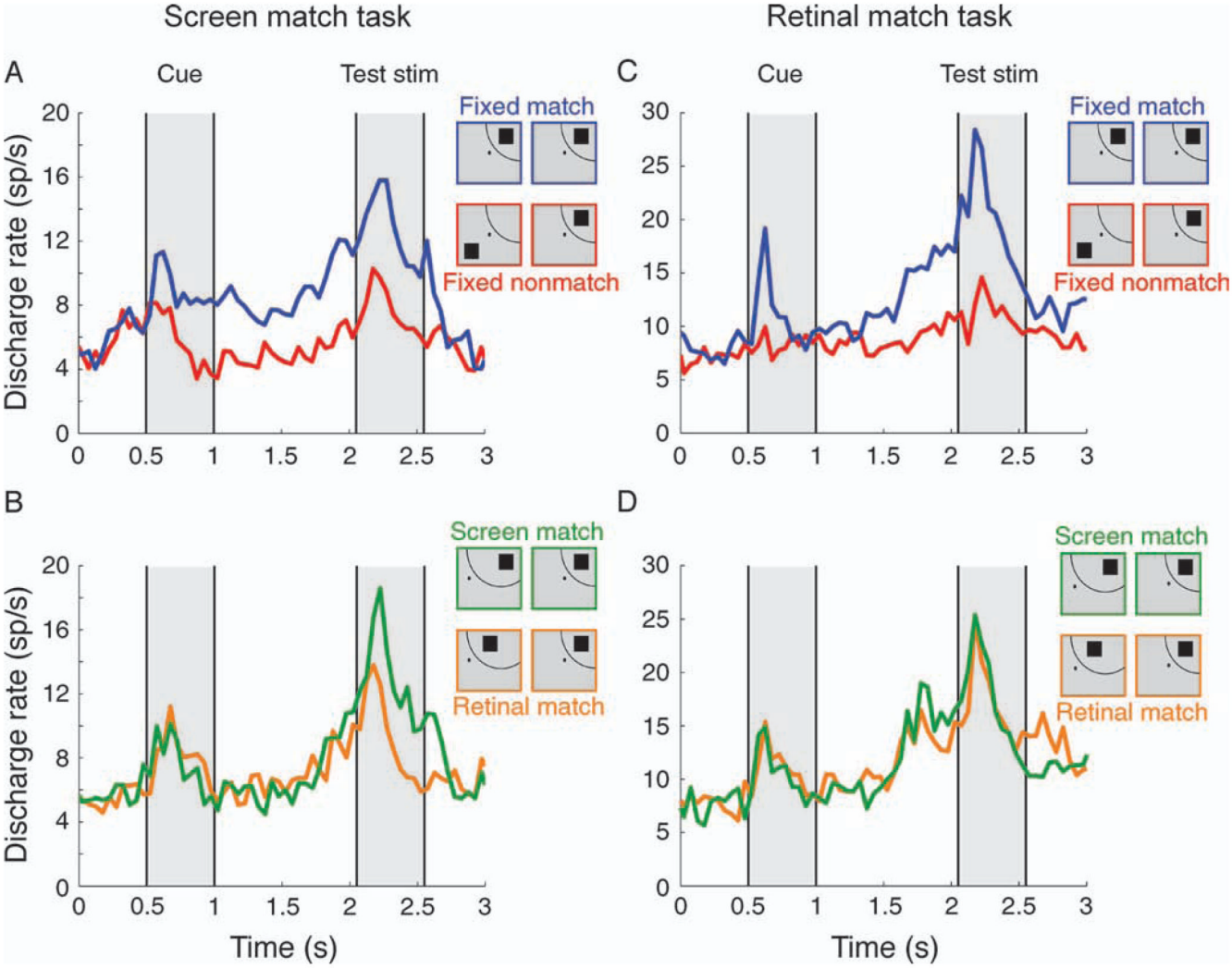

Figure 5.

Population responses of match-preferring neurons. PSTHs are shown for the population of neurons with higher mean responses for a Fixed Match over a Fixed Nonmatch stimulus (N = 21 for Screen Match Task, N = 28 for Retinal Match Task). Insets to the right of each panel represent condition averaged by each trace. The location of the stimulus (black square) relative to the receptive field (arc) is depicted schematically; these differed for each neuron included in the population average. Left column (A, B) represents responses from the Screen Match Task, right column (C, D) from the Retinal Match Task. Top row (A, C) represents neuronal responses under no fixation movement. Bottom row represents neuronal responses with a moving fixation point. The blue line represents the Fixed Match condition; the red line represents the Fixed Nonmatch; the green line represents the Screen Match; and the yellow line represents the Retinal Match.

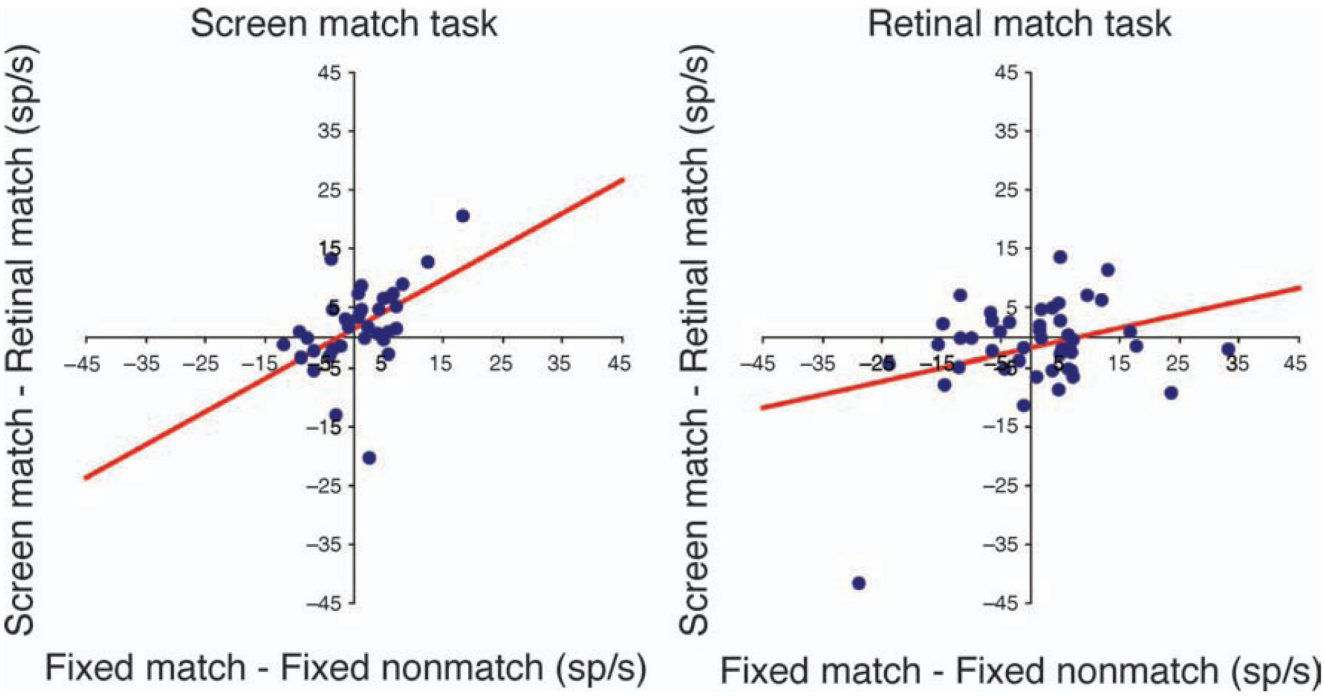

Figure 6.
Relationship between Match and Nonmatch responses. Scatter plots of the difference in firing rate between the Fixed Match and Fixed Nonmatch responses are plotted against the difference between the Retinal Match and Screen Match responses. Each dot represents one Task-Selective neuron. Points falling along the diagonal indicate neurons with identical difference of responses to the two conditions.

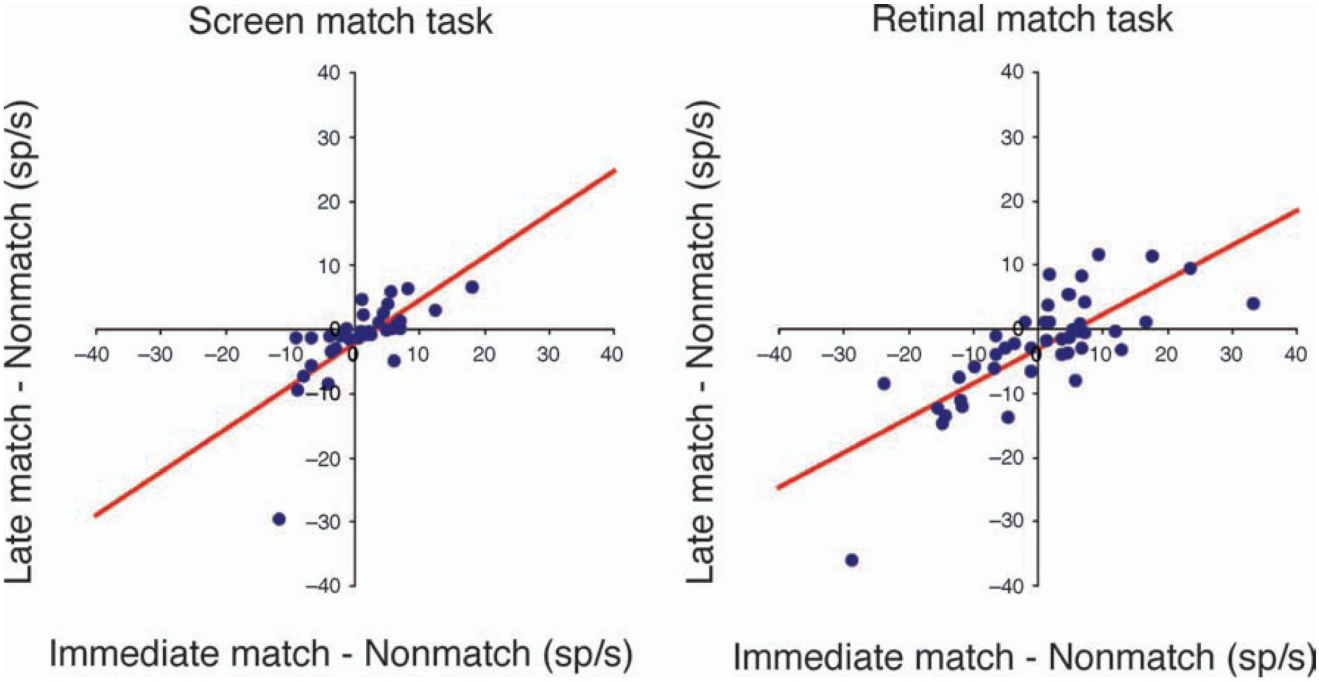

Figure 7.
Differences between immediate and late Match responses. Scatter plots of the difference in firing rate between match and nonmatch stimuli appearing after intervening nonmatch stimuli, plotted against the difference in firing rate between match and nonmatch stimuli appearing immediately after the cue. Neurons appearing on the diagonal represent neurons with identical response differences to the two conditions.

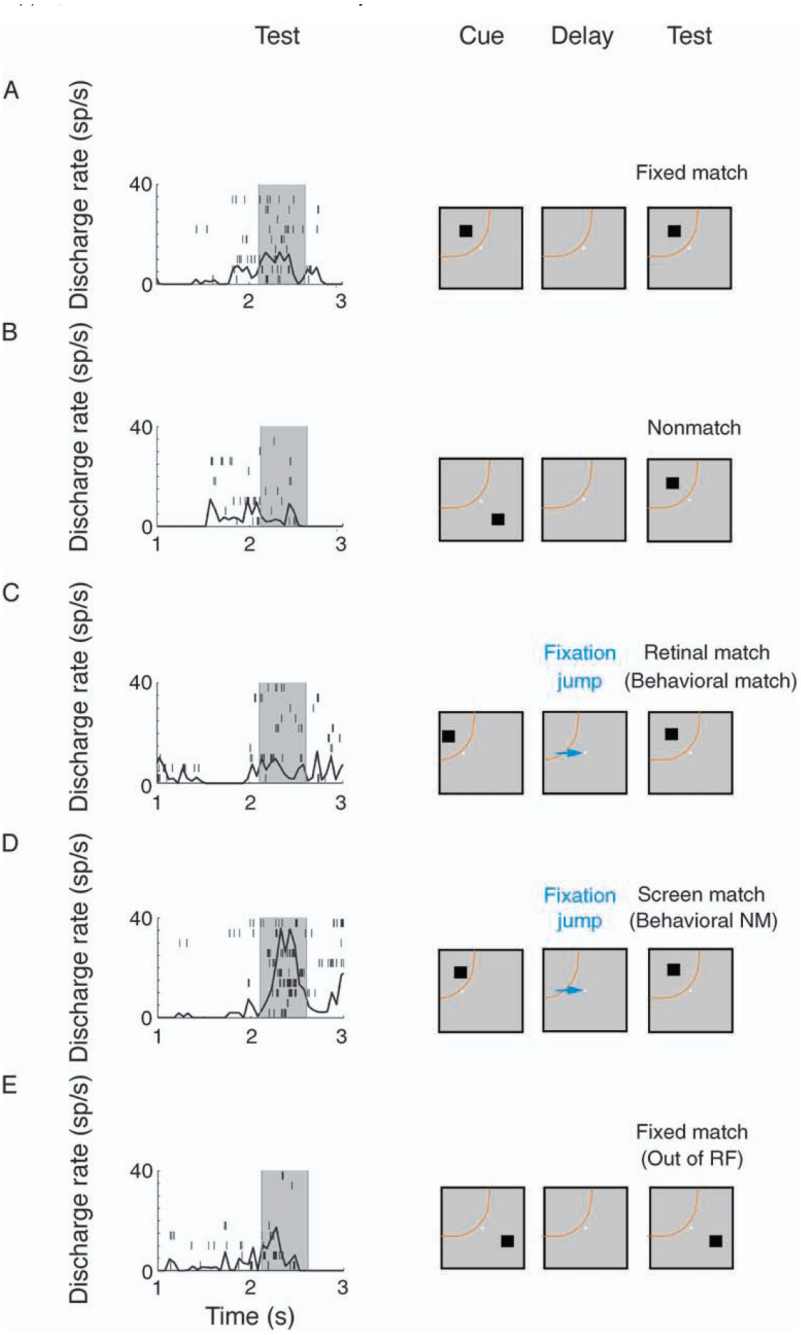

Figure 8.

Sample neuron in Retinal Match Task. Conventions are the same as in Figure 2. (A) Match stimulus presentation in the receptive field elicited a strong response. (B) Nonmatch stimulus presentation in the receptive field elicited a weaker response. (C) The neuron responded weakly to a retinal match, although this was a behavioral match. (D) The neuron responded strongly to a screen match stimulus, although this was no longer a behavioral match in this task (did not require a lever release). (E) The neuron did not respond to a match stimulus out of the receptive field.