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Eye position encoding in the macaque posterior parietal cortex

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Abstract

In two previous studies, we had demonstrated the influence of eye position on neuronal discharges in the middle temporal area, medial superior temporal area, lateral intraparietal area and area 7A of the awake monkey (Bremmer *et al.*, 1997a,b). Eye position effects also have been found in visual cortical areas V3A and V6 and even in the premotor cortex and the supplementary eye field. These effects are generally discussed in light of a coordinate transformation of visual signals into a non-retinocentric frame of reference. Neural network studies dealing with the eye position effect succeeded in constructing such non-retinocentric representations by using model neurones whose response characteristics resembled those of 'real' neurones. However, to our knowledge, response properties of real neurones never acted as input into these neural networks. In the present study, we thus investigated whether, theoretically, eye position could be estimated from the population discharge of the (previously) recorded neurones and, if so, we intended to develop an encoding algorithm for the position of the eyes in the orbit. The optimal linear estimator proved the capability of the ensemble activity for determining correctly eye position. We then developed the so-called subpopulation encoding of eye position. This algorithm is based on the partition of the ensemble of neurones into two pairs of subpopulations. Eye position is represented by the differences of activity levels within each pair of subpopulations. Considering this result, encoding of the location of an object relative to the head could easily be accomplished by combining eye position information with the intrinsic knowledge about the retinal location of a visual stimulus. Taken together, these results show that throughout the monkey's visual cortical system information is available which can be used in a fairly simple manner in order to generate a non-retinocentric representation of visual information.

Introduction

A fundamental problem in the control of visually guided movement consists of the different frames of reference in which sensory and motor signals occur. The incoming sensory signals are organized in a retinotopic manner throughout several stages of the visual system, whereas the outgoing motor commands are encoded with respect to singular muscles. Considering a typical interaction with an environment, e.g. reaching out for a target, the problem obviously arises in how to relate the incoming sensory signal with the required motor output. One hypothesis for solving this problem is a so-called coordinate transformation from retinocentric signals to signals encoded in a cranio-, ego- or even allocentric frame of reference (Andersen & Zipser, 1988; Zipser & Andersen, 1988; Andersen *et al.*, 1990, 1993; Pouget *et al.*, 1993; Pouget & Sejnowski, 1997). Initially, studies on awake monkeys had shown that the visual, memory and saccade-related responses of neurones in posterior parietal cortical areas were affected by eye position (Andersen & Mountcastle, 1983; Andersen *et al.*, 1985). The strength, for example, of a saccade-related discharge was dependent on the initial position of the eyes in the orbit, although the neuronal tuning for the metrics of the saccade (amplitude, direction) was always the same. It was suggested that these eye-position-dependent cells could be involved in the generation of an implicit representation of visual information in a non-retinocentric frame of reference by combining eye position information with information about the retinal location of a visual stimulus.

Most theoretical studies concerning a possible coordinate transformation carried out so far were based on the influential study by (Zipser & Andersen (1988). Briefly, Zipser and Andersen trained a three-layer back propagation network to represent in the output layer spatial information in a non-retinocentric frame of reference. By studying cell characteristics of the trained network, they found that the discharge characteristics of neurones in the hidden layer considerably resembled the real discharge characteristics of neurones in parietal area 7A. However, none of the models developed so far used experimental data as their input signal.

In our study therefore, we first tested whether, theoretically, the recorded neuronal discharges were capable of representing the actual eye position. This was carried out by means of a well-established mathematical algorithm called the optimal linear estimator (OLE). The OLE was applied to the discharges of a

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subset of previously recorded neurones, i.e. neurones from parietal areas LIP (lateral intraparietal area) and 7A, tested during fixation in darkness. In a second step we set out to develop a concept whose implementation had to be biologically plausible and which had to be capable of recovering eye position from neuronal discharges. This resulted in a concept which we called the subpopulation encoding of eye position (SPE). Two pairs of linear-independent ensemble response planes represent the average discharge of subgroups of neurones. Depending on the actual eye position, the average discharge increases for the one subgroup and decreases for the other. Equal activity values are achieved for eye positions located almost along the horizontal- and vertical-zero-meridians. Eye position simply can be encoded as the difference of discharge values in the different subpopulations. As an example, a difference value of roughly zero for both subgroups would indicate an eye position almost straight ahead. A difference value of zero for the horizontal subgroups, but a positive value for the vertical subgroups would indicate an upward eye position on the vertical meridian, etc. Combining this information about eye position together with the available information about the location of a visual stimulus on the retina would allow (e.g. by simple vector summation) for encoding of the location of a visual stimulus with respect to the head.

Materials and methods

In previous studies we had investigated the eye position effect in neurones of the middle temporal area (MT), medial superior temporal area (MST), lateral intraparietal area (LIP) and area 7A in different behavioural paradigms. For the sake of clarity, we will present the entire procedure of data analysis for only one subset of cells, tested in only one behavioural paradigm. As a representative subset we selected the neurones in the posterior parietal cortex (areas LIP and 7A) tested in the fixation paradigm in darkness (see below). This subset was chosen for two reasons. (i) response characteristics of neurones from areas LIP and 7A have already been modelled by several other studies. Applying our model allows direct comparison with the outcomes of other experimental and theoretical studies on posterior parietal neurones. (ii) The population size ($n = 89$) of this subset was big enough to test for effects at the population level and furthermore allowed assembling of subgroups of reasonable size for testing the dependence of remaining error on sample size (see below). Finally, by presenting data from two other samples of cells, we will demonstrate that the computational results are alike for all subsets of neurones, tested in all behavioural paradigms, and that the model holds as a general scheme for an implicit encoding of eye position.

Data recording and analysis

The procedures for monkey training, electrophysiological recordings as well as data analysis were described in detail in previous papers (Bremmer *et al.*, 1997a,b). Monkeys had been surgically prepared for recordings: under general anaesthesia and sterile surgical conditions each animal had been implanted with a device for holding the head. A recording chamber for microelectrode penetrations through the intact dura was placed flat to the skull, scleral search coils for monitoring eye position were implanted. All procedures were in accordance with published guidelines on the use of animals in research (European Communities Council Directive 86/609/EEC). During an experiment the animal sat in a primate chair with the head restrained, facing a translucent screen.

In the fixation paradigm, used for recordings in areas LIP and 7A, targets were back-projected in random order at nine different locations on the screen without any further visual stimulation. Locations were the centre of the screen plus eight concentrically located points 15° away from the centre ([x, y] = [0°,0°], [0°, ±15°], [±15°,0°], [±10.6°, ±10.6°]). Presentation of fixation targets lasted for 1000 ms after the animal's eye position had been located continuously within an electronically defined window for at least 300 ms. Mean neuronal activity was computed for each fixation location.

In the pursuit paradigm, used for recordings in areas MST, LIP and 7A, the monkey had to pursue a target which (after an initial fixation period) started moving in random order from one out of five different locations, always with the same speed into the previously determined preferred direction. Starting locations for pursuit were 15° apart from the centre and the centre itself ([x, y] = [± 10.6°, ± 10.6°], [0°, 0°]). Target movement lasted for 1200 ms. For analysing neuronal activity in the pursuit paradigm individual trials were aligned to the onset of the initial saccade preceding the smooth pursuit phase. Trials typically were divided into two characteristic epochs. Epoch 1 was defined as the time window beginning with trial onset (fixation light ON) until 100 ms before the initial saccade, taken as background activity. Epoch 2, taken as raw activity, was defined as beginning 100 ms after saccade onset until the end of the pursuit target movement, thus lasting for about 1000 ms. Discharge rates (relative activity) were computed as activity difference between raw activity (epoch 2) and background activity (epoch 1).

Differences in activity were tested for statistical significance with a distribution free ANOVA. Two-dimensional linear regression analysis was applied to quantify the eye position effect. For validating the planar model as fit to the observed data an *F*-test was employed.

At the end of the experimental sessions small electrolytic lesions were made in the recorded hemisphere by passing small direct current (10 μA for 20 s) through the recording electrode. The monkey then was given an overdose of sodium pentobarbital and after respiratory block and cessation of all reflexes transcardially perfused. Frontal sections were made at 50-μm thickness and stained alternately with the Gallyas method for myeloarchitecture and with cresyl violet for cytoarchitecture. As a standard procedure, two-dimensional maps of the recorded hemispheres were constructed (after: van Essen & Maunsell, 1980; Ungerleider & Desimone, 1986; Distler *et al.*, 1993). Recording locations were reconstructed by relating the penetration scheme to the electrolytic lesions.

Results

The eye position effect at the single cell level

Two-thirds (60/89) of the investigated neurones revealed an influence of the position of the eyes in the orbit on their activity during fixation in darkness. This modulatory effect was quantified utilizing 2-dimensional linear regression analysis. An example is shown in Figure 1. For this neurone recorded in area 7A discharges were strongest for fixation locations below the horizontal-zero-meridian (ANOVA: $P < 0.001$). Activity decreased for eye positions further up. The shaded plane depicts the regression plane approximated to the mean discharge values.

All target positions were located at equal distance from the screen centre, i.e. for all eye positions gaze angle (φ) varied relative to straight ahead (left, left and up, etc.) while gaze

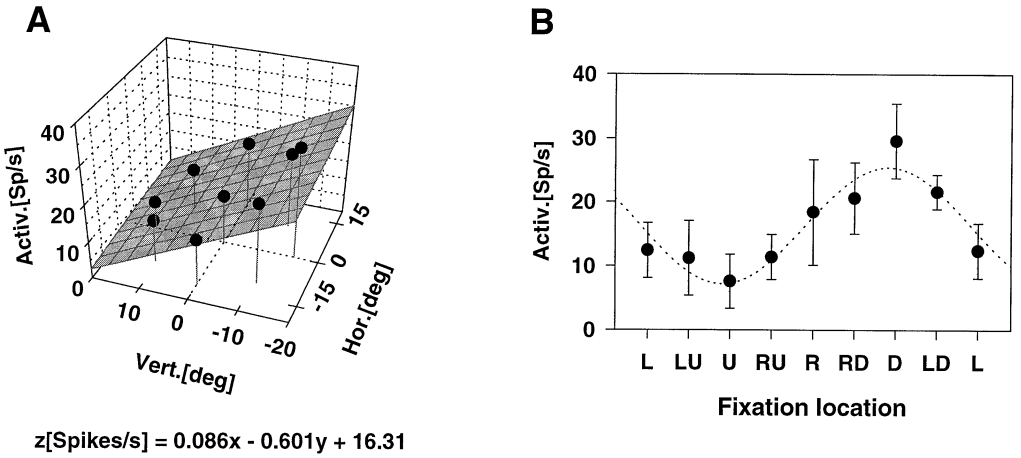

FIG. 1. Eye position effect during fixation in darkness: single cell level. (A) The shaded plane represents the 2-dimensional linear regression to the mean discharge values of a neurone from area 7A ($r^2 = 0.863$, $P < 0.003$). The *x*–*y* plane in this plot represents the central 40 by 40 degrees of the tangent screen. The base point of each drop line depicts the fixation location on the screen, and the height of each line depicts the mean activity value during fixation at this location. (B) Mean activity values (± standard deviation [SD]) of the very same neurone as in A (C = centre; LU = left up; U = up; RU = right up; R = right; RD = right down; D = down; LD = left down; L = left). Discharges were strongest for fixation locations below the horizontal-zero-meridian (ANOVA: $P < 0.001$). The dotted line represents the values obtained from the regression plane in A for isoamplitude (15°) eye positions.

amplitude was kept constant ($r = 15°$). With $x = r\cos\varphi$, and $y = r\sin\varphi$, the equation of a regression plane in Cartesian coordinates

$$z = a\,x + by + c$$

can be re-written as

$$z = ar\cos\varphi + br\sin\varphi + c = (a, b) \times (r\cos\varphi, r\sin\varphi)^T + c.$$

The product term can be interpreted as the scalar product between the gradient of the regression plane $\mathbf{g} = (a, b)$ and the vector of the actual eye position $\mathbf{e} = (r\cos\varphi, r\sin\varphi)$ and thus leads to

$$z = \mathbf{ge} + c = ge\cos\psi + c$$

with ψ the angle between vectors **g** and **e**. Thus, approximation of a regression plane with horizontal and vertical eye position as independent variables is equivalent to the approximation of a cosine function with gaze angle as independent variable for a fixed gaze amplitude (15°). As shown by (Sanger (1994) and Salinas & Abbot (1994) this cosine tuning is optimal for application of the OLE (optimal linear estimator). The variance of this linear estimate depends on the neuronal tuning function, and the smallest variance is obtained for a cosine tuning. We thus employed the OLE as mathematical tool for testing the capability of the population of recorded neurones to encode eye position.

The optimal linear estimator

This algorithm consists in estimating eye position, E^*, by a linear combination of the vector, **A**, corresponding to the activities of *n* neurones.

$$E^* = W\mathbf{A}$$

The estimator is optimal in the sense that *W*, the weight matrix, is chosen to minimize the square error, *SE*, between the true eye position, E_i, and the estimated values, E_i^*.

$$SE = \Sigma_i \; E_i - E_i^{*\;2}$$

In our case, *i* varied from 1 to 9, because the activities of the neurones were recorded for nine different eye positions. Several numerical methods are available for finding *W*. We chose to use a stochastic gradient descent procedure. This method treats *W* as the weights of a two-layer network in which the input units correspond to the neurones, and the output layer contains two units encoding the horizontal and vertical eye position. The network is then trained on pairs of activity vectors and corresponding eye positions. The entries in *W* are adjusted after each example according to the delta-rule. This method is guaranteed to reach the global minimum of the mean square error although this minimum might not necessarily be zero (Widrow & Hoff, 1960).

Using the activity values recorded from the 89 cells for nine different eye positions, we trained such a network and found that the optimal *W* leads to a residual *SE* of 10^{-5}. In other words, application of the OLE could prove the capability of retrieving an unbiased estimate of eye position from the activity of the recorded neurones.

The eye position effect at the population level and the subpopulation encoding of eye position

The eye position effect, which could be observed at the single cell level, was balanced out at the population level. This is shown in Figure 2. The histogram on the left depicts the average discharge values of the population of neurones for the different fixation locations. Statistical analysis proved these values to be not significantly different (ANOVA: $P > 0.9$). The shaded plane on the right represents the very same result by showing the population discharge plane which was obtained by averaging the parameters (a, b and c) of the individual regression planes.

The symmetry of the population response, i.e. the flatness of the population discharge plane, could result, for example, from a roughly equal distribution of eye position effects for all parts of the oculomotor range. It could, however, result also from a small number of neurones firing at high rates in one part of the oculomotor range and a large number of neurones firing at relatively low rates for the opposite part of the oculomotor range. We therefore analysed also the distribution of the gradients of the regression planes, i.e. the amount and the direction of the steepest increase of activity with eye position. For the population of neurones, regression slopes were normally distributed, whereas gradient directions proved to be uniformly

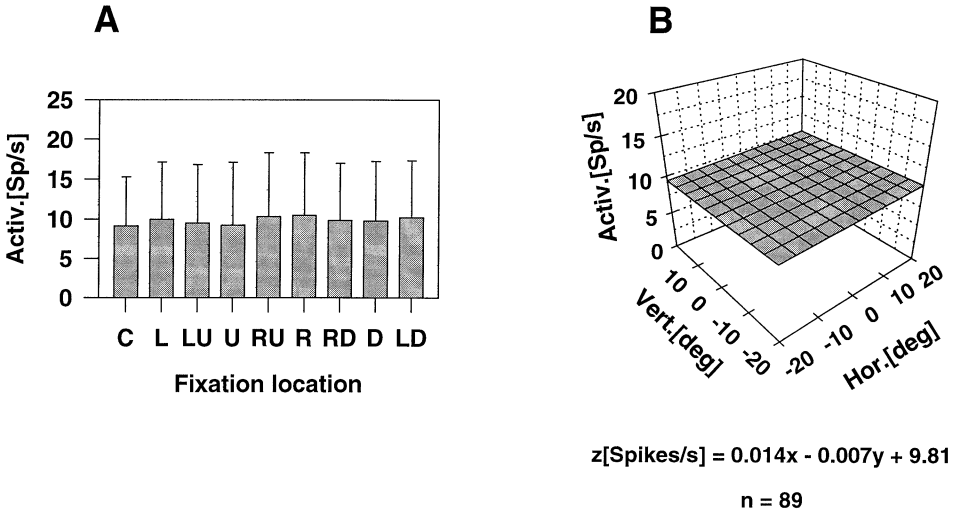

FIG. 2. Eye position effect during fixation in darkness: population level. A: mean activity (± SD) for the nine different eye positions (C = centre; LU = left up; U = up; RU = right up; R = right; RD = right down; D = down; LD = left down; L = left). The discharge values for the different eye positions were not significantly different (ANOVA $P > 0.9$) indicating that the modulatory effect of eye position is balanced out at the population level. B: the mean population response plane was obtained by averaging all linear regression planes. The resulting discharge plane proved to be flat.

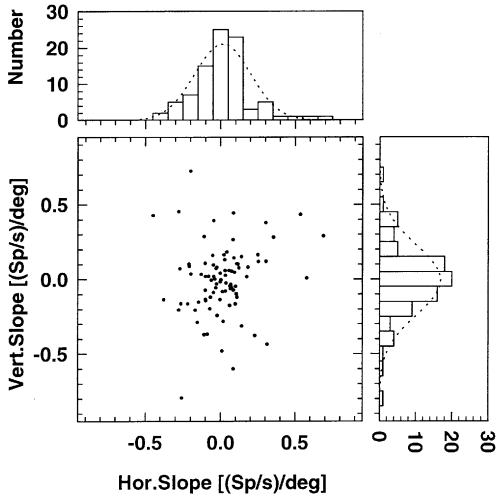

FIG. 3. Distribution of the gradients of the regression planes. In the central scatter plot each single dot represents the gradient of an individual linear regression plane. Statistical analysis proved the directions of the gradients to be uniformly distributed. A normal distribution as shown by the dotted lines in the histogram aside and on top of the central scatter diagram turned out to be the best fit for both the values of the horizontal and the vertical slopes.

distributed (χ^2-test: $P > 0.9$), as can be estimated from Figure 3. In general, for a given number of neurones (like the one in Fig. 1), with increasing activity for downward eye positions (gradient directions) there exists an almost equivalent number of neurones with roughly the same increasing activity for upward gradient directions. The same is true considering rightward vs. leftward gradient directions. This led us to consider the whole population of neurones as being built up by two pairs of subpopulations: one subpopulation of cells with increasing discharge for eye positions below the horizontal-zero-meridian (H-0-M) and the other with increasing discharge for eye positions above the H-0-M. Another pair of subpopulations would respond better for eye positions at the right or left of the vertical-zero-meridian (V-0-M), respectively. The same neurones thereby might share different subgroups, i.e. a neurone might be part of a vertical as well as a horizontal subpopulation.

We applied this consideration by computing the average activity planes of these up vs. down subpopulations. The number of neurones with stronger activity for downward eye positions ($n = 44$) was almost identical to the number of neurones with a preference for upward eye positions ($n = 45$). We resulted in two ensemble planes z_{y-} and z_{y+} which nearly had no slope in horizontal direction, and about the same slope in vertical direction, however, with an inverted sign. Furthermore, these planes had about the same intercept, indicating that their activity levels were almost equal near the H-0-M:

$$z_{y-} = -0.021x - 0.177y + 10.45 \ (n = 44)$$

$$z_{y+} = 0.048x + 0.158y + 9.19 \ (n = 45)$$

The analogue symmetrical behaviour was obtained for the left vs. right subpopulations:

$$z_{x-} = -0.129x - 0.023y + 10.40 \ (n = 41)$$

$$z_{x+} = 0.136x + 0.006y + 9.31 \ (n = 48)$$

The two resulting ensemble response z_{x-} and z_{x+} planes had almost no slope in vertical direction, about the same slope in horizontal direction (with an inverted sign) and approximately the same intercept. Thus, equal activity levels for the second pair of response planes were located around the V-0-M. Locations of equal activity are given by the following equations:

$$y = -0.206x + 3.76 \text{ for the first pair of planes and}$$

$$x = -0.109y + 4.13 \text{ for the second pair of planes.}$$

On average the difference between real and estimated eye position (mean remaining error MRE) is the same as the remaining error (RE) for straight ahead direction:

$$\text{MRE } [°] = \text{RE}_{([x, y] = [0°, 0°])} = \text{sqrt}(3.762^2 + 4.132^2) = 5.58.$$

Considering these relationships the actual eye position could be retrieved from neuronal discharges of a population of neurones in a push–pull manner by subtracting the ensemble activity of one

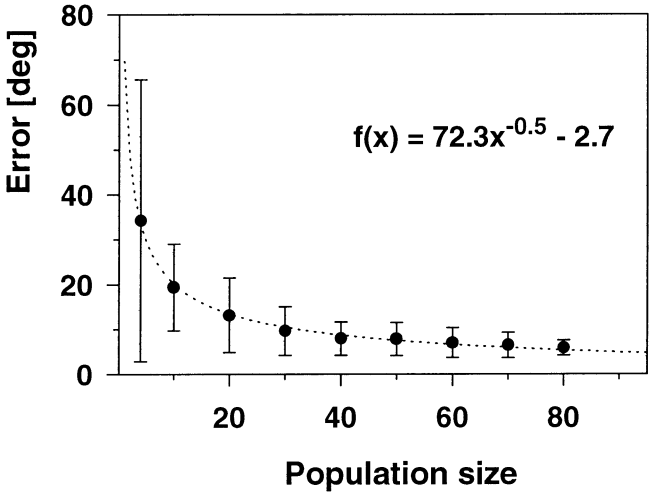

FIG. 4. Mean remaining error as function of the population size. Nine subsets of different size (n = 2, 4, 10, 20, 30, 40, 50, 60, 70 and 80) were chosen by a random process from the complete sample of neurones (n = 89). One-hundred different subsets of each size were generated and mean remaining error between real and estimated eye position was computed for each subset. This error (mean ± SD shown by black circles and respective error bars) proved to be a function of the sample size and could be fit by an inverse square root function. This estimate predicts less than 700 neurones necessary to achieve a remaining error smaller than 10^{-1} degree.

subpopulation from the activity of the other. A net zero activity within one pair of subpopulations would indicate eye positions almost along a meridian. Increasing activity levels would indicate more eccentric eye positions with respect to this meridian. This computation could easily be conducted if the neurones in the follow-up structures would have antagonistic inputs, depending on whether the input neurones had stronger discharges for eye positions on one side of the meridian or the other.

Encoding of a visual stimulus in a head-centred frame of reference then could be accomplished, e.g. by simple vector summation. If **e** depicts the vector representing eye position and **r** the vector representing the retinal location of a visual stimulus, then **h** = **e** + **r** would give the location of a visual stimulus in head-centred coordinates.

The influence of population size on the remaining error

We were also interested in the question whether the mean remaining error (MRE) we observed was potentially influenced by the number of neurones considered in our computation. To answer this question, we selected by a random process differently sized subsets of neurones from the entire sample of neurones. For these subsets we computed the remaining error between estimated and given eye positions in the above described manner. Computation was replicated 100 times for each subset. This resulted in a quite robust estimate of the MRE as a function of sample size, as is shown in Figure 4. Non-linear regression proved the MRE to be inversely related to the square root of the sample size, indicating less than 700 neurones to be necessary as to obtain a remaining error less than 10^{-1} degree. This implies that with a large enough number of neurones the subpopulation encoding is, on average, capable of providing an unbiased, i.e. correct estimate, of the actual eye position.

The subpopulation encoding in another experimental paradigm

So far we have presented data only for one specific subgroup of cells tested in only one paradigm, i.e. neurones from areas LIP and 7A tested in the fixation paradigm. To validate the subpopulation encoding as a general scheme for an implicit representation of eye position we also applied it to data obtained from two different ensembles of neurones tested in the pursuit paradigm. The first ensemble comprises neurones from the same two areas as before (areas LIP and 7A), the second ensemble of neurones stems from the MST area. As shown previously (Bremmer *et al*., 1997a,b), the activity of the majority of neurones from both ensembles was also influenced by eye position in this task. In addition, as for the discharges observed in the fixation paradigm, the whole population of neurones revealed a symmetric response, i.e. no discharge bias for any eye position. As before, gradient directions of the approximated regression planes were uniformly distributed for both neurone ensembles. Application of the subpopulation encoding scheme led to essentially the same results as before, as shown in Figure 5. The upper two panels (A, B) represent the result for splitting up the population of MST neurones according to the sign of the horizontal (A) or vertical (B) slope of the approximated regression planes. Analogue results are shown for areas LIP and 7A in the bottom panels (C, D). The MRE proved to be 3.49° for data from the MST area and was as small as 0.79° for data from areas LIP and 7A.

Discussion

A number of theoretical studies suggested that the functional properties of neurones affected by eye position might be used for accomplishing a coordinate transformation of the incoming sensory signals and the generation of a non-retinocentric representation of visual information. The most influential work from (Zipser & Andersen (1988) could show that, by combining information about the location of a stimulus on the retina with information about the position of the eyes in the orbit, it was possible to train a neural network on generating an output in head centred coordinates. Modelling was performed by means of a back-propagation network. The input layer of this network received (i) a visual input organized in a retinocentric frame of reference and (ii) an extraretinal input, signalling eye position with respect to the horizontal and vertical meridian. The neurones in the output layer generated a head-centred representation of the visual environment while the units in the intermediate hidden layer revealed functional properties resembling the discharge patterns described for ‘real neurones’ in area 7A. From this finding it was suggested that area 7A might be capable of generating a non-retinocentric space representation.

More recent studies were mainly based on the model by Zipser and Andersen. The major goal of the study of Mazzoni *et al*. (1991) was to be biologically more plausible than the original back-propagation approach. Goodman & Andersen (1989, 1990) evaluated in more detail the characteristics of a network generating such a head-centred representation of visual information. Finally, Pouget *et al*. (1993) provided a computational explanation for *why* gain fields can be used for sensory motor transformations. None the less, to our knowledge, even these more recent studies did not use real experimental data to be put in the respective algorithms in order to test for an ongoing coordinate transformation.

From our point of view it therefore seemed to be necessary, given that the neuronal discharge was capable of encoding eye position, to develop a concept which is based on the data collected in experimental sessions and which uses these data to generate the hypothesized coordinate transformation. As a data base we used discharges from posterior parietal neurones observed in a fixation paradigm. Utilization of the OLE unveiled the potential of the observed discharges to encode actual eye position.

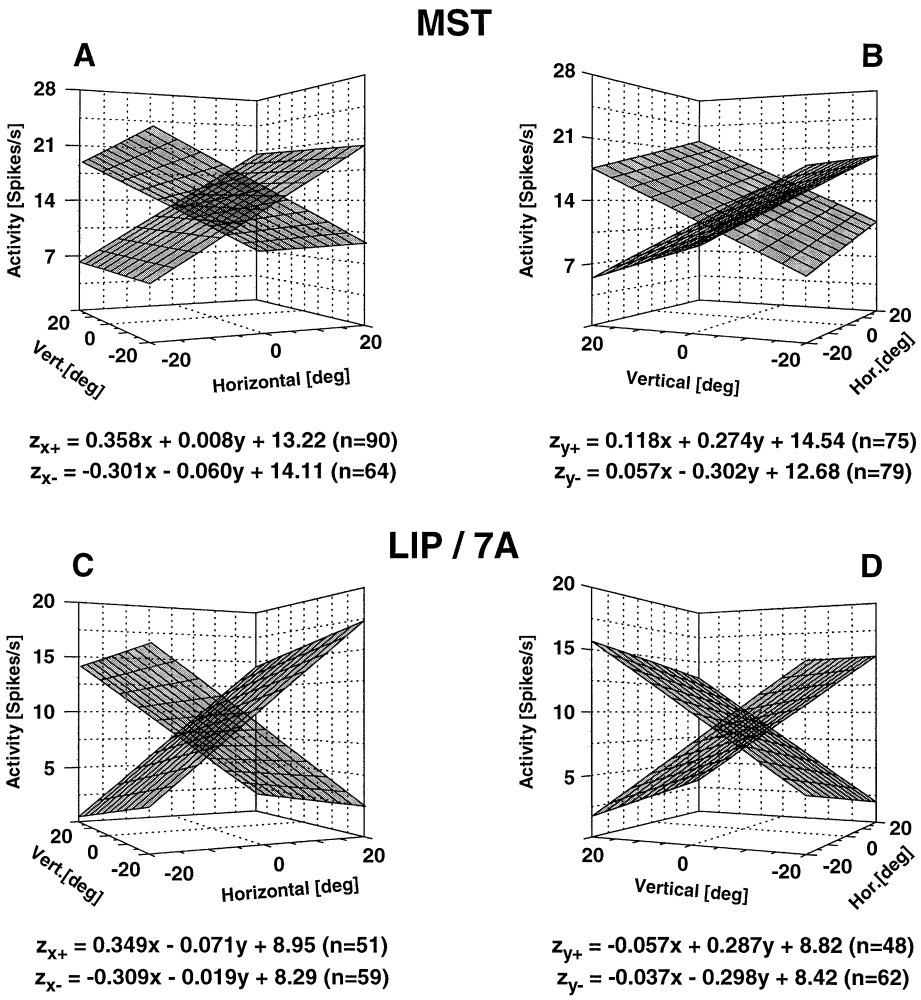

FIG. 5. The subpopulation encoding for pursuit related activity. Data are shown for recordings from areas MST (A, B; medial superior temporal) and LIP (lateral intraparietal) and 7A areas (C, D). The two planes in each left panel (A, C) represent the relative activity (see Materials and methods for definition) of the subpopulations whose discharge was stronger or less strong with respect to the vertical-zero-meridian (V-0-M). Analogue data, yet with respect to the horizontal-zero-meridian (H-0-M), are shown in the two right panels (B, D). Equations for the two respective average discharge planes and the number of neurones within in each subpopulation are given below each panel.

In considering the entire population of neurones as being built up by subpopulations, we succeeded in the generation of two pairs of ensembles of neurones whose difference in activity could be encoded via a push–pull mechanism the distance between actual eye position and the H-0-M and V-0-M. Yet, such a push–pull mechanism would require specific projections from eye-position-dependent neurones to their follow-up structures. However, this seems to be reasonable to assume because such specific projections of subpopulations of neurones recently have been shown to exist, e.g. for the cortical contribution to the optokinetic system (Ilg & Hoffmann, 1993). The division of the entire population of neurones into subgroups firing strongly or less strongly for eye positions above or below the H-0-M or left or right from the V-0-M seems to be arbitrary. It is in fact true that this specific choice of the two meridians as 'dividing lines' for splitting up the population into subgroups is not the only possible one. As can be estimated from Figure 3 all divisions of the entire ensemble of neurones using axes almost perpendicular to each other (like the H-0-M and the V-0-M) would generate subpopulations with an encoding relative to these axes.

However, when reflecting on the central processing of sensory information let us consider specifically the H-0-M and the V-0-M as dedicated axes, as both are 'represented' in biological systems. First, early visual signal processing strongly separates information coming from the contra and ipsilateral visual hemifield, i.e. with respect to the V-0-M. Secondly, the otolith system of the vestibular organ is dedicated for signalling not only linear acceleration but also tilt of the head, i.e. deviation with respect to the H-0-M. Thus, inherent signal processing properties in biological systems make both meridians potential candidates for selecting them as reference axes for the classification of neurones.

Application of the classical population code

As shown at the beginning, the response of a single neurone can be written as $z = \mathbf{ge} + c = ge\cos\psi + c$. This equation describes neuronal activity z for an eye position defined by a vector **e** comprising an angle ψ between itself and the direction of the gradient **g** of the neurone's eye position affected discharge plane. This equation matches the equation given by Georgopoulos *et al*. (1986) for the directional tuning of neurones in primate primary motor cortex investigated in an isoamplitude reaching task. As for the neurones from motor cortex, the parietal cell's activity is broad and cosine tuned with respect to

the preferred (gradient) direction. Furthermore, as all preferred directions are equally represented (as shown in Fig. 3), this suggests the possibility of application of a weighted vector summation algorithm to our data. We did test the performance of this population code on the LIP/7A neurones tested in the fixation paradigm and this resulted in a relatively small mean directional error of 7.9 degrees. However, only the direction of eye position is represented by this type of encoding. Different amplitudes, as required for a non-retinocentric encoding of spatial locations, cannot result from this type of population code.

Different concepts of space representation in monkey cortex

The hypothesis of a distributed network of neurones generating an implicit non-retinocentric representation of the visual environment is not the only theory concerning spatial information processing in primate cortex. At least two different concepts are suggested. The first is the concept introduced by Duhamel *et al*. (1992) who proposed an oculocentric space representation within monkey cortical area LIP. The authors could show the shifting of visual receptive fields of single neurones prior to a saccade and proposed this shifting as an argument for the updating of the representation of visual space by intended eye movements. With this concept a coordinate transformation of the incoming sensory signals no longer seems to be necessary. The controversy about the two different encoding schemes yet has not been resolved. However, from our point of view the one hypothesis (non-retinocentric encoding by means of a coordinate transformation) does not rule out the other (oculocentric encoding by means of a perisaccadic updating mechanism). One could imagine both mechanisms working in parallel. The updating mechanism, e.g. could be used for generating visual stability across saccadic eye movements. As was shown in all experimental studies on the influence of the position of the eyes in the orbit, these effects proved to be tonically active, whereas the shifting effect per definition occurs phasically. It thus might be two processes acting independently of each other in order to guarantee visual stability and space constancy during the continuously ongoing alternating scheme of constant fixations and redirections of gaze.

The second alternative concerns the finding of neurones whose visual receptive fields remain spatially constant regardless of eye position, i.e. which encode visual spatial information in a non-retinocentric frame of reference. Neurones of this type have been described for posterior parietal cortex areas V6 (Galletti *et al*., 1993) and VIP (Bremmer *et al*., 1996). The question arises whether the finding of such an explicit non-retinocentric encoding at the single cell level rules out the functional significance of retinocentric neurones influenced by eye position, which could perform such kind of encoding implicitly. The above-mentioned studies on areas V6 and VIP also described neurones whose discharge was influenced by eye position. It thus might be that specific projections from eye-position-dependent neurones in hierarchically lower dorsal stream areas or even functional circuits within areas V6 or VIP lead to the responses of the non-retinocentric neurones, as shown theoretically by Pouget & Sejnowski (1997). Thus, the finding of neurones with spatial instead of retinal visual receptive fields does not contradict the existence of neurones with an influence of eye position on their discharge.

The eye position effect as common encoding scheme

Our results apply to neuronal responses previously recorded from all areas (MT, MST, LIP and 7A) in all behavioural paradigms. This is because the following holds as a general result: (i) the directions of the gradients of the regression planes are uniformly distributed; (ii) neuronal discharges are unbiased at the population level, i.e. for an ensemble of cells there exists no specific eye position eliciting a stronger or weaker average activity compared with others. In this respect, our results are in good agreement with what Andersen *et al*. (1990) reported for the eye position effect on visual, memory, and saccade-related activities for neurones in areas LIP and 7A. It furthermore seems to be very similar to what Galletti and colleagues described for area V6 (Galletti *et al.*, 1991, 1995). Results from area V3A appear a little different, because the very same authors found a preponderance of cells with highest activity for fixations in the hemifield contralateral to the recording site (Galletti & Battaglini, 1989).

All areas mentioned so far belong to the so-called dorsal stream of the macaque visual cortical system. However, the occurrence of an eye position effect on neuronal discharges is not restricted to these dorsal stream areas. Preliminary data suggest that an eye position effect can also be found in ventral stream area V4 (Bremmer & Hoffmann, 1995). Finally, even activity of neurones in the supplementary eye field (Schlag *et al.*, 1992) and the premotor cortex (Boussaoud *et al.*, 1993; Boussaoud, 1995) are influenced by eye position. We thus consider the modulatory influence of eye position on neuronal discharges to be a common phenomenon throughout the monkey cortical system subserving probably an implicit representation of spatial information in a non-retinocentric frame of reference.

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Abbreviations

H-0-M	horizontal zero meridian
LIP	lateral intraparietal area
MRE	mean remaining error
MT	middle temporal area
MST	medial superior temporal area
OLE	optimal linear estimator
SPE	subpopulation encoding of eye position
V-0-M	vertical zero meridian
VIP	ventral intraparietal area

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