

SINGLE neuron activity was recorded in monkey motor cortex during the execution of pointing movements in six directions. The amount of prior information was manipulated by varying the range of precued directions. A distribution of neural population activation was constructed in the space of movement directions. This population representation of movement direction was preshaped by the precue. Peak location and width reflected the precued range of movement directions. From this preshaped form, the population representation evolved continuously in time and gradually in parameter space toward a more sharply peaked distribution centered on the parameter value specified by the response signal. A theoretical model of motor programming generated a similar temporal evolution of an activation field representing movement direction.

**Key words:** Behaving monkey; Dynamic models; Motor cortex; Motor programming; Neuronal population; Single-neuron recording

## Prior information preshapes the population representation of movement direction in motor cortex

Annette Bastian,<sup>1,CA</sup> Alexa Riehle,<sup>1</sup>  
Wolfram Erlhagen<sup>1,2</sup> and  
Gregor Schöner<sup>1</sup>

<sup>1</sup>Center for Research in Cognitive Neuroscience, CNRS, 31, chemin Joseph Aiguier, 13402 Marseille Cedex 20, France;

<sup>2</sup>Institut für Neuroinformatik, Ruhr-Universität Bochum, Germany

<sup>CA</sup>Corresponding Author

### Introduction

Movement preparation takes place, in human subjects as well as in primates, even if only partial information about the upcoming movement is available.<sup>1,2</sup> The number and the probability of choices affects reaction time.<sup>3</sup> This suggests that the task setting, i.e. the ensemble of potential movement targets in a particular experimental protocol, affects movement preparation. It is possible that such prior information about upcoming movements is used to partially prepare movements. It has been demonstrated, for example, that subjects prepare a 'default' response that depends on the range of possible responses.<sup>4,5</sup> By training subjects to initiate a movement at an externally paced point in time while providing specific information about the upcoming movements at variable stimulus–response intervals, Ghez and collaborators<sup>6</sup> have shown that a structured distribution of movement parameter values is defined early in the stimulus–response interval. This distribution evolves continuously in time and gradually in parameter value to a distribution centered on the specified movement parameter value.

Erlhagen and Schöner have modeled this continuous and graded evolution of the representation of movement parameters (in preparation). Single movement parameters (such as direction) are represented

by a distribution of activity in the corresponding parameter space. Each potential value of the movement parameter is represented by an activation variable. Localized distributions of activation thus specify the parameter value on which they are centered, while broad distributed patterns of activation represent incomplete information about possible parameter values. In the model, prior information about upcoming movements is represented by a preshaping input to the field dynamics, preactivating the field in the relevant locations (Fig. 1). The response signal is modelled by a localized input centered on the specified parameter value, in response to which the field evolves continuously. Interactions in the field stabilize the final form.

Neurons in motor and premotor cortex vary their firing rate in response to prior information about upcoming movement parameters.<sup>7,8</sup> What remains unclear, however, is whether the change of neural activity in response to partial information about upcoming movements is specific to that information. How can we observe a prestructuring of the representation of movement parameters at the level of cortical neurons? Our answer to this question was based upon the following: (1) The observation by Georgopoulos and colleagues<sup>9</sup> of broad tuning of motor cortical neurons to movement direction which is relatively uniform across neurons is used to define

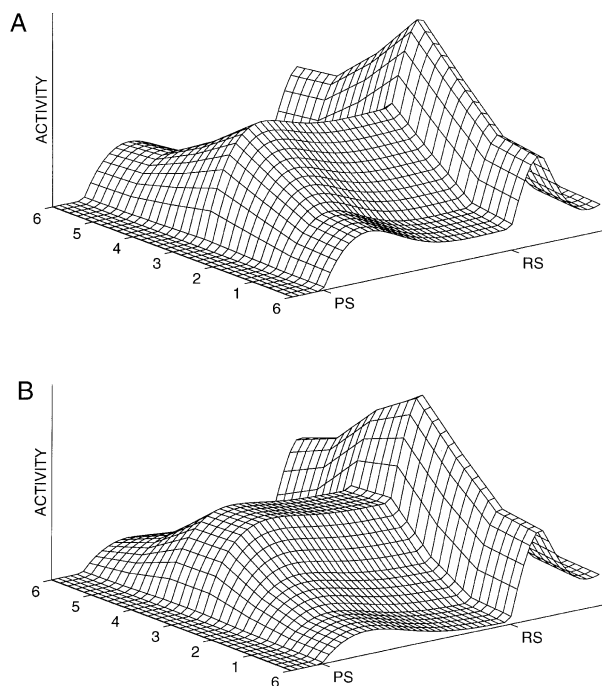


FIG. 1. The dynamic field model of movement preparation represents the movement parameter 'direction' ( $\phi$ ), by an activation field,  $u(\phi, t)$ . Peaks of activation represent the parameter value at which they are localized. The field evolves continuously in time as governed by a dynamic system:

$$\begin{aligned} \tau_u \dot{u}(\phi, t) &= -u(\phi, t) + \int w(\phi - \phi') f(u(\phi', t)) d\phi' \\ &\quad + v(t) + h(t) + S(\phi, t) \\ \tau_v \dot{v}(t) &= -v(t) + c_f f(u(\phi', t)) d\phi' \end{aligned}$$

Sensory information associated with the preparatory signal, PS, and the response signal, RS, is modelled as localized excitatory input,  $S(\phi, t)$  and global excitatory input,  $h(t)$ . Interaction within the field (local excitation, global inhibition,  $w(\phi - \phi')$ ) stabilizes a single localized peak of activation as the target state of the field. The activation induced by input stimulation is transiently suppressed again by an inhibitory process,  $v(t)$ . The figure shows the temporal evolution of the activation field in two cases. (A) When the preparatory signal specifies completely the movement direction (at target 3), the corresponding input preshapes the field at the specified location. The response signal drives this localized peak transiently to higher levels of activation. (B) When, by contrast, the preparatory signal specifies two neighboring targets (at targets 3 and 4) the field is more broadly preshaped and its maximum is centered on the average of the two precued movement directions. The response signal now leads not only to an increase of activation, but also to a shift of the peak location toward the specified target (target 3) and a sharpening of the distribution.

an estimation procedure through which a distribution of activation over the movement parameter 'direction' can be constructed. (2) The notion of preshaping of neural representations is employed to search for specific use of prior information. By extrapolating the estimation procedure for population representations into periods in which incomplete information about movement direction is available, the preshaping of these representations can be observed. (3) To detect experimentally such preshaping, the amount and metric range of prior information is varied by precueing either one, two or three adjacent movement targets.

## Materials and Methods

A monkey (*Macaca mulatta*) was trained to perform pointing movements. It was cared for in the manner described in the *Guiding Principles in the Care and Use of Animals of the American Physiological Society*. The animal sat in a primate chair in front of a vertical panel on which seven touch sensitive light emitting diodes (LED) were mounted, one in the center and six equidistantly on a circle around the center. A trial started when the center target was illuminated. The animal had to touch the center target and wait for the preparatory signal (PS), consisting of the illumination of one or several targets in green. After a preparatory period (PP) of 1 s, one of the green targets turned red, thus providing a response signal (RS), which instructed the animal to release the center button and to point at the specified target. Three different types of prior information were presented: (i) complete information in which a single target was illuminated; (ii) partial information with two adjacent targets illuminated; (iii) partial information with three adjacent targets illuminated. Each of the three types of prior information was presented in a separate block of about 120 trials. Within each block, all possible movement directions were presented randomly.

After training, the animal was prepared for surgery. A circular recording chamber was placed under halothane anesthesia (< 0.5% in air) over the dorsal premotor cortex contralaterally to the task performing arm. A T-bar was fixed on the skull in order to immobilize the animal's head during the experimental session. A multi-electrode microdrive (Reitboeck device, Uwe Thomas Recording, Marburg) was used to transdurally insert seven independently driven micro-electrodes (impedance 1–4 M $\Omega$  at 1 kHz) into the motor cortex. Action potentials of single neurons were recorded extracellularly and isolated using a window discriminator. Only neurons that changed significantly (one-factor analysis of variance) their activity as a function of movement direction during reaction time (time from the occurrence of the RS until the initiation of movement observed as the release of the center button), or during movement time (time from the initiation of movement until the hand touches the target) were selected for the further analysis at the population level. The activity of 40 of 56 neurons (71%) recorded in the condition of complete information, 46 of 57 neurons (81%) recorded in the condition of partial information with a precue of two targets, and 41 of 49 neurons (84%) recorded in the condition of partial information with a precue of three targets reached statistical significance.

The construction of a population representation of movement direction is technically similar to the

methods used by Georgopoulos and colleagues<sup>9</sup> to construct the population code, although the goal pursued with this construction is different. Inquiries into population code typically ask which movement parameters are represented by populations of neurons in motor cortex. Although movement direction is clearly coded for in motor cortex, neural firing may also depend on parameters such as movement extent, arm configuration, or shoulder joint angle.<sup>10-12</sup> We simply conclude from the tuning of single neurons to movement direction that motor cortical neurons contribute to the representation of that parameter, among the potentially many other representations that they might contribute to. To inquire about movement direction, we projected from this potentially high-dimensional space onto the axis representing movement direction,  $\phi$ . This can be done by constructing a population distribution of activation defined over the space of movement directions. The distribution was built from basis functions, which we chose as the tuning curves of each neuron. By weighting (multiplying) the tuning curve with the current firing rate, population representations were constructed for the various experimental conditions and at different points in time. Specifically, for each of the three types of prior information (complete, two-target, three-target), a population representation was constructed for each value of the preparatory and response signal, that is, for each possible direction. The combination of targets presented as preparatory and response signal is designated in the formula as 'configuration'.

The mathematical definition reads

$$u_{\text{configuration}}(\phi, t) = \sum_{\text{neurons } i} \text{tuning}_i(\phi) \cdot \text{firingrate}_{\text{configuration}}(i, t)$$

where the index  $i$  indicates the individual neurons in the population. The firing rate of neuron  $i$  in a particular configuration was obtained by averaging within a time slice beginning at time  $t$ . Thus, the population representation could be estimated as a function of time. A normalization factor was introduced to smooth the density at which the parameter 'movement direction' was sampled by the preferred directions of the cells. The tuning curves were obtained from neural firing rates averaged over the reaction time interval. Note that computing the population representation during the reaction time interval is thus somewhat tautological, but extrapolating this estimator into other periods is not.

Means were computed from the population representation by treating it as a probability distribution and using circular statistics.<sup>13</sup> The width of the population representation was obtained by using the concentration measure of circular statistics. Because the population representation is unnormalized, the

concentration was calculated after the areas under the population distributions at different configurations were all equaled by adding or subtracting appropriate constants.

Population representations of movement direction were computed on the basis of the recorded activity of 40 neurons for the condition of complete information and 22 neurons for each of the two conditions of partial information.

## Results

The temporal evolution of the population representation is shown for the condition of complete information (Fig. 2A) and for the condition of two target information (Fig. 2B). The following statements hold true for all movement directions: (1) Neuronal activation increased in response to the preparatory signal and in response to the response signal. After a first maximum of activity following

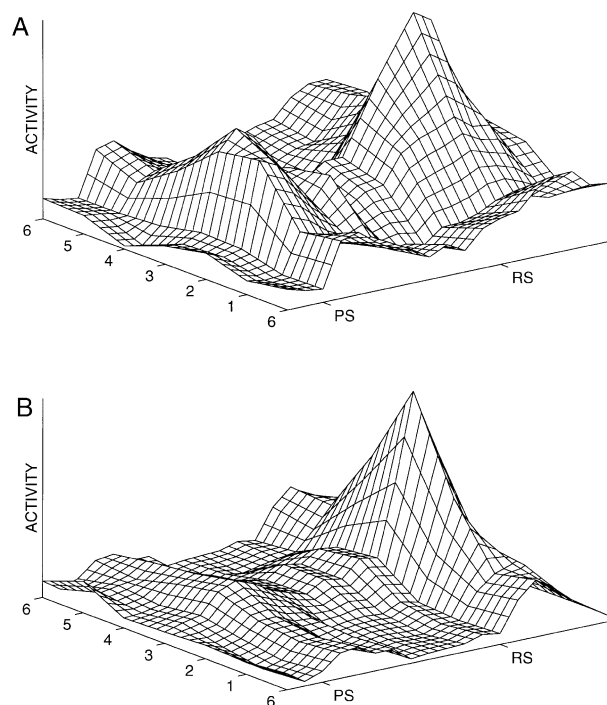


FIG. 2. The population representation of movement direction as constructed from neural responses of a population of motor cortical cells is shown when complete prior information (A, target 3 was precued at PS and specified at RS) and two target prior information (B, targets 3 and 4 were precued at PS and target 3 was specified at RS) is provided. The time slices for the computation of the population distribution are 100 ms. Note how the population distribution is preshaped in response to the preparatory signal. Location and width of activation reflect the range and contents of prior information. If complete information is provided (A) the activation peak is localized over the precued target during the preparatory period and the distribution increases in activation and contents subsequent to the RS. At two target prior information (B), the preshaped distribution is centered broadly on the precued range, whereas after presentation of the RS its peak shifts towards the specified value while sharpening.

the PS there was a slight decrease during the preparatory period, but activity remained at levels well above spontaneous discharge rate. (2) The neuronal activation after the occurrence of the preparatory signal was spatially structured. It peaked at the precued parameter value (complete information) or within the range of precued parameter values (partial information). (3) This prestructure of the population representation reflected the amount of prior information: the distribution was broader when two targets were precued than when a single target was precued and even broader when three targets were precued. (4) The population distribution sustained its preshape throughout the preparatory period. (5) After the response signal, the prestructured distribution evolved continuously toward a sharp, strongly activated distribution centered on the specified parameter value. Thus, for incomplete prior information, the width of the distribution decreased, and the peak shifted continuously from the average among the precued targets toward the specified target. Quantitative analysis of the activity distribution demonstrated that the width of the population representation varied as a function of task condition (Fig. 3). The less information that was provided in advance, the broader the distribution was during the preparatory period. This relationship persisted in the reaction time period as a consequence of the gradual development of the representation.

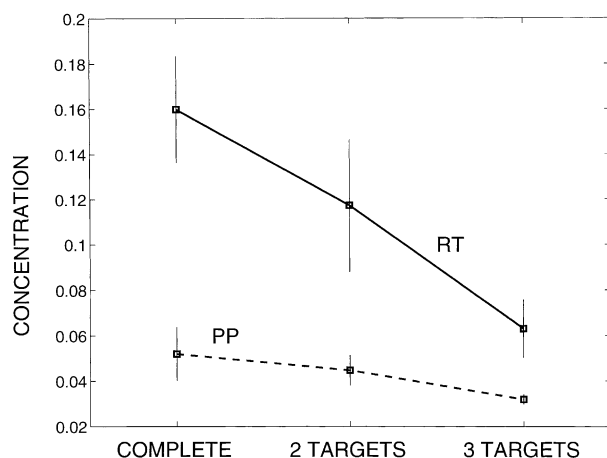


FIG. 3. The width of the population representation is assessed using the concentration measure of circular statistics, shown here as a function of the amount of prior information. The population distribution was computed from neuronal firing rates averaged over the first 500 ms of the preparatory period (PP) and from firing rates averaged over the reaction time period (RT). Averages across the six population representations (one for each of the six possible movement directions specified by the RS) are shown jointly with their standard error. Note that during the preparatory period, sharpness decreases with increasing range of prior information. This dependence carries over into the reaction time period, because the sharpening of the population distribution subsequent to the response signal is gradual. Note also that distributions are always sharper during the reaction time period than during the preparatory period.

Direct comparison with the theoretical model (Fig. 1) further confirms the conclusion that we have observed preshaping of the representation of the movement parameter direction in the sense of the model.

## Discussion

The aim of this study was to demonstrate how populations of motor cortical neurons participate in the preparation of movement. We used an experimental protocol which allowed us to vary the amount and content of prior information about movement direction. The results demonstrate that neuronal activity during the preparatory period reflects information about the required movement not only when this information is complete, but also when partial information is provided and the movement cannot be fully prepared in advance. Evidence that information about single movement parameters is correlated with responses of individual cells in motor cortical areas has been provided earlier.<sup>2,7,8</sup> Because in these studies precued information was always either complete or absent, the question of how partial precue information is represented on the cortical level could not be addressed. When prior information is varied in a graded manner by precuing different ranges of movement directions, the population representation of movement direction was shown to reflect this change through the width of the activity distribution. In terms of the dynamic field model, our observations reveal preshaping at the level of population representations. The gradual evolution of the neuronal population representation after specific input has been provided by the response signal is in line with the gradual specification process of movement parameter values observed in psychophysical studies<sup>5,6</sup> and validates the model of movement preparation.

This new way of looking at neuronal activity prior to movement initiation raises a number of interesting questions. What is the relationship between space and time in the population representation? Do sharper distributions evolve faster than broad distributions? How does the shape of the population distribution relate to reaction time? How does it relate to the accuracy of the movement? Future work can now address these issues using the techniques we have introduced.

## Conclusion

Neuronal populations in motor cortex represent the movement parameter 'direction' during the preparatory period. The shape of the population representation during the preparatory period depends on the range of precued parameter values. From this

preshape the population representation evolves continuously in time to the final representation of the specific motor response once the response signal has been presented. These findings are consistent with a theoretical model of movement preparation, in which the movement representation evolves from a preshaped field to the specified form in response to specific input.

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