Comparison of neural activity preceding reaches to auditory and visual stimuli in the parietal reach region

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We examined the responses of neurons in the parietal reach region (PRR) during reaches to the remembered locations of auditory or visual stimuli. We found that the firing rate of PRR neurons contained information about the location of auditory and visual stimuli. For neurons tested with visual stimuli, the amount of information remained constant throughout the task. In contrast, for neurons tested with auditory stimuli, the amount of target-location information increased as the trial evolved. During the reach period of the task, the amount of information that was carried by neurons tested with auditory stimuli was not statistically different from the amount carried by neurons tested with visual stimuli. We interpret these data to suggest that the type of information that PRR neurons encode evolves throughout a task. *NeuroReport* 13:891–894 © 2002 Lippincott Williams & Wilkins.

Key words: Auditory; Information; Monkey; Posterior parietal cortex; Reach

INTRODUCTION

Parietal activity is correlated with different cognitive intermediates of the sensorimotor transformation [1,2]. Parietal activity has been shown to be related with a monkey's intention to form a motor plan [3]: neurons in the lateral intraparietal area (area LIP) are modulated preferentially when a monkey plans an eye movement, whereas neurons in the parietal reach region (PRR) are modulated preferentially when a monkey plans a reach. Parietal activity has also been correlated with changes in the locus of a monkey's attention [2], stimulus saliency [4], and decisions to saccade to a particular spatial location [5,6]. Interestingly, recent examinations of activity in area LIP have demonstrated that the quantity being encoded by a neuron is dynamic and changes as a task progresses [5–7]. For instance, LIP neurons may initially encode a monkey's expectancy but later in the trial, encode his movement plan. To further examine this issue, we probed whether the modality of a sensory target affects the manner in which PRR activity evolves during a delayed reach to an auditory or visual target.

MATERIALS AND METHODS

We studied two adult male rhesus macaque monkeys (*Macaca mulatta*) who were trained to make reaches to the remembered location of an auditory or visual stimulus. Monkeys sat in a completely dark room and made reaches to an array of touch-sensitive buttons placed in front of the monkey. Eye position was sampled with a scleral search coil [8] at a rate of 500 Hz and button presses were monitored with 2 ms resolution. Extracellular neural activity was recorded using tungsten electrodes inserted daily into the PRR [9]. The neurons reported in this paper were collected as part of a series of studies that investigated the reference frame of neurons in the PRR [10,11]. One monkey learned auditory reaches prior to learning visual reaches, while the second monkey learned visual reaches prior to learning auditory reaches. Since we did not observe any systematic differences in the behavior of these monkeys or in the responses of their neurons, data were pooled for presentation. The error rate, however, of the monkeys did vary as a function of stimulus type: on auditory trials, the error rate was ~50%, whereas on visual trials the average error rate was ~20%. Chance performance would produce an error rate of 87.5%. NIH guidelines were strictly followed for the use and care of the animals.

The delayed-reach task began with a monkey fixating and depressing the illuminated central button (Fig. 1). Next, a 300 ms cue was presented from one of the eight buttons that formed a square around the central button. In auditory trials, the cue was a 1–15 kHz noise burst from a speaker (Audax, TWO25V2) that was located within each button. In visual trials, the cue was a flash from a green light-emitting

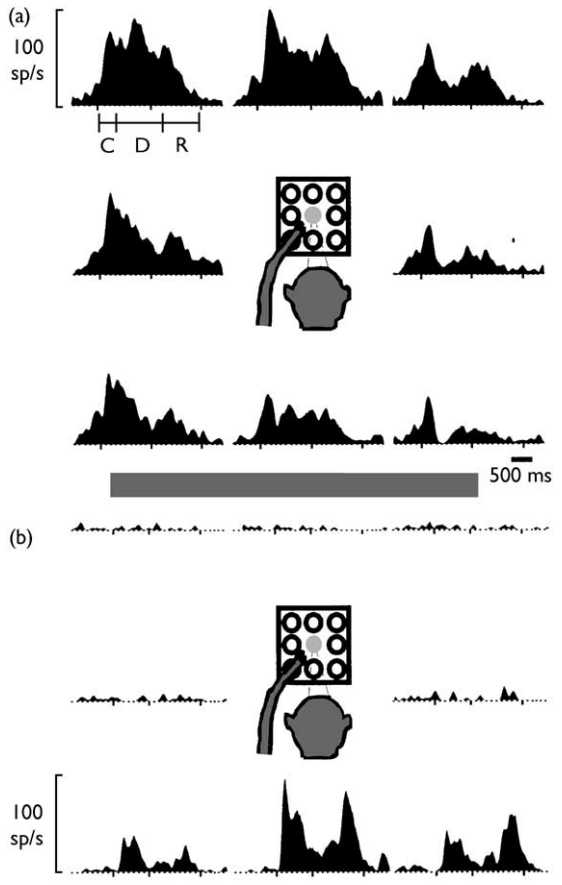

Fig. 1. Behavior of (**a**) an auditory tested and (**b**) a visually tested PRR neuron. Each panel contains a schematic of the monkey's initial hand and eye position and a PRR response profile; the monkey fixated and pressed the central button (grey circle). In each schematic, the circles indicate the relative position of each button assembly. The response profiles are arranged as a function of stimulus location, and neural activity is represented by spike–density histograms. The histograms are aligned relative to the onset of the cue, which is identified by the first long tic mark on the time axis. Tick interval = 100 ms. The black bar in the lower-right corner of (a) indicates 500 ms. The C, D, and R in (a) indicate the times of the cue, delay, and reach periods, respectively.

diode that was within each button. After a random delay, which ranged between 700 and 1000 ms, the light from the central button was extinguished, and the monkey made a reach to the remembered location of the cue while maintaining fixation at the central button. Monkeys usually made five reaches to each target location; in 3% of the neurons that were probed with visual stimuli, only three reaches were made to each target location.

As described in other PRR studies, neural activity was divided into several intervals. The baseline period was the 500 ms that began after the monkey fixated and pushed the central button. The cue period was the 300 ms that began 50 ms after the introduction of the auditory or visual stimulus. The delay period was the 600 ms that began 100 ms after cue offset. The reach period was the 700 ms period that began after extinction of the central LEDs. Neural activity during each of these periods was expressed as the number of action potentials per second (i.e. firing rate).

Target location information was calculated from the firing rate of each PRR neuron during the cue, delay, and reach periods. Target-location information is a non-parametric index of a neuron's spatial selectivity or tuning width. We used a method analogous to one described previously [12–14] to calculate target-location information. In brief, firing rates, from correct trials, were binned to form a matrix in which target location constituted one dimension and firing rate was the other dimension; an analysis of data from incorrect trials will be presented separately. The binning along the firing-rate dimension of the matrix was proportional to the standard deviation of the baseline period firing rate; this binning size allows for a conservative estimate of the information content of each neuron [12,13]. The matrix was normalized to estimate the joint probability and marginal probability densities. Target location information was given by

$$I = \Sigma_s \Sigma_r P(s, r) \log_2(P(s, r)/P(s)P(r)),$$

where s is the index of each target location, r is the index of the firing-rate bins, P(s,r) is the joint probability, and P(s) and P(r) are the marginal probabilities.

To facilitate comparisons across monkeys and stimulus modalities, data are reported in terms of relative information [12]. We computed relative information, on a cell-by-cell basis, by calculating the amount of target location information from the original data and from bootstrapped trials. In bootstrapped trials, the relationship between a neuron's firing rate and stimulus location was randomized and then the amount of information was calculated. This process was repeated 100 times and the median value from this distribution of values was determined. The amount of relative target location information was calculated by subtracting the median amount of information obtained from bootstrapped trials from the amount obtained from the original data.

RESULTS

PRR activity was strongly modulated by reaches to the remembered location of auditory or visual targets. Figure 1a shows an example of a response profile that was obtained from a monkey making delayed reaches to auditory stimuli (an auditory tested PRR neuron). Figure 1b shows an example of a response profile that was obtained from a monkey making delayed reaches to visual stimuli (a visually tested PRR neuron). As seen in both of these response profiles, PRR activity is spatially selective. The auditory-tested PRR neuron in Fig. 1a responded maximally to stimuli located up and to the left of fixation. The visually tested neuron shown in Fig. 1b responded maximally to stimuli located below fixation.

A neuron was spatially tuned if delay period activity was different from baseline period activity and if this difference was dependent on stimulus location [11]. If the interaction term of a two-way ANOVA analysis (task period *vs* stimulus location) rejected the null hypothesis at a level of $p < 0.05$, a neuron is termed spatially tuned. Forty-four percent ($n = 44/99$) of auditory tested PRR neurons were spatially tuned. Fifty-nine percent ($n = 67/113$) of visually tested PRR neurons were spatially tuned. During a recording session, neurons were identified and isolated based on their responses to the delayed reach task. Consequently, these percentages may overestimate the number of PRR neurons that are

activated by the delayed-reach task and that are spatially tuned. All further analyses discussed in this paper focus on the properties of those neurons that were spatially tuned.

Target location information: While auditory tested and visually tested PRR neurons were spatially tuned, the responses of auditory tested and visually tested PRR neurons were not the same. To quantify these differences in tuning, the amount of relative target location information (see Materials and Methods) carried by each PRR neuron was calculated. Histograms of relative target location information for the cue, delay and reach periods are shown in Fig. 2. Since each distribution is shifted significantly (Wilcoxon test; $p < 0.05$) toward positive values, it implies that in the population, PRR neurons carry information about delayed reaches to auditory and visual stimuli during the cue, delay and reach periods.

Figure 2 displays, for our population of PRR neurons, how the amount of target location information changed as a function of task period. The amount of target location information carried by auditory tested PRR neurons (grey bars in Fig. 2) during the cue (median 0.15 bits; s.d. 0.19), delay (median 0.24 bits; s.d. 0.21), and reach (median 0.27 bits; s.d. 0.32) periods was different (Kruskal-Wallis; $p < 0.05$). In contrast, the amount of target location information carried by visually tested PRR neurons (black bars in Fig. 2) during the cue, delay, and reach periods was not different (Kruskal-Wallis; $p > 0.05$). The median amount of information during these three periods was 0.32 ± 0.21, 0.39 ± 0.17 and 0.36 ± 0.22 bits, respectively.

The amount of target location information differed for auditory tested and visually tested PRR neurons. During both the cue and memory periods, visually tested PRR neurons carried more target location information than did auditory tested PRR neurons (Wilcoxon; $p < 0.05$). During the reach period, the amount of target location information was not statistically different for auditory tested and visually tested PRR neurons (Wilcoxon; $p > 0.05$).

DISCUSSION

The firing rate of PRR neurons contained information about the location of auditory and visual stimuli. This information was present during the cue period and remained throughout the trial. The amount of information that was carried in the firing rate of auditory tested PRR neurons increased throughout the task and eventually became similar to the amount present in visually tested PRR neurons. Below we discuss some caveats of the experimental paradigm and interpret the results of this study.

Experimental considerations: One important caveat of this study is that the responses of PRR neurons during visual and auditory reaches were examined in separate populations of neurons. We do not believe, though, that the observed differences in target location information would be minimized or eliminated if we had examined how each PRR neuron responded during delayed reaches to auditory stimuli and during delayed reaches to visual stimuli. Indeed, a related study demonstrated that, when activity from individual neurons was recorded while monkeys participated in delayed saccades to auditory and visual

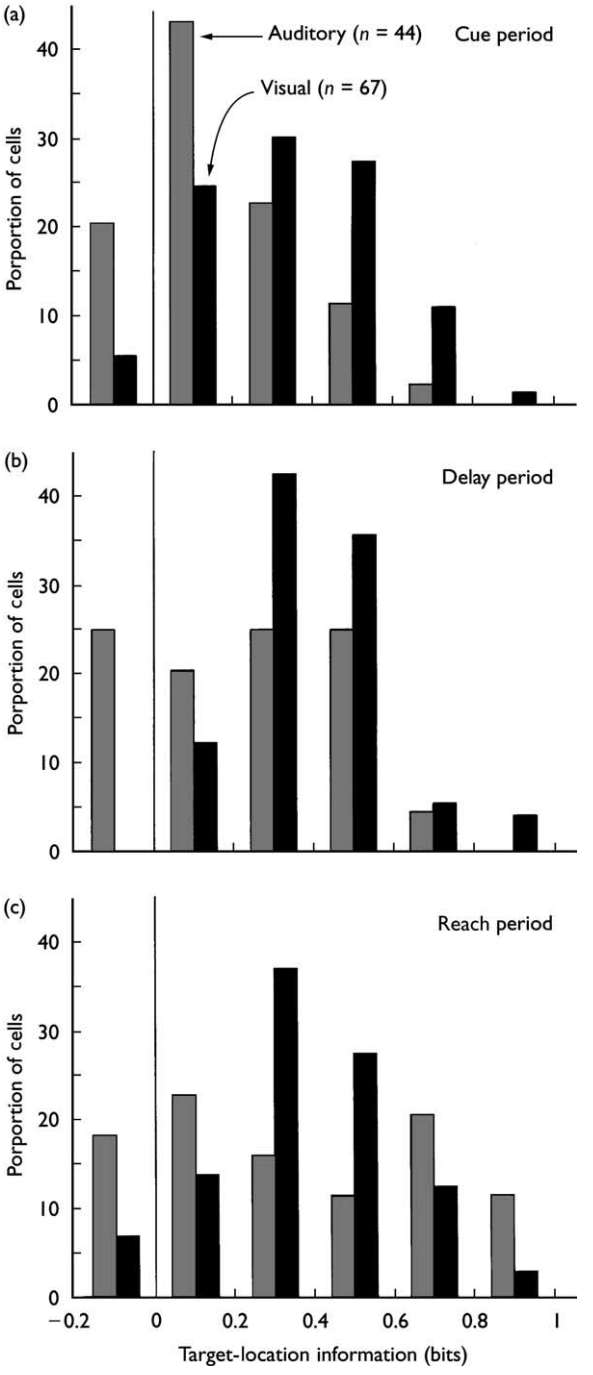

Fig. 2. Distribution of target location information for the cue (**a**), delay (**b**) and reach (**c**) periods. The grey bars indicate the distribution of target location information for auditory tested PRR neurons and the black bars indicate the distribution for visually tested PRR neurons.

targets, neurons in the lateral intraparietal area responded differently [12,15]. Moreover, since, during recording sessions, neurons were identified and isolated based on their responses during delayed reaches to auditory or visual stimuli, it is reasonable to believe that these neurons contributed substantially to the computations underlying the delayed-reach task and that the responses of these

neurons were indicative of those PRR neurons that participated in the task. Thus, we believe that it is unlikely that bimodal PRR neurons or an as of yet unidentified population of PRR neurons would respond in a manner that is substantially different than the responses report in this study. However, it is important to examine the responses of individual PRR neurons during delayed reaches to both auditory and visual stimuli in order to make direct comparisons between these two conditions.

Interpretation: During the cue period, auditory tested PRR neurons carried less target location information than did visually tested PRR neurons. There are many possible explanations for this observation. The most parsimonious interpretation of this difference is that it reflects differences in how localizable auditory and visual stimuli are for primates (including humans) [16–20]. Indeed, the observation that the error rate during auditory trials was substantially greater than the error rate during visual trials (50% *vs* 20%, respectively) supports the notion that differences in PRR activity may be due, in part, to differences in the localizability of the auditory and visual stimuli.

Following the cue period, auditory tested PRR neurons and visually tested PRR neurons behaved differently. For visually tested PRR neurons, the amount of target location information remained constant. In contrast, for auditory tested PRR neurons, the amount of target location information increased throughout the trial and eventually became similar to the amount seen in visually tested PRR neurons. We interpret these observations to suggest that PRR neurons initially encode information conveyed by the stimulus modality of the reach instruction. However, in latter portions of the task, PRR neurons appear to be encoding information relating to the reach plan. That is, the quantity being encoded in the firing rate of PRR neurons is dynamic and changes as the sensory, cognitive, or motor demands of the task change.

Such dynamic encoding of different aspects of a task has been reported in other parietal studies. For instance, in one study [7], monkeys were trained to saccade to a specific location cued on an object. After the location had been cued, the object rotated. Initially, neurons in the lateral intraparietal area encoded aspects of the visual stimulus, but, as the task evolved, these same neurons began to encode the direction of the planned saccade. In another study [6], the reward and target probabilities were found to influence the early period of a saccade task but not the later period when the monkeys had selected a target for a saccade. Finally, in an experiment by Shadlen and Newsome [5], monkeys were trained to judge the motion of randomly moving dots on a visual display and to saccade in the direction of the motion. Initially, neurons in the lateral intraparietal area were modulated by the monkey's judgments of the direction of motion in the visual display but not in later epochs of the task when the monkeys had selected a saccadic target.

What processes might underlie the changes in the amount of information carried by auditory tested PRR neurons? In other words, how are initially sensory-based signals transformed into ones that encode a reach plan? One possibility is that, following the presentation of the auditory stimulus, monkeys recruited memories of the precise reach endpoint, which they had learned to associate with that sound location. This may result in an increasingly refined prediction of the reach endpoint, both behaviorally and neurally. Another possibility is that cognitive mechanisms may have transformed the initial and poorly defined representation of target location into one that was appropriate to represent an accurate reach endpoint. Further work is needed to determine (1) which of these possibilities, or others, is correct and (2) the neural computations that underlie such transformations.

CONCLUSION

When auditory or visual stimuli were present in the environment, PRR neurons responded in a modality-dependent manner. However, as the task progressed, modality-dependent differences were minimized and, during the reach period, PRR neurons did not encode stimulus modality. These results suggest that the quantity that PRR neurons (and neurons in the lateral intraparietal area [5–7]) represents is dynamic and changes with demands of the task.

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