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Reaches to Sounds Encoded in an Eye-Centered Reference Frame

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Summary

A recent hypothesis suggests that neurons in the lateral intraparietal area (LIP) and the parietal reach region (PRR) encode movement plans in a common eye-centered reference frame. To test this hypothesis further, we examined how PRR neurons encode reach plans to auditory stimuli. We found that PRR activity was affected by eye and initial hand position. Population analyses, however, indicated that PRR neurons were affected more strongly by eye position than by initial hand position. These eye position effects were appropriate to maintain coding in eye coordinates. Indeed, a significant population of PRR neurons encoded reaches to auditory stimuli in an eye-centered reference frame. These results extend the hypothesis that, regardless of the modality of the sensory input or the eventual action, PRR and LIP neurons represent movement plans in a common, eye-centered representation.

Introduction

The posterior parietal cortex contains functional subdivisions, some of which are involved in encoding specific types of movement plans (Snyder et al., 1997, 2000; Andersen et al., 1998). For instance, the lateral intraparietal area (LIP) contains neurons that respond preferentially to eye movement plans. Similarly, the parietal reach region (PRR) contains neurons that respond preferentially to reach plans.

Activity in the PRR and LIP appears to be encoded in a *common* eye-centered reference frame. This reference frame is "common" since it is independent of both motor effector and stimulus modality (Andersen et al., 1998; Batista et al., 1999). LIP neurons encode eye movement plans in an eye-centered reference frame, regardless of whether the sensory stimulus is a light (Bushnell et al., 1981; Gnadt and Andersen, 1988; Andersen et al., 1990a; Goldberg et al., 1990; Brotchie et al., 1995) or a sound (Stricanne et al., 1996). Similarly, PRR neurons encode reach plans in an eye-centered reference frame (Batista et al., 1999).

The hypothesis that movement-planning activity is encoded in a common reference frame makes a rather nonintuitive prediction: reach plans to auditory stimuli should also be encoded in an eye-centered reference frame. This hypothesis is nonintuitive since the head-centered representation (Irvine, 1986) of a sound source can be converted directly into a limb-centered representation that is useful for reaches. In this study, we found that the tuning properties of a significant population of PRR neurons is affected more strongly by eye position than by limb position. A further analysis indicated that a significant population of PRR neurons encodes reaches to sounds in an eye-centered reference frame.

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Results

PRR neurons were recorded from two hemispheres of two rhesus macaque monkeys (*Macaca mulatta*). The PRR was identified through both its anatomical location and its physiological properties. Anatomically, the PRR is medial and posterior to area LIP (Snyder et al., 1997) and appears to overlap with area MIP and dorsal aspects of area PO (Snyder et al., 2000; see also Colby and Goldberg, 1999). Since the PRR overlaps with these regions, it may not be a distinct brain region but, instead, may reflect the functional properties of MIP and PO; further anatomical studies of the PRR are necessary to resolve this important issue. Physiologically, PRR neurons were characterized by having more activity in the delay period of a memory-guided reach than in a comparable period during a memory-guided saccade (Snyder et al., 1997). For monkey D, all of the neurons ($n = 26$) reported in this study were "reach specific" since they had significantly ($p < 0.05$) more activity during the delay period preceding a reach than during the delay period preceding a saccade. For monkey G, this motor specificity was not established until after all of the cells ($n = 55$) reported in this study had been recorded. Since, in our stimulus array, the location of the auditory and visual targets was the same, we wanted to decrease the possibility that any eye-centered neural activity resulted from monkey G learning to associate the location of an auditory target with the location of a visual target. In other words, we wanted to control for the possibility that training history may affect the responsiveness of PRR neurons to auditory stimuli (Grunewald et al., 1999). Thus, we did not train monkey G to make memory-guided saccades until after the reference frame data had been collected. After training monkey G to make memory-guided saccades to visual targets, 11 of 11 neurons were reach specific. Thus, we are confident that, in both animals, we recorded from the PRR.

The reference frame of PRR neurons was examined by determining how their tuning properties were affected under two conditions (see schematics in Figure 1). In the first condition, identical reaches were made to remembered sound source locations from two different fixation positions. In this condition, the monkey's initial hand position was on the central button, and he maintained fixation either 18° to the left or to the right of the central button. In the second condition, different reaches were made to remembered sound source locations from the same fixation position. In this condition, the monkey fixated the central button and his initial hand position was on the button that was either 36° to the left or to the right of the central button. It should be noted that these initial hand positions were adjacent to the 3×3 array of buttons that served as auditory reach

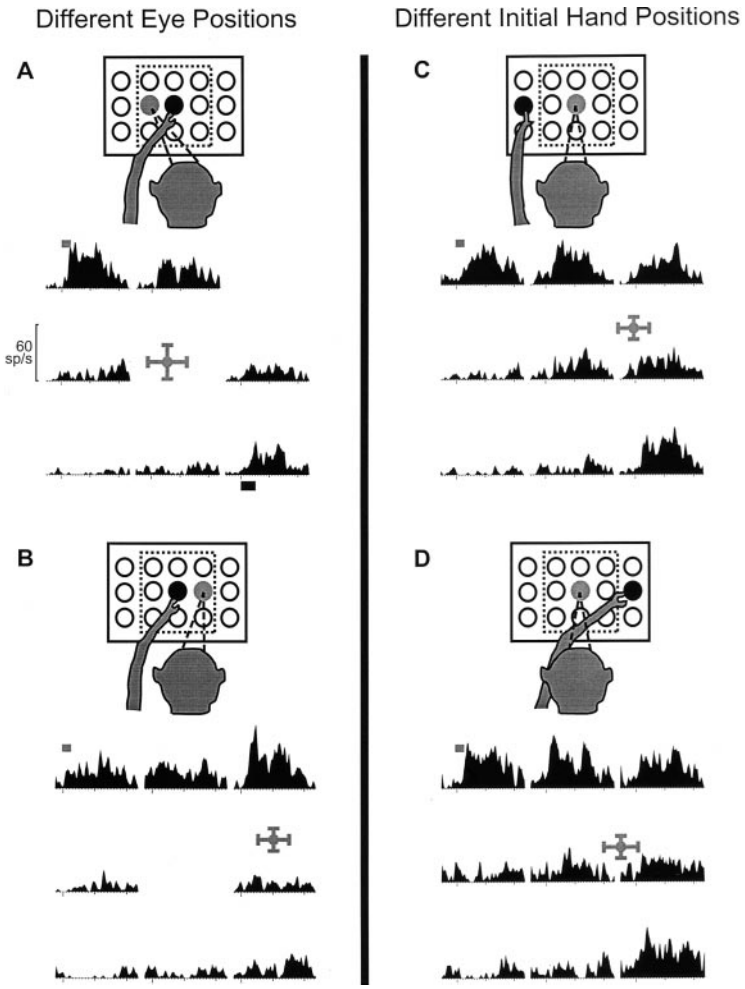

Figure 1. Behavior of a PRR Neuron in the Reference Frame Task

Each panel contains a schematic of the monkey's initial hand and eye positions and a PRR response profile, which was generated when the monkey's hand and eye positions were in the configuration shown in the schematic. In each schematic, the circles indicate the relative position of each button assembly, and the dotted square outlines the 3 × 3 target grid. The black circle indicates the button that the monkey pressed initially, and the gray circle indicates the button that the monkey fixated. The response profiles are arranged as a function of speaker location, and neural activity is represented by spike density histograms. The histograms were generated by convolving a triangular kernel with raster plots and indicate the time course of spike activity during five trials to each target location. The histograms are aligned relative to the onset of the noise burst, which is identified by the first long tick mark on the time axis. The solid gray bar, in the upper left corner of each response profile, shows the timing of the noise burst. The gray circle indicates the center of mass of the response profile; error bars represent 1 standard deviation. The center of mass was determined by multiplying each auditory target location by the delay period activity that was elicited when the monkey made a reach to that location, summing up these values, and then dividing this quantity by the sum of the delay period activity.

(A and B) Two response profiles generated with the same initial hand position but different eye positions. In this condition, the monkey did not reach to the center button on the button array, since this was the location of his initial hand position. On the day this neuron was recorded, the monkey would not reach up and to the right when his eye position was directed to the left; this behavior occurred rarely.

(C and D) Two response profiles generated with the same eye position but different initial hand positions. When eye position varies, the peak of the response profile shifts. In contrast, when initial hand position varies, the response profiles do not shift. Tick interval, 100 ms. The black bar in the lower right corner of (A) indicates 500 ms.

targets (see schematics in Figure 1). We positioned the monkey's hand at these locations so that we could maximize the number of reach targets; if the monkey's hand is located initially on a particular button, a reach cannot be made to that location. This hand position does not bias our analysis since it makes it even more likely to detect cells in a limb-centered reference frame.

These different conditions (i.e., two initial hand positions and two eye positions) allowed us to examine independently the effects of PRR activity when reaches were made to target locations in eye-centered or limb-centered reference frames. More specifically, if a PRR neuron encodes sound source location in an eye-centered reference frame (i.e., a neuron's activity reflects the difference between gaze position and the location of a sensory stimulus), the location of its response profile peak (or "center of mass") should shift as a function of eye position. If a PRR neuron encodes sound source location in a limb-centered reference frame (i.e., a neuron's activity reflects the difference between current and desired hand position), the location of the center of mass of its response profile should shift as a function of initial hand position. Alternatively, if PRR activity is in a head-, body-, or world-centered reference frame, the location of the center of mass of a PRR response profile should be invariant to these manipulations of eye and hand position. Additionally, the amplitude or "gain" of PRR activity may be modulated by such factors as eye and initial hand position (e.g., Zipser and Andersen, 1988; Brotchie et al., 1995; Graziano et al., 1997; Andersen et al., 1998). Indeed, as shown in area LIP, eye, head, body, or even world position can modulate neural activity (Andersen et al., 1997, 1998). An analysis of this gain will be presented in a future paper.

We found that eye position and initial hand position had a substantial effect on PRR activity. An example neuron is shown in Figure 1. Changes in eye position appeared to alter the spatial response profile of this neuron. When the monkey shifted its eye position from left to right, the response profile's center of mass shifted from the left to the right (compare Figures 1A and 1B). In contrast, changes in initial hand position had only a moderate effect on the location of the center of mass: the center of mass was located up and to the right of

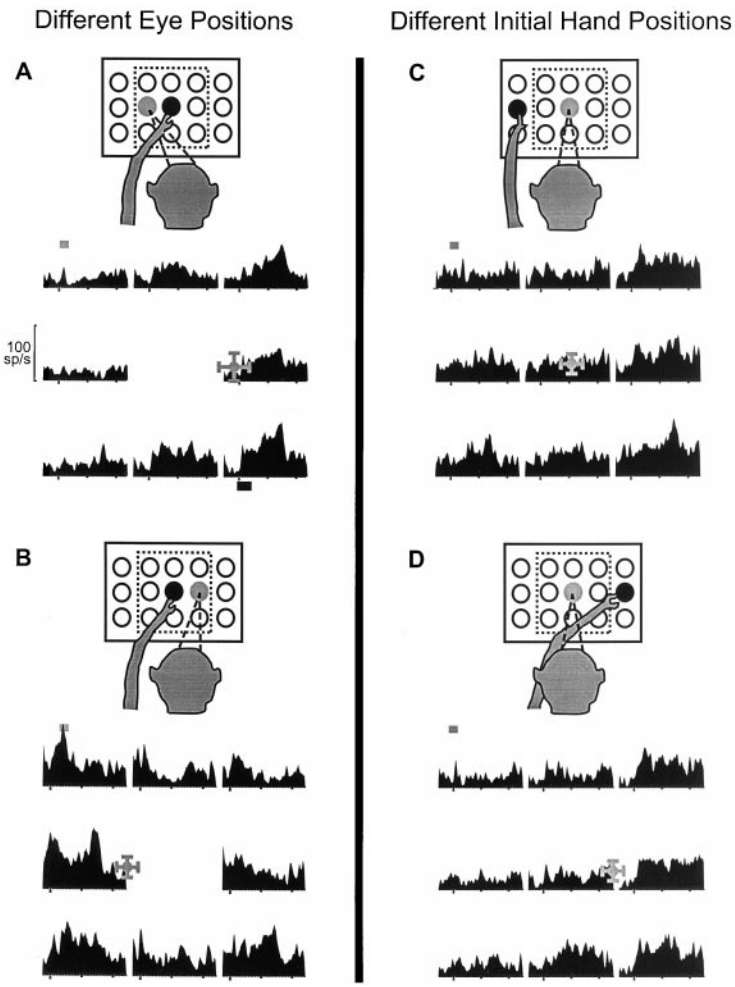

Figure 2. Behavior of a PRR Neuron in the Reference Frame Task

Same conventions as described in Figure 1.

the monkey's eye position, independent of initial hand position (compare Figures 1C and 1D). Another example neuron is shown in Figure 2. This example illustrates how, in some neurons, eye and hand position affected PRR activity in a complex manner. When the monkey shifted his eye position from left to right, the response profile's center of mass shifted from the right of the monkey's initial hand position to the left of his initial hand position (compare Figures 2A and 2B). When the monkey shifted its initial hand position from the left to the right, the center of mass shifted moderately to the right (compare Figures 2C and 2D). In addition, the overall magnitude or gain of activity appeared to change to a degree.

To summarize the results for the population, we calculated the correlation coefficient between the two response profiles generated with different eye positions and the correlation coefficient between the two response profiles generated with different initial hand positions (Batista et al., 1999). Since the result of this correlation analysis was the same for both monkeys, the data were pooled for presentation. Figure 3 summarizes this analysis, on a cell-by-cell basis, for our population of 81 cells. In this figure, a data point's position along the horizontal axis represents the correlation between the two response fields that were generated when the monkey's eye position was constant. The position along the vertical axis represents the correlation between the two response fields that were generated when the monkey's initial hand position was constant. If a data point lies above the diagonal line (which represents the line of equal correlation), it suggests that the tuning properties of a PRR neuron were affected more by changes in initial hand position than changes in eye position. If a data point lies below the diagonal, it suggests that the tuning properties of a PRR neuron were affected more by changes in eye position than changes in initial hand position. If a neuron is not sensitive to one of these manipulations or is only gain modulated by changes in eye or initial hand position, its correlation value should, in theory, be equal to one. As can be seen, both eye and initial hand position affected the tuning properties of PRR neurons. This observation is consistent with the notion that individual PRR neurons may encode information about target position in a reference frame that takes into account both initial hand and eye position. However, we found significantly (Wilcoxon, $p < 0.05$) more neurons that were altered more by changes in eye position than by changes in initial hand position. In other words, while the tuning properties of individual cells were affected by eye or hand position, in the population, PRR activity was more sensitive to changes in eye position than changes in initial hand position.

What is the nature of this sensitivity to eye position?

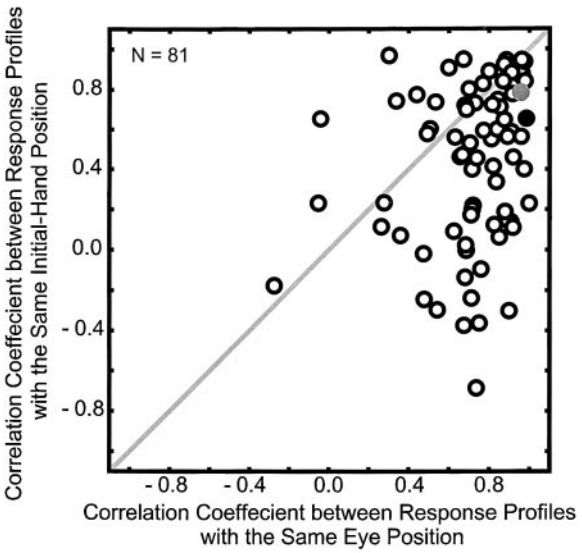

Figure 3. Correlation Analysis of PRR Cells

One a cell-by-cell basis, the correlation value of the two response profiles with different initial hand positions (same eye position) is plotted on the abscissa, and the correlation value of the two response profiles with different eye positions (same initial hand positions) is plotted on the ordinate. A high correlation coefficient indicates that the two response profiles are similar. The solid black circle indicates the correlation values calculated for the two pairs of response profiles illustrated in Figure 1. The solid gray circle indicates the correlation values calculated for the two pairs of response profiles illustrated in Figure 2. The solid gray line is the line of equal correlation.

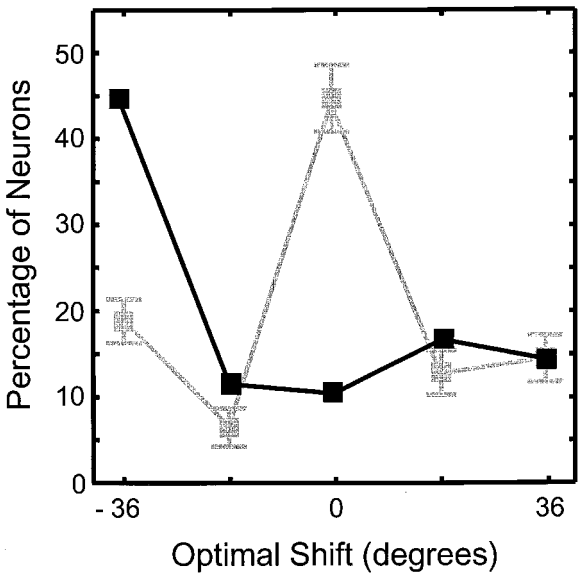

Figure 4. Histogram of Optimal Shift Values

The black line is the distribution of optimal shift values. The gray histogram is the distribution of optimal shift values generated with a bootstrap analysis and indicates the distribution that would be expected by chance. The error bars on this histogram represent the standard error of the mean.

This sensitivity to eye position is consistent with the notion that PRR activity encodes, in part, reaches to sounds in an eye-centered reference frame. To explicitly test this hypothesis, we calculated the cross-correlation coefficient between the two response profiles generated with different eye positions (Shenoy et al., 1999). This analysis was done by calculating the correlation coefficient when one response profile was held constant and the other was shifted horizontally, relative to the first response profile; the curves were shifted horizontally since the two eye positions used in this study varied along the horizontal dimension. Since the two fixation positions were located 18° to the left and 18° to the right of the central fixation position, the range of possible shifts was limited to ±36°. In other words, the response profiles were shifted (relative to one another) either by −36°, −18°, 0°, +18°, and +36°. After shifting the response profile by one of these shift values, we correlated the response profiles in the region of overlap. The *optimal shift* was the relative horizontal shift with the maximum correlation coefficient. In this analysis, the two response profiles were aligned, relative to initial eye position, when one response profile was shifted by −36°. Thus, if a cell had an optimal shift of −36°, it implied that it aligned best in an eye-centered reference frame. A 0° optimal shift suggested that the activity of a PRR neuron was insensitive to initial eye position. Neurons with this optimal-shift value may be in other reference frames, such as head centered. Intermediate shift values indicated alignment in between. This analysis was done for the population of 55 cells collected from monkey G but was not done on the data collected from monkey D. Since monkey D was trained to reach to only a subset of the targets, when the two response profiles were shifted, there were few common target locations in the region of overlap and, consequently, few pairs of data points to correlate; correlation values derived from such a limited data set are difficult to interpret.

Figure 4 plots the results of the cross-correlation analysis, on a cell-by-cell basis, for the population of cells from monkey G. We found a large proportion (42%, 23 of 55 neurons) of PRR cells had an optimal shift of −36°, the optimal-shift value expected for an eye-centered reference frame. An additional 7 neurons (13%) had an optimal-shift value of −18°, the optimal-shift value that is intermediate between an eye-centered and a head-centered (or body-centered) reference frame.

Since, in this analysis, the number of responses profiles in each region of overlap differed, we were concerned that the distribution shown in Figure 4 may reflect the changing number of data points and its effect on correlation values rather than the underlying tuning properties of the neural data. To examine this possibility, we performed a bootstrap analysis. For this analysis, we, on a cell-by-cell basis, picked randomly (with replacement) two response profiles and cross-correlated them, as described above, in order to obtain their optimal shift. For each cell of the 55 cells in the population, this process was repeated 100 times in order to obtain a distribution of "expected" optimal-shift values. This distribution was then binned to form a histogram. The histograms generated from each of the 55 cells were then averaged together to obtain the distribution of "expected" optimal-shift values. If the distribution of optimal-shift values that was obtained from the actual data simply reflected the changing number of data points, then this distribution should be quite similar to the one obtained with the bootstrapped data. However, as can

be seen, this was not the case. Specifically, we found more cells had optimal-shift values of $-36°$ and $-18°$ than predicted by the bootstrapped distribution (Mann-Whitney, $p < 0.05$). In contrast, at other optimal-shift values, the proportion of cells observed was nearly equal to or less than that expected by chance. We interpret these results to mean that the cross-correlation analysis was sensitive to the tuning properties of the PRR neurons. Moreover, the significant number of PRR neurons with optimal-shift values of $-36°$ suggests that a population of PRR neurons encodes reach plans to auditory targets in an eye-centered reference frame.

Discussion

The results of this study demonstrate that the tuning properties of individual PRR neurons were affected by eye and initial hand position. These effects were complex and included full or partial shifts in a response profile's center of mass and changes in the gain of neural activity. In the population, eye position effects were greater than effects due to initial hand position. Moreover, as the cross-correlation analysis indicated, a significant population of PRR neurons encoded reaches, at least in part, in an eye-centered reference frame. This population representation of an eye-centered reference frame could allow another cortical area to "read out" the eye-centered location of a reach target by integrating the information from a limited number of neurons (Zipser and Andersen, 1988; Brotchie et al., 1995), even though the individual neurons may show a high degree of variability. These observations support and extend the hypothesis that movement plans in the PRR and in area LIP are encoded in a common eye-centered reference frame, a reference frame that is independent of the type of action planned and the sensory stimulus that initiates the action (Andersen et al., 1998).

There are advantages for encoding movement plans in a common reference frame. For instance, since natural scenes contain both auditory and visual objects, it may be computationally simpler to encode motor plans in a similar reference frame (Sabes and Jordan, 1997; Batista et al., 1999). Similarly, this common reference frame may ease and facilitate the coordination and integration of activity across area LIP and the PRR (Andersen et al., 1998). Everyday tasks often require complex hand and eye movements. By encoding motor plans in a common reference frame, the computations underlying these complex movements may be facilitated.

Many aspects of auditory perception seem to be dependent on eye position or the location of visual stimuli. For example, a person's perception of sound source location depends on his/her eye position (Lewald and Ehrenstein, 1996; Lewald, 1998). Similarly, the perceived location of a sound source is profoundly impacted by misplaced visual stimuli: if we see a person's lips moving, we perceive that it is the source of the speech, regardless of the fact the speech source originates elsewhere (Driver, 1996). The neural bases of these phenomena may be related, in part, to the eye-centered representations of sound source location found in area LIP (Stricanne et al., 1996) as well as the PRR (current study).

An important question to consider is where does auditory information get transformed from its original head-centered reference frame (Irvine, 1986) to the eye-centered representations that are found in area LIP and the PRR (Andersen et al., 1998)? This question is confounded by the fact that auditory spatial information is encoded in both cortical and midbrain pathways (Cohen and Knudsen, 1999). Consequently, it is possible that the transformation from a head-centered reference frame to an eye-centered reference frame occurs independently in both the cortical pathway and the midbrain pathway or in an area of the ascending auditory pathway that contributes to both of these cortical and midbrain pathways. At present, though, we do not have sufficient knowledge of the cortical sound localization pathway to address this issue. One attractive hypothesis is that, since the posterior parietal cortex receives both auditory, visual, and eye position signals (Pandya and Kuypers, 1969; Andersen et al., 1990b), it may be a site of this transformation. To determine if this hypothesis is correct, the reference frame of cells in auditory areas leading to the posterior parietal cortex needs to be examined in order to determine the locus of this transformation.

Experimental Procedures

Animal Preparation

Experiments were conducted in two hemispheres of two adult, male rhesus monkeys (*Macaca mulatta*). In a sterile surgical procedure under sodium pentobarbital anesthesia, a methylmethacrylate implant was fitted to the skull and a scleral eye coil was implanted; the scleral eye coil was used to monitor eye position. Behavioral training began no sooner than 1 week after surgery. Monkeys received juice rewards for correct performance during both behavioral training and experimental sessions. Adequate performance levels were reached after several months of training. A subsequent surgery was performed to open a craniotomy and to implant a stainless-steel cylinder, which provided chronic access to the PRR for electrophysiological recording. The Caltech Institutional Animal Care and Use Committee approved all protocols. Further details about these procedures can be found in Snyder et al. (1997) and Shenoy et al. (1999).

Recording Techniques

Extracellular action potentials were recorded with varnish-coated tungsten microelectrodes, with $\sim$2 MΩ impedance at 1 kHz. A stainless-steel guide tube was advanced manually dorsoventrally through the dura, and the electrode was extended further into the brain with a hydraulic micropositioner. Action potentials were amplified and single neuron waveforms were isolated with a two-window, time–voltage discriminator (Bak Electronics).

Behavioral Tasks and Data Analysis

Saccades and reaches were made to an array of touch-sensitive buttons placed in front of the monkey. The buttons were 4 cm in diameter and were separated by 18° in azimuth and 23° in elevation. Each button contained a red and a green light-emitting diode (LED), which were side-by-side and centered in front of a speaker (Audax, TWO25V2). A trial began with illumination of a red and a green LED. The monkey looked at and pressed this "central" button. A 300 ms cue was then presented from one of the buttons that formed a 3×3 grid centered on the central button. If the cue was a red LED flash, it signaled an eventual saccadic eye movement. If the cue was a green LED flash, it signaled an eventual reach. After a delay period (>900 ms), the central LEDs were extinguished and the monkey made a saccade or reach to the remembered location of the flashed LED. Importantly, during saccade trials, the monkey did not move his hand, and during reach trials, the monkeys maintained fixation at the location of the now-extinguished red LED. The contralateral limb was used in all experiments and the room was darkened.

PRR neurons were characterized as being "reach specific" (Snyder et al., 1997) if there was significantly (bootstrap analysis, $p <$

0.05) more activity during the delay period (100–800 ms after stimulus onset) preceding reaches than during the delay period preceding saccades.

The reach task was modified so that we could examine the reference frame in which reaches to auditory targets (300 ms noise bursts) are encoded (Figure 1). In this task, monkeys made reaches to the remembered location of an auditory target. Four conditions with different eye and initial hand positions were used. In two conditions, the monkey's initial hand position was on the central button, and he maintained fixation either 18° to the left or to the right of the central button. In the other two conditions, the monkey fixated the central button, and his initial hand position was on the button that was either 36° to the left or to the right of the central button. Each of these four initial configurations was interleaved randomly with five repetitions of reaches to each randomly chosen auditory target. Monkey D could only be trained to make reaches to six of the targets on the 3×3 grid.

The reference frame of a PRR neuron was only examined if it was spatially tuned. A cell was spatially tuned if neural activity during the delay period varied significantly (ANOVA, $p < 0.05$) as a function of auditory target location.

The reference frame of PRR neurons was characterized through a correlation analysis (Shenoy et al., 1999). The formula to compute the correlation coefficient was:

$$r(x, y) = \frac{\sum_{i=1}^{n} (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum_{i=1}^{n} (x_i - \bar{x})^2} \sqrt{\sum_{i=1}^{n} (y_i - \bar{y})^2}}$$

Using this formula, the correlation coefficient between the two response profiles with different eye positions was calculated: x_i was the average delay period firing rate to a target i from the leftward eye position and y_i was the average delay-period firing rate to a target i from the rightward eye position. $\bar{x}$ was the average of the x_i, and $\bar{y}$ was the average of the y_i. An analogous formula was used to compute the correlation coefficient between the two response profiles with different initial hand positions.

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References

Andersen, R.A., Bracewell, R.M., Barash, S., Gnadt, J.W., and Fogassi, L. (1990a). Eye position effects on visual, memory, and saccade-related activity in areas LIP and 7a of macaque. J. Neurosci. *10*, 1176–1196.

Andersen, R.A., Asanuma, C., Essick, G., and Siegel, R.M. (1990b). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. J. Comp. Neurol. *296*, 65–113.

Andersen, R.A., Snyder, L.H., Bradley, D.C., and Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. Annu. Rev. Neurosci. *20*, 303–330.

Andersen, R.A., Snyder, L.H., Batista, A., Buneo, C.A., and Cohen, Y.E. (1998). Posterior parietal areas specialized for eye movements (LIP) and reach (PRR) use a common reference frame. In Novartis Foundation Symposium 218: Sensory Guidance of Movement (Chichester, UK: Wiley), pp. 109–118.

Batista, A., Buneo, C.A., Snyder, L.H., and Andersen, R.A. (1999). Reach plans in eye-centered coordinates. Science *285*, 257–260.

Brotchie, P.R., Andersen, R.A., Snyder, L.H., and Goodman, S.J. (1995). Head position signals used by parietal neurons to encode locations of visual stimuli. Nature *375*, 232–235.

Bushnell, M.C., Goldberg, M.E., and Robinson, D.L. (1981). Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J. Neurophysiol. *46*, 755–772.

Cohen, Y.E., and Knudsen, E.I. (1999). Maps versus clusters: different representations of auditory space in the midbrain and forebrain. Trends Neurosci. *22*, 128–135.

Colby, C.L., and Goldberg, M.E. (1999). Space and attention in parietal cortex. Annu. Rev. Neurosci. *22*, 319–349.

Driver, J. (1996). Enhancement of selective listening by illusory mislocation of speech sounds due to lip-reading. Nature *381*, 66–68.

Gnadt, J.W., and Andersen, R.A. (1988). Memory related motor planning activity in posterior parietal cortex of macaque. Exp. Brain Res. *70*, 216–220.

Goldberg, M.E., Colby, C.L., and Duhamel, J.-R. (1990). Representation of visuomotor space in the parietal lobe of the monkey. Cold Spring Harbor Symp. Quant. Biol. *60*, 729–739.

Graziano, M.S., Hu, X.T., and Gross, C.G. (1997). Visuospatial properties of ventral premotor cortex. J. Neurophysiol. *77*, 2268–2292.

Grunewald, A., Linden, J., and Andersen, R.A. (1999). Responses to auditory stimuli in macaque lateral intraparietal area. II. Effects of training. J. Neurophysiol. *82*, 330–342.

Irvine, D.R.F. (1986). The Auditory Brainstem (New York: Springer-Verlag).

Lewald, J. (1998). The effect of gaze eccentricity on perceived sound direction and its relation to visual localization. Hear. Res. *115*, 206–216.

Lewald, J., and Ehrenstein, W.H. (1996). The effect of eye position on auditory lateralization. Exp. Brain Res. *108*, 473–485.

Pandya, D.N., and Kuypers, H.G.J. (1969). Intra- and interhemispheric connections of the neocortical auditory system in the rhesus monkey. Brain Res. *13*, 49–65.

Sabes, P., and Jordan, M.I. (1997). Obstacle avoidance and a perturbation sensitivity model for motor planning. J. Neurosci. *17*, 7119–7128.

Shenoy, K.V., Bradley, D.C., and Andersen, R.A. (1999). Influence of gaze rotation on the visual response of primate MSTd neurons. J. Neurophysiol. *81*, 2764–2786.

Snyder, L.H., Batista, A., and Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. Nature *386*, 167–170.

Snyder, L.H., Batista, A., and Andersen, R.A. (2000). Intention-related activity in the posterior parietal cortex: a review. Vis. Res. *40*, 1433–1441.

Stricanne, B., Andersen, R.A., and Mazzoni, P. (1996). Eye-centered, head-centered, and intermediate coding of remembered sound locations in area LIP. J. Neurophysiol. *76*, 2071–2076.

Zipser, D., and Andersen, R.A. (1988). A back-propagation programmed network that simulates response properties of a subset of posterior parietal neurons. Nature *331*, 679–684.