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Population coding of arm-movement-related neurons in and below the superior colliculus of *Macaca mulatta*

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Abstract. It has been shown for the motor cortex of primates, that an arm trajectory is coded as a population vector formed by many neurons with activities correlated with arm movements. Recently, neurons in the primate superior colliculus that also display activities related to arm movements have been described. In the present paper we show that a subpopulation of this type of neuron is able to code for limb movement by the population vector. However, the cosine function cannot describe these neurons adequately. Rather the Fisher distribution yields a much better description of arm-movement-related cells in the superior colliculus.

1 Introduction

In the literature many models have been described for the control of voluntary movements. The common ideas of these different models can be grouped into two classes of systems: the equilibrium-point hypothesis (EPH) and the vector-coding scheme (VCS).

The first class of system describes the regulation of voluntary arm movements at the level of the spinal cord (Merton 1953; Feldman 1966, 1986; Bizzi et al. 1989; Latash 1992, 1994a,b; McIntyre and Bizzi 1993; Dornay and Sanger 1993). Models of the EPH type are normally described as feedback systems, in which the physiological parameters of neurons and muscles are encoded in the matrix of inertia of the feedback system.

The second class of system describes the steering of voluntary movements – of the eyes at the midbrain level and of the arm at the cortical level (Schiller and Stryker 1972; Wurtz and Goldberg 1972; Sparks et al. 1976; Georgopoulos et al. 1983, 1988; Lee et al. 1988). These models infer that neurons encode movement directions and that the neural discharge differs for movement directed towards different directions. The discharge patterns of neurons for movements toward different directions are described by using a vector of a parameter space which encodes the difference of the discharge by a basic physiological function. The term 'basic physiological function' covers any mathematical description for the variation of a behaviour or the discharge rate of a neuron by a stimulus. In this sense a model consists of a set of rules which describe the use of these basic physiological functions. These rules should be an attribute of the investigated brain area. On the condition that the dispersion of preferred directions is uniform, every monotonic function can, in principle, be a possible basic physiological function (Mussa-Ivaldi 1988; Sanger 1994). For a VCS, it has been shown that the quality of a population reponse depends upon the dimensions of the parameter space and the signal-to-noise ratio of the individual neurons (Snippe and Koenderink 1992a,b). When determining the minimization of the sum of squares of errors as a measure of quality, the best tuning function in a statistical sense is one of the gaussian type (Snippe and Koenderink 1992a,b).

A formulation of a VCS has been described by Georgopoulos and co-workers for the motor cortex (Georgopoulos et al. 1982, 1983, 1988; Caminiti et al. 1990, 1991; Schwartz 1992) and the pre-motor cortex (Kalaska et al. 1983; Caminiti et al. 1991). This formulation has become known as the population-coding hypothesis and is derived from the use of a cosine as the basic physiological function. In the superior colliculus (SC) a VCS has been proposed for visually evoked saccades (Schiller and Stryker 1972; Wurtz and Goldberg 1972; Sparks et al. 1976; Gisbergen et al. 1987; Lee et al. 1988; Opstal and Gisbergen 1990; Glimcher and Sparks 1992) as well as for saccades towards remembered targets (White et al. 1994; Stanford and Sparks 1994). The formal description for the generation of saccades by the oculomotor neurons in the SC starts with a gaussian-type function as a basic physiological function.

There is now convincing evidence that next to saccade-related cells, in and below the SC, there are also neurons which modulate their discharge rate in relation to arm movements (Werner 1993). The aim of this paper is to demonstrate a VCS which would also code for arm trajectories of these neurons. For this purpose we have tested a VCS using either a cosine or a gaussian-type function as the basic physiological function. We will show that the use of a vector description of a gaussian-type function (Fisher 1953)

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enables us to construct a VCS for the arm-movement-related neurons in the SC.

2 Materials and methods

2.1 Animals and task

Two rhesus monkeys (*Macaca mulatta*) were trained in several eye and arm movement tasks. The animals were seated in a comfortable primate chair with their head fixed, facing a vertical Plexiglas plate. The distance between the plate and the monkey's eyes was 30 cm for monkey P and 20 cm for monkey E. The non-working arm was loosely restrained by a plastic cylinder around the upper and lower arm. During the arm movement task the monkeys had to perform an arm movement so as to touch a target located on the screen with their fingers. Screen targets included the central fixation light at eye level and up to eight targets positioned on a circle with an eccentricity of 15° centred on the fixation point. Each trial began when the monkeys touched with their right hand a metal bar (touchbar) positioned close to their hip. This resulted in the onset of a central red fixation light projected onto the screen. After a variable period of time, a peripheral red target light was turned on. The monkeys had to maintain fixation of the central light until it was extinguished, and then were required to make a saccade to the peripheral target. After the saccade, the monkeys had to maintain eye position within a window of 5° to 8° radius surrounding the target position. Then a tone (200 ms duration), which served as a go signal, allowed them to release the touch bar and to start a pointing movement in order to touch the target. This temporal dissociation of different events made it possible to distinguish visual, saccadic and skeletomotor neuronal responses. The duration of the fixation light, that of the target, their overlap in time, the timing of the go signal and the position of the target occurred in a pseudorandomized order. The total duration of a single trial was 3–6 s. The implantation of search coils and recording cylinders as well as data acquisition have been described elsewhere (Werner 1993).

2.2 Data analysis

Standard statistical techniques (Draper and Smith 1981; Snedecor and Cochran 1989) were used to analyse the data. Three time epochs were distinguished for every trial. A period of 500 ms before the appearance of the go signal defined the *control time* (CT). The *movement time* (MT) began with the release of the hand from the touchbar and ended with the contact of the target. The *total experimental time* (TET) was defined as the time from the go signal to the contact of the target. The mean discharge frequency and the variance between the trials (inter-trial variance) were calculated for each of these epochs. The activity of the arm-movement-related neurons was analysed further by a multiple linear weighted regression to determine whether the discharge rate varied in an orderly fashion with the arm movement in three-dimensional space.

The cosine model of Georgopoulos (Georgopoulos et al. 1983; Schwartz et al. 1988) was tested as well as a gaussian-type model based on the Fisher distribution (Fisher 1953). The cosine model is defined as (Schwartz et al. 1988):

$$d(\mathbf{M}) = b_i + k_i * \cos(\Theta_{\mathbf{C}_i\mathbf{M}}) \quad (1)$$

where $\Theta_{\mathbf{C}_i\mathbf{M}}$ is the angle formed by the neurons' preferred direction $\mathbf{C}_i$ and the direction of movement $\mathbf{M}$. The vectors $\mathbf{C}_i$ and $\mathbf{M}$ are of unit length. b_i defines an offset and k_i the amplitude. The parameters b_i and k_i as well as the neurons' preferred direction $\mathbf{C}_i$ in (1) were calculated by standard techniques of weighted regressions (Draper and Smith 1981). The weights were determined by the inter-trial variance of the mean activity. A regression coefficient of $r^2 \geq 0.7$ was used as a criterion of a satisfactory fit.

The gaussian-type model is defined by the Fisher distribution (Fisher 1953):

$$d(\mathbf{M}) = c(\kappa_i) * \exp(\kappa_i * \cos(\Theta_{\mathbf{C}_i\mathbf{M}})) \quad (2)$$

where κ_i defines a tuning strength for each neuron and $c(\kappa_i)$ defines the normalizing factor. The Fisher distribution forms a two-dimensional gaussian function in a three-dimensional space. It decribes the probability of an event (an action potential in our case) occuring within a defined cone in space. The value κ_i is the reciprocal equivalent to the variance of a gaussian function (Fisher 1953).

Equation (2) can be logarithmically transformed (Gould 1969) to

$$\ln(d(\mathbf{M})) = \ln(c(\kappa_i)) + \kappa_i * \cos(\Theta_{\mathbf{C}_i\mathbf{M}}) \quad (3)$$

This equation can be solved by the same regression technique as the cosine model. With respect to the logarithm, the weights are determined by the inter-trial variance normalized to the mean discharge frequency.

The extrapolation of a specified arm movement $\mathbf{M}$ with the cosine function was done as follows: First, the spike rate has to be estimated by the cosine function. Then the preferred direction $\mathbf{C}_i$ has to be weighted with this value. The population vector is then calculated as the resultant vector of all weighted preferred directions. In contrast to the cosine function, the Fisher distribution predicts spike probabilities. To calculate the population vector, the spike rate has to be estimated with respect to the total spike rate measured for each neuron.

The prediction of the population vector from a population of arm-movement-related neurons was compared with the vectors for movements. The spherical correlation coefficient (Fisher and Lee 1986) was used as a measurement for the quality of the prediction.

The coordinate system was defined for all calculations as the x-axis to the right of the monkey, the y-axis upward and the z-axis towards the monkey.

2.3 Neuronal database

A total of 389 arm-movement-related neurons recorded in the SC or ventral to the SC were considered in this study. For inclusion in the population scheme, the cells had to satisfy the following criteria: (1) nine target positions were tested, (2) at least 15 trials existed for each position, (3) the direction of movement caused a significant effect on the mean discharge frequency in MT/TET versus CT (Wilcoxon rank sum test, 1% level). In total, 34 neurons fulfilled all three requirements. One of these neurons is shown in Fig. 1.

3 Results

When comparing different systems, the rules governing the decision to accept or reject a system are the heart of the problem. The rules depend on the model to be introduced, but the proof of the system depends on the physiological data base. For our purposes we have divided the comparison of the two possible basic physiological functions into two steps. The first is the description of the physiological data with the two basic physiological functions (see also rules a–c in Georgopoulos et al. 1983). The second is the prediction of movement direction (see rule d in Georgopoulos et al. 1983). Two different statistical tests were used. For the first step, a regression coefficient of $r^2 \geq 0.7$ in the multiple linear regression was chosen for the best fit (Georgopoulos et al. 1983; Schwartz et al. 1988). For the second step the spherical correlation coefficient was used as a measurement of the quality of prediction (Fisher and Lee 1986). For our data this means that we have first selected neurons which could be described by one of the basic physiological functions, and then used the mathematical description of the neurons to predict several movement directions and measured the quality of the prediction.

Figure 1 shows the mean activity of a directional arm-movement-related neuron in the SC with movements in nine directions. The arrangement of the plots is related to the position of the targets on the screen. The neuron showed negligible activity before the go signal, an increasing discharge shortly before the release of the touchbar (t = 0)

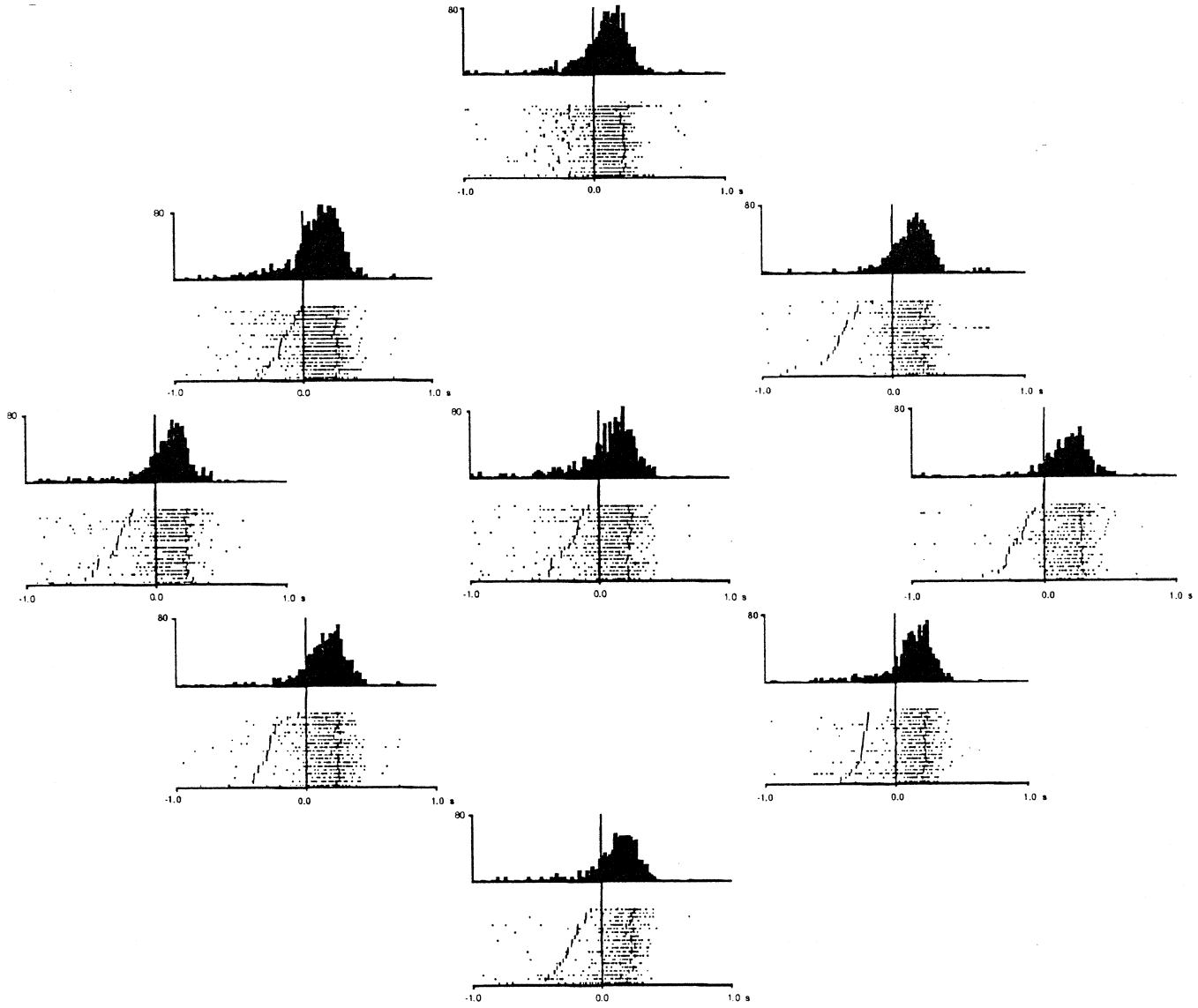

Fig. 1. Peri-stimulus time histograms (PSTHs) and raster displays of the discharge rate of one neuron with movements towards nine targets. The arrangement of the plots is related to the position of the targets on the screen. PSTHs and raster displays are aligned to the release of the hand from the touchbar. The time ranges from 1 s before movement onset (t = 0) until 1 s after. The *first bar* in each trial of the raster displays marks the go signal; the *second bar* marks the contact with the target. The scale of the ordinate in the PSTHs is 80 impulses/s

and strong activity in the movement time until target contact. Neuronal activity decreased again after this. It can be clearly seen that the activity differed for movements toward different targets. The mean activity was highest for movements to the upper left position [76 impulses/s (imp/s)] and decreased gradually for other movement directions with a minimum at the right target position (37 imp/s, see MT in Table 1). The behaviour of this neuron resulted in an estimation of the preferred direction at the point θ = 109°, ϕ = 105° with r^2 = 0.86 for the cosine function. The estimated preferred direction for the Fisher distribution was θ = 110°, ϕ = 105° with r^2 = 0.84. The estimated preferred directions are quite similar, but the parameters of the regression equation showed a strong difference between the two models. Following (1) the parameters for the cosine function were k = 521 and b = −452. This would mean that outside a cone with an angle of 30° the equation predicted negative spike rates. In contrast, the Fisher distribution predicted positive spike rates for all directions. The tuning strength was estimated with κ = 9.5 with respect to the behaviour of the neuron.

The mean discharge rates and inter-trial variances were calculated for each direction of movement (n = 9). Then, the parameters for the proposed basic physiological functions were calculated for each neuron (n = 34). For MT, a total of 10 neurons could be described by the Fisher distribution and 11 cells by the cosine function. For TET, 15 neurons could be described by the Fisher distribution and 11 cells by the cosine function. The results (summarized in Table 2) show that in a statistical sense both basic physiological functions are able to describe the behaviour of the neurons.

In order to measure the quality of prediction for movement directions, we used the data from neurons which were described by each of the basic physiological functions. Due

Table 1. Mean activity (impulses/s) of the neuron in Fig. 1

Position	MT (mean±SD)	TET (mean±SD)	n
Right	36.7 ± 9.2	24.3 ± 10.1	20
Right-up	49.4 ± 12.5	22.7 ± 9.2	20
Up	67.4 ± 14.5	43.3 ± 14.3	19
Left-up	75.6 ± 11.2	54.8 ± 15.8	19
Left	55.0 ± 18.2	30.4 ± 13.3	20
Left-down	50.2 ± 9.1	27.7 ± 8.6	20
Down	45.7 ± 17.1	25.1 ± 7.6	20
Right-down	47.3 ± 11.8	26.6 ± 9.2	20
Center	57.5 ± 11.1	37.9 ± 12.3	20

MT, movement time; TET, total experimental time

Table 2. Number of fitted ($r^2 \geq 0.7$) arm-movement-related neurons (n = 34)

	MT		TET	
Monkey	Cosine	Fisher	Cosine	Fisher
E	5	6	4	7
P	6	4	7	8
Σ	11	10	11	15

MT, TET = time epochs; cosine, Fisher = supposed distributions

to the difference in size of the two monkeys, movement trajectories differed for the nine targets. Consequently, movement directions for the trajectories of monkey P and E were predicted separately.

The spherical correlation coefficient was used to compare the movement direction predicted by the model with the real trajectories in the experiment (Fisher and Lee 1986). Similar to the linear correlation coefficient, the spherical correlation coefficient allows a comparison of vector groups (here the real trajectories of the experiment versus the predicted trajectories of the model). This would mean that for a value $\rho = \pm 1$ the groups are equal. The sign marks the orientation of the groups with respect to each other. A value $\rho \approx 0$ means that the groups are independent from each other. A value $0 < |\rho| < 1$ gives the dependency of the groups on each other (Fisher and Lee 1986).

The model based on the cosine distribution resulted in a good prediction for one of four cases only (Table 3: $\rho_{(P,TET)} = 0.923$). In two cases the prediction was poor (Table 3: $\rho_{(P,MT)} = 0.460$, $\rho_{(E,TET)} = 0.223$) and in the fourth case a total loss of the prediction was found (Table 3: $\rho_{(E,MT)} = 0.000$). The model based on the Fisher distribution resulted in a good prediction of the movement directions for all four cases (Table 3: $0.839 \leq \rho \leq 0.883$). This means that the Fisher distribution is able to predict every movement direction tested in our experiment, independently of the animal and the selected time window.

Table 3. Spherical correlation coefficient for different movement directions

	Movement directions	
	Directions of P	Directions of E
MT		
Cosine (n = 11)	0.460	0.000
Fisher (n = 10)	0.883	0.874
TET		
Cosine (n = 11)	0.923	0.223
Fisher (n = 15)	0.839	0.877

Table 4. Spherical correlation coefficient of the directions used in the experiment by Georgopoulos

MT		TET	
Cosine (n = 11)	Fisher (n = 10)	Cosine (n = 11)	Fisher (n = 15)
0.048	0.370	0.001	0.729

The space sampled by the nine trajectories was relatively small. The population coding hypothesis is a general coding system for trajectories that allows the population vectors for different trajectories, including trajectories that have not been explicitly tested, to be calculated (Georgopoulos et al. 1988, appendix 3). In order to enlarge our field of analysis, we calculated the trajectories used in the experiments by Georgopoulos et al. (1988) that were not tested in our experiment. We have selected those trajectories because they describe a uniform distribution in three-dimensional space. To those trajectories we applied our data on neurons which were described by the two basic physiological functions: cosine and Fisher distribution. The results show that the cosine function did not result in a reasonable prediction for those trajectories (Table 4: $\rho_{(MT)} = 0.048$, $\rho_{(TET)} = 0.001$), whereas the Fisher distribution yielded a better prediction for MT (Table 4: $\rho_{(MT)} = 0.370$) and a good prediction for TET (Table 4: $\rho_{(TET)} = 0.729$).

In order to visualize the different statistical results of Table 4, the dispersion of the neurons' preferred directions and the population vectors for TET are shown for the cosine and the Fisher distribution in Fig. 2. The coordinate system was defined as follows: the monkey's right as the x-axis, the upward direction as the y-axis, and direction towards the animal as the z-axis. The positive directions of the axes are marked with capital letters. The figure shows a view along the z-axis into the x/y-plane. The trajectories of the experiments done by Georgopoulos et al. (1988) are marked with the numbers 1–8 and are drawn with small arrowheads. The different shadows of the arrowheads depend on different projections in the drawing plane. The trajectories 1, 4, 5, and 8 mark directions behind the drawing plane; trajectories 2, 3, 6 and 7 mark directions in front of the drawing plane. The calculated population vectors are marked with $1'$–$8'$ respectively and are drawn with large arrowheads. If the estimation of the population vectors were perfect ($\rho = \pm 1$), the population vectors would be drawn in the same positions as the trajectories of the experiment. Errors in the estimation of the population vectors lead to the drawing of different vectors (i.e. trajectory 1 and population vector $1'$ in Fig. 2a). The amount of the prediction error is estimated and expressed by the spherical correlation coefficient (shown in Table 4 and illustrated in Fig. 2). The population vectors calculated by the cosine model (Fig. 2a) are all found in the same region in front of the drawing plane. This fact clearly indicated the inability of the cosine model to predict population vectors from our data. In contrast, the model based on the Fisher distribution (Fig. 2b) estimated the directions accurately. Of course the Fisher distribution was not a perfect prediction of all trajectories but it was more accurate than the cosine distribution.

To analyse the reason why the two models differed in the prediction of trajectories, it was necessary to look at

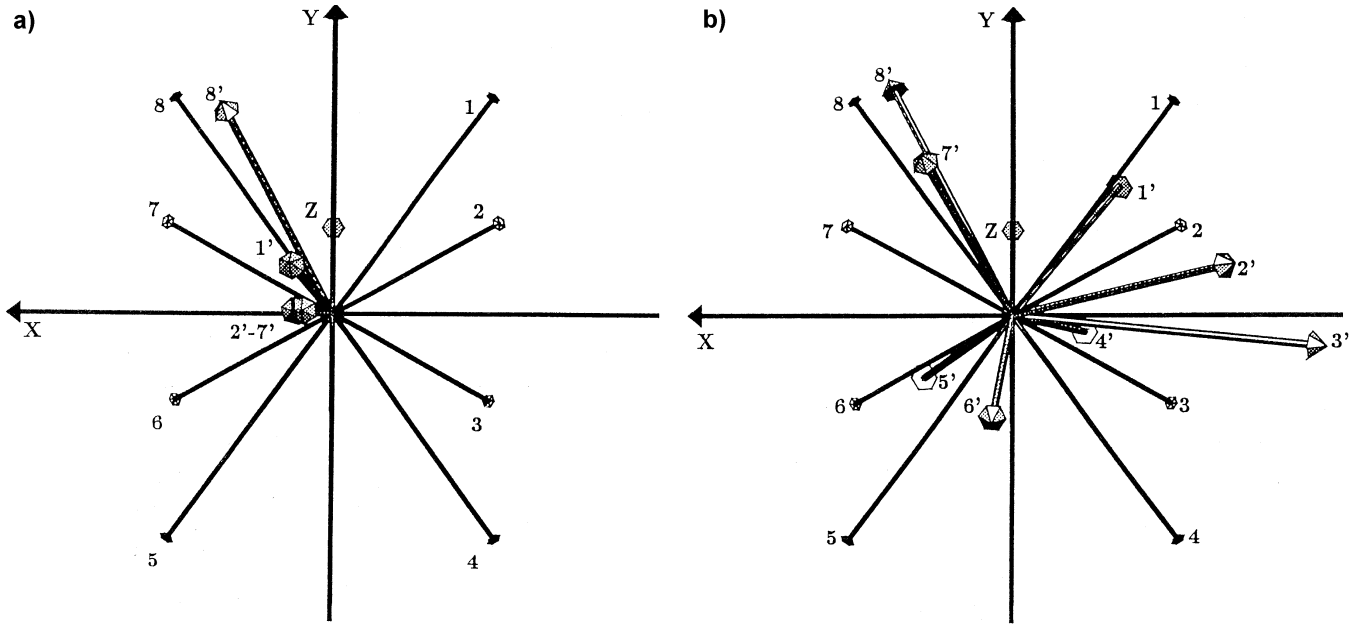

Fig. 2. Population vectors of the neurons estimated by the supposed distribution (**a** cosine function, **b** Fisher distribution), viewed from in front of the animal. The coordinate system was defined as follows: the monkey's right as the x-axis, the upward direction as the y-axis, and direction towards the animal as the z-axis. The positive directions of the axes are marked with *capital letters*. The figure shows a view along the z-axis into the x/y-plane. The trajectories of the experiments done by Georgopoulos et al. (1988) are marked with the *numbers 1–8* and are drawn with *small arrowheads*. The different *shadows* of the arrowheads depend on different projections in the drawing plane. The calculated population vectors are marked with *1′–8′* respectively and are drawn with *large arrowheads*. From Kutz (1995); reproduced with permission of the publisher

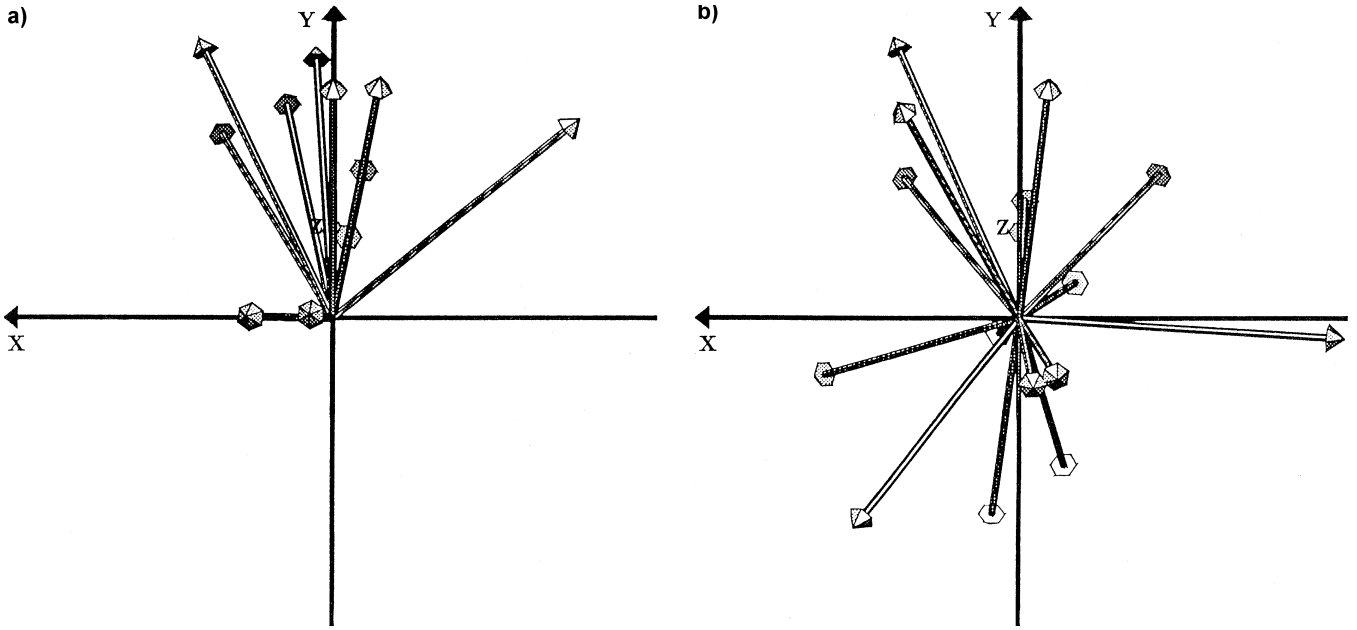

Fig. 3a,b. Preferred direction of the neurons estimated by the supposed distribution, viewed from in front of the animal. **a** cosine function (n = 11), **b** Fisher distribution (n = 15). For details see legend of Fig. 2. From Kutz (1995); reproduced with permission of the publisher

the estimated preferred directions of the neurons (Fig. 3). In Fig. 3a the preferred directions estimated by the cosine model are shown: there is clearly a bias towards the upper region. Thus, the cosine function is able to estimate the behaviour of a neuron adequately only if the estimated cell is broadly tuned, while it fails to do so when the cell is sharply tuned. In contrast, the Fisher distribution allowed a much better estimation of the preferred directions in both cases (Fig. 3b). This is due to the fact that the tuning strength κ of the Fisher distribution fits well with the activity of broadly and sharply tuned neurons.

4 Discussion

The present results show that a VCS can be applied to the arm-movement-related neurons in the SC. We have used two functions as basic physiological functions of a VCS: the co-

sine, which was proposed by Georgopoulos et al. (1983), and the Fisher distribution (Fisher 1953) as a gaussian-type function. However, it should be noted that the best basic physiological function is of gaussian type. The main problem with the cosine function is the possibility of yielding negative spike rates, that of course do not have a counterpart in the physiological structures. In contrast to the data of Georgopoulos (Georgopoulos et al. 1986, note 8), in our experiments the cosine function would have predicted negative values for a large part of the possible movement trajectories. On the other hand, the Fisher distribution predicted positive spike rates in all cases. Note that although all neurons tested exhibit a direction-dependent modulation of the discharge rate, only some of them can be described by one of the functions of the VCS (cosine or Fisher) within the small space covered by the nine trajectories tested. The number of neurons (Table 2), as well as the quality of prediction of the trajectories in our experiment (Table 3), allows a decision for the Fisher distribution.

To prove this, a theoretical experiment was designed according to the idea that the population coding hypothesis is a general coding system for trajectories (Georgopoulos et al. 1988, appendix 3). The prediction of a population of arm-movement-related neurons in the SC for TET (ρ = 0.729) is better than the value published by Georgopoulos et al. (1988) for a population of motor cortex neurons. Those cortical neurons have been described by the cosine function (Georgopoulos et al. 1988, ρ = 0.466, table 2, eq. 7). It is important to note that the number of neurons in the population of Georgopoulos (n = 475) is more than 30 times greater than in our population (n = 15). These results lead to the conclusion that the arm-movement-related neurons in the SC could be better described by a gaussian-type function such as the Fisher distribution than by the cosine function.

The adaption of a gaussian-type function as a tuning function leads to the transformation of the population coding hypothesis of Georgopoulos et al. (1983) into classical description theories for physiological functions. In fact it has been shown that gaussian-type functions (Seelen 1968; Snippe and Koenderink 1992a,b) and their derivatives (Koenderink and Doorn 1990a,b, 1992) represent the best possible models for describing adequately many sensory and motor systems. The description of receptive fields of cells in many visual areas represents one example of the use of gaussian-type functions (Enroth-Cugell and Robson 1966; Enroth-Cugell et al. 1983; Dawis et al. 1984). Bremmer et al. (1994) and Lappe et al. (1994) described the visual response of neurons in area MST to rotating or contracting stimuli. It was found that derivatives of a gaussian-type function (a sigmoidal function) yielded a good explanation of the neuronal discharge. The description of saccade generation in the SC is an example of the use of a gaussian-type function on the motor side (Ottes et al. 1986; Gisbergen et al. 1987). The advantage of a gaussian-type function is that there is no need to extract the first Fourier component from the sensory signal. The research on saccade generation in the SC shows the advantage of describing sensory and motor systems in the same way. A gaussian-type function as a basic physiological function for the steering of the skeletomotor system leads to a consistent description of the sensory and motor system.

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