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Hints for a topographic map of tuning properties in primate motor cortex

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Abstract - **The spatial organization of tuning properties of neurons in the primate motor cortex is still unknown. Here, we analyze the directional tuning of neurons and local field potentials recorded in the motor cortex of monkeys performing center out arm movements. We found that the tuning of nearby neurons, and of single neurons and local field potentials recorded from the same electrodes is more similar than expected by chance. These findings are in agreement with a spatial organization of tuning properties in motor cortex.**

Keywords - **behaving monkey, single-unit activity, local field potentials, topographic map**

I. INTRODUCTION

As is well known, the primate motor cortex shows a somatotopic organization. Moreover, single-unit recordings demonstrated that many motor cortical neurons are tuned to physical parameters (e.g. direction, force) of arm movements. Unlike in the visual cortex, however, the question to what extent a map of tuning properties exists within the motor cortex is still unresolved and debated (e.g. [1,2]).

Here, we investigated correlations between the directional tuning of local field potentials (LFPs, [3,4]) and single neurons, and among nearby neurons recorded in the motor cortex of a trained rhesus monkey. Specifically, we tested, whether the tuning curves of neurons and LFPs recorded from the same electrode were more similar than could be expected from randomly assigned tunings.

Assuming that the neural activity recorded from the same electrode originates from sources which are spatially close, a topographic map of tuning properties would result in a relation in the tuning among nearby neurons and between LFPs and single neurons recorded from the same electrode.

II. METHODS

A. Experimental procedures

Single-unit activity and LFPs we simultaneously recorded from the motor cortex of a rhesus monkey (*Macaca mulatta*) during performance of a center out task (Fig. 1, for details see [5,6]). Briefly, the monkey grasped two manipulanda (one with each hand) that were movable in the horizontal plane and controlled two cursors on a vertical screen in front of the monkey. In response to a visual cue, the monkey had to move either the left or the right arm to one of eight directions (regularly arranged on a circle, 45° apart). Single-unit activity (SUA) and LFPs were recorded simultaneously from four glass-coated tungsten electrodes (arranged at relative distances of 350 to 700 μm) in each hemisphere. All experimental procedures were in accordance with the Hebrew University and NIH regulations for the Care and Use of Laboratory Animals.

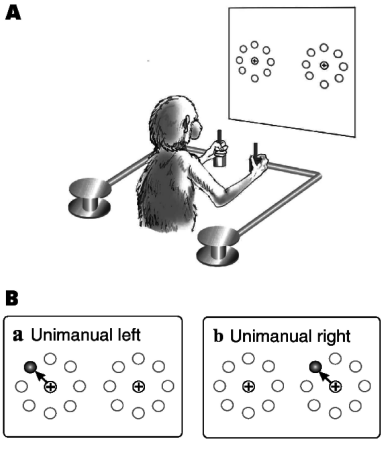

Fig. 1 Experimental setup. (Figure modified from [6])

B. Data analysis

In total, we analyzed 58 SUA/SUA and 57 SUA/LFP pairs from 16 recording days. We considered only recordings with at least 15 trials for each target and aligned all trials at the beginning of movement (algorithm developed by A. Arieli).

As shown by [7], the trial-averaged LFP has a characteristic shape, typically exhibiting four distinct peaks (Fig. 2). To measure the strength of a particular peak, we used the square root of the integral of the square (rms) of the averaged LFP enclosed of the area around the peak [7]

$$rms = \sqrt{\int_{\text{peak}} \overline{LFP}^2(t)\,\mathrm{d}t} \qquad (1)$$

Thus, we determined the tuning curve for each peak of each LFP by the rms as a function of the target.

The tuning curve of a neuron was defined by the mean firing rate as a function of the target. For each point in time we computed the tuning curve after convolving the spike train with a Gaussian kernel of 50 ms standard width. In addition to this time-resolved tuning, we computed the tuning curve in four fixed time windows (Fig. 2): the first interval enclosing most of the reaction time (-250 ms to 0 ms, where 0 ms is at the onset of movement) is termed "RT". The second interval includes RT and 500 ms of movement time (termed "RMT"). The third interval includes the late phase of the movement ("LMT") and the last interval (from -250 ms to 1000 ms) includes all the above and is termed "ALL".

In order to compare the tuning curves of either two nearby neurons or of a single neuron and an LFP we used two different measures of similarity: (a) The signal correlation (r_s), i.e. the correlation coefficient between the tuning curves. To assess the significance of a non-zero signal correlation, we used the distribution of this parameter for the case of uncorrelated tuning curves. We generated a random sample from this distribution by a shuffling procedure and computed the the significance level (p-value) using the Mann-Whitney test. (b) The angular difference (AD) between the preferred directions (PD). The PDs were determined by a cosine fit. The AD ranges between 0 and 180 degree, since the sign of the AD does not matter. For uncorrelated tuning-curves the distribution of the ADs is homogeneous. The Kolmogorov-Smirnov test was used to determine the significance of a deviation from the uniform distribution.

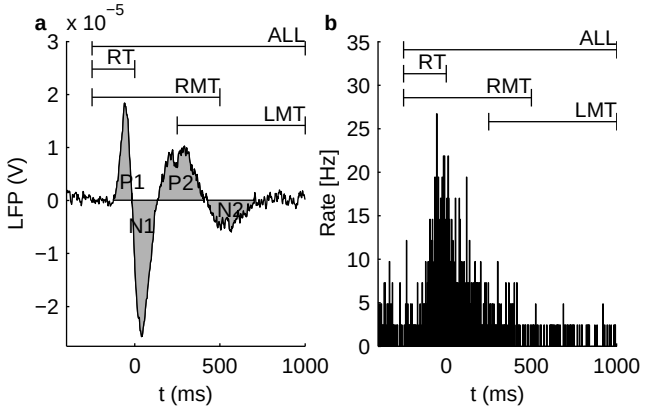

Fig. 2 (a) Mean evoked LFP and **(b)** average firing rate of a neuron recorded from the same electrode. As shown in [7], the mean evoked potential typically exhibits four peaks: a negative peak around movement onset (N1), a preceding and a successive positive peak (P1,P2) and a negative peak (N2) up to 500 ms after P2. The black bars in **(b)** depict the different time windows which were used to compute the tuning curves of each neuron. Further explanation in the text.

III. RESULTS

A. Signal correlation between neurons and LFPs

Fig. 3 shows the signal correlation between the time-resolved tuning of neurons and the tuning of each of the four LFP peaks averaged over all 57 SUA/LFP pairs recorded from the same electrode. The strength of the correlation is clearly time-dependent, exhibiting a maximum for P2 and a minimum for N2 around movement onset. For all four peaks we determined the time where the absolute value of the correlation was maximal (indicated by stars in Fig. 3). The distribution of the signal correlation at these time points is shown in Figs. 4a,c,e,g. All four distributions are broad with averages only slightly above or below zero (Fig. 4i). However, for peak P2 and peak N2 the deviation from zero was highly significant with p-values of $5 \cdot 10^{-7}$ and $3 \cdot 10^{-4}$, respectively.

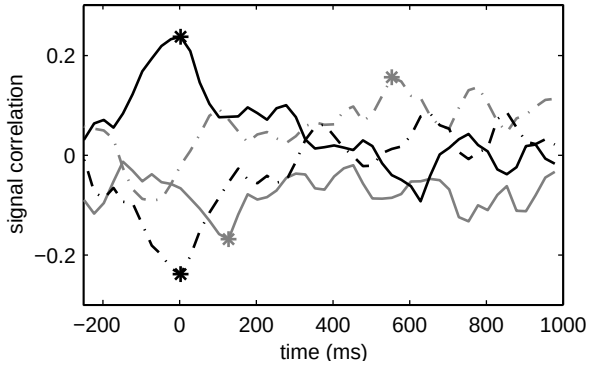

Fig. 3 Signal correlation between the time-resolved tuning of the neurons and the tuning of the four LFP peaks: P1 (gray solid), P2 (black solid), N1 (gray dash-dotted), N2 (black dash-dotted). Stars indicate the time points of maximal correlation or anti-correlation.

For the same points in time, we compared the preferred directions of the single neurons with the preferred directions of the LFP peaks and plotted the distribution of angular differences (Figs.4b,d,f,h). This distribution is significantly different from homogeneous for P2 (Fig. 4d) and N2 (Fig. 4h) whereas for P1 (Fig. 4b) and N1 (Fig. 4f) the deviation from homogeneity is much less significant. The angular difference between the preferred direction of LFP peak P2 and the neuron is for most pairs smaller than 60°. By contrast, the AD distribution between LFP peak N2 and the neurons is concentrated between 120°-180°. Whether this shift is a result of a 180° flip of the PD of the LFP between P2 and N2 is currently investigated. Taken together, our results from the analysis of ADs are in close agreement with our results from the analysis of the signal correlation. Both types of analysis demonstrate that single neurons and LFPs recorded from the same electrode have a weak but significant similarity in their directional tuning properties.

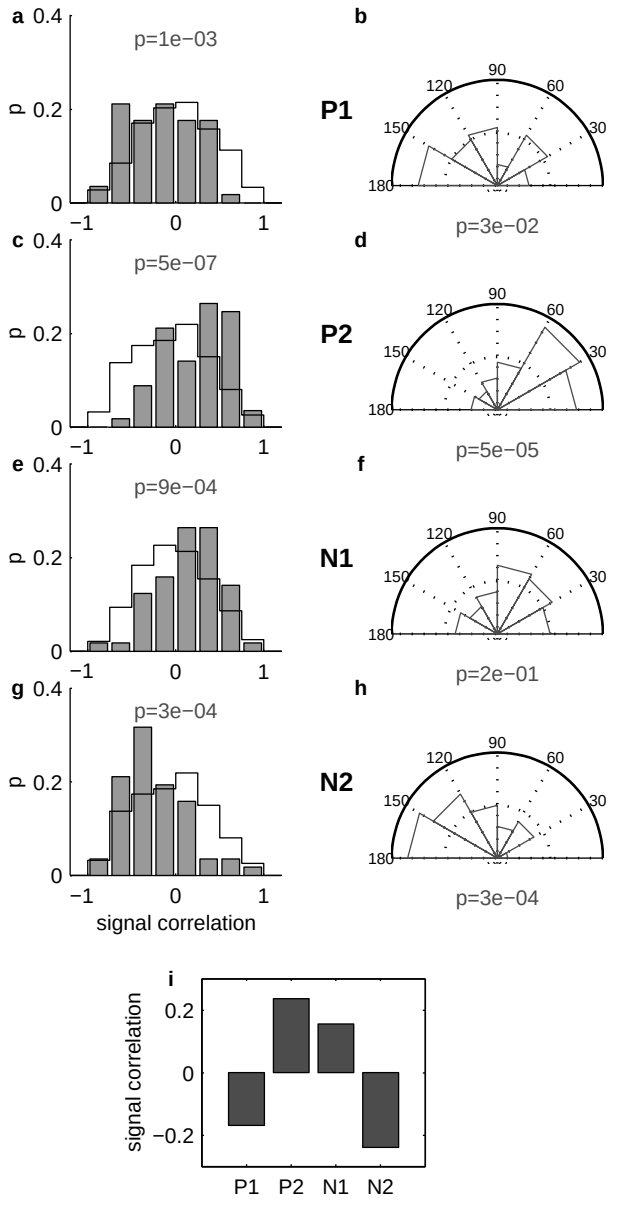

Fig. 4 Signal correlation between single neurons and LFPs recorded from the same electrode. **a,c,e,g:** Distribution of the signal correlation between single neurons and the four LFP peaks (gray bars) P1,P2,N1,N2 respectively. The black histograms show the distribution as expected for no correlation. Gray numbers indicate the significance level for deviation from no correlation. **b,d,f,h:** Distribution of the angular differences in PDs between a single neuron and the PDs of the four LFP peaks P1,P2,N1,N2 respectively. Gray numbers depict the p-values for deviation from a uniform distribution. **(i)** Average signal correlation between single neurons and the four peaks of the LFP.

B. Signal correlation between nearby neurons

We compared the tuning of pairs of single neurons recorded from the same electrodes. For all four time windows (RT, RMT, LMT, ALL) we found a broad distribution of signal correlations (Figs. 5a,c,e,g) covering the whole range of possible values. The average signal correlation (Fig. 5i) was slightly above zero for all time windows. The highest average signal correlation was observed for the time windows RMT, LMT and ALL, with all three average correlations being significantly different from zero. The distributions of the ADs for the time windows RMT, LMT and ALL were significantly non-homogeneous with a strong bias towards small angular differences (Figs. 5b,d,f,h). This similarity of PDs of nearby neurons is in agreement with results from a recent study [2].

C. Significant signal correlations are not caused by a non-homogeneous distribution of PDs

A possible explanation for a non-homogeneous distribution of ADs could be a non-homogeneous distribution of PDs. For SUA such a non-homogeneous distribution has been described [9]. For our data, however, we could not reject the null hypothesis of a homogeneous distribution of PDs for single neurons ($p > 0.6$ for all time windows). Moreover, by comparing the distribution of ADs to a distribution generated by randomly sampling two PDs from the distribution of observed PDs, we confirmed our main results. In particular, the similarity of PDs between SUA and LFP is significant ($p < 10^{-3}$) for P2 and N2 while the similarity of PDs between nearby neurons is significant ($p < 10^{-2}$) for the time windows RMT and LMT.

IV. DISCUSSION

We examined the relationship between the directional tuning curves of the LFP and single neurons recorded from the same electrodes. The mere fact that we find tuning in the LFP, a signal supposedly composed of activities from thousands of individual neurons, in itself suggests a topographic organization. Indeed, our results reveal the presence of a weak, but significant correlation, both between the tuning of LFPs and single neurons, and between the tunings of neighboring neurons alone. It is reasonable to assume that the activities obtained from one electrode originate from a spatially confined region. Thus, our results support the notion of a topographic mapping of tuning properties in the motor cortex.

A number of reasons may account for the apparent weakness of the similarities in the tuning curves of nearby neurons. These include the selection of the correct tuning parameter [8,9] and possible difficulties in the determination of the tuning curves due to high noise levels and also recording stability across trials. However, it is also possible that the actual topographic organization in the motor cortex is indeed weak.

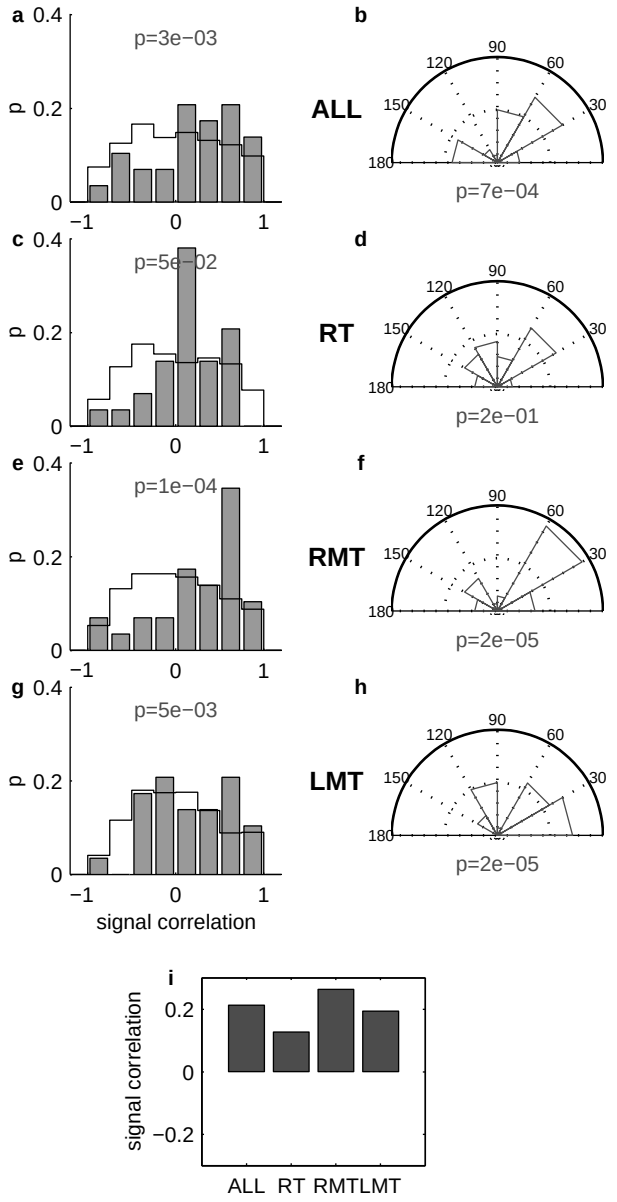

Fig. 5 Signal correlation between single neurons recorded from the same electrodes. **a,c,e,g** Distribution of the signal correlations between the tuning of two neurons in fixed time windows ALL,RT,RMT,LMT (gray bars). The black histogram shows the distribution as expected for no correlation. Gray numbers indicate the significance value for a deviation from no correlation. **b,d,f,h** Distribution of the angular differences in PDs between two single neurons. Gray numbers depict the p-values for deviation from a uniform distribution.**(i)** Average signal correlation between the tuning of nearby neurons for the tuning in the four different time windows.

Further research, including alternative tuning models especially for the LFP, is necessary to address these issues. The same holds for the functional interpretation of the observed LFP tuning. These issues are the subject of current research in our laboratory.

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