Attention improves object discriminability in monkey area V4
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Introduction
Attention improves processing of objects within complex scenes. Improved processing manifests itself in lower thresholds, faster responses and better recognition of stimulus shape as compared to non-attended stimuli. On the neuronal level it was found that attention can modulate firing rates, which corresponds to increasing the signal-to-noise ratios (SNR) of feature representations [1]. Alternatively, neuronal representations of objects could also be improved by modifying the corresponding population activities such that they become more distinct [2].

The purpose of this project is to investigate the impact of attention on population representations of objects by using recordings of local field potentials (LFPs) from two macaque monkeys engaged in a stimulus recognition task. This task was chosen because it cannot be performed correctly without attention [3]. Here, we quantify the improvements of stimulus representations through attention by classifying the presented objects from the LFP data using standard support vector machines (SVMs) [4], and we identify which properties of the signals are modulated by attention.

Figure 1: Left: Two monkeys were trained to attend to one of two sequences of objects, which were simultaneously presented in both hemifields of a computer screen. The task required the monkeys to attend to the left or right hemifield by releasing a lever. Right: Classification performance P of the initial shape (650 to 2200 ms) under attention with respect to the position of the electrodes in the array (black circles). The performance level is color-coded according to the color bar shown to the right of the array, and in addition displayed above each electrode position. The numbers in brackets denote the gain in performance through attention. For the grey colored squares, classification performance did not differ significantly (p = 0.01) from the chance level of 18% (indicated by the black horizontal line in the color bar). The electrode selected for the frequency analysis (Fig. 2) is marked by grey arrows.

Setup and Methods
Two monkeys were trained to an extended delayed match to sample paradigm (see Fig. 1(left) for details) where the monkey had to respond to the recurrence of the initial shape in one of two presented pattern sequences. LFPs were recorded with a chronically implanted array of 36 (second monkey: 37) epidural electrodes while the monkeys were performing the task. The array covered parts of area V1 and V4 with 3 mm electrode spacing. The signals were continuously recorded at a sampling rate of 1 kHz. To suppress the effect of the common reference and minimize spatial smearing, the current source density (CSD) was computed. For analysis in the time frequency (TF) domain the CSD signal of each trial and electrode was convoluted with complex Morlet’s wavelets. For further details of signal pre-processing see [5].

The resulting wavelet power coefficients were averaged over time in each frequency band and then used for a trial-by-trial based pattern classification with the help of SVMs [4]. For this purpose, the data from...
correctly executed trials only was split into a training and a test data set of equal size. To exclude effects from ongoing adaptation processes, the splitting has been done in an interleaved fashion.

**Results**

During the experiment, the monkeys succeeded to identify the re-occurrence of the initial shape in 80% of all valid trials. The number of successful trials used in the SVM analysis was 2760 (800) for the attended, and 2750 (760) for the non-attended condition (values for the second monkey in brackets).

![Figure 2: Classification performance $P$ using the power of the wavelet coefficients from the main V4 electrode obtained under attention during the initial period (650 ms to 2200 ms after trial onset). The performance is shown in color-code for various subsets of power coefficients in different frequency ranges.](image)

Pooling data from all electrodes during presentation of the initial shape, we found a SVM performance of up to 94% correct (1200 ms window, chance level: 17%), i.e. the information contained in the LFP-data was nearly sufficient for perfect object identification. Pooling 5 electrodes covering area V4 resulted in 52% classification performance for non-attended stimuli, and 63% for attended stimuli. Considering data only from single electrodes, classification performance reaches peak values of 67\% and 42\% in the two regions corresponding to areas V1 and V4, respectively (see Fig. 1(right)). Furthermore, we classified whether the initial shape was attended by the animal. In this case, the LFP signal corresponding to a single electrode located above V4 reached 75\% performance (chance level: 50\%). Similar performances were also obtained from the data recorded in the second monkey.

![Figure 3: Scaling factor or ratio $\Gamma_c(f_0)$ of the mean wavelet power coefficients for attended versus non-attended conditions, in dependence on the pattern class (shape) $c$ and the frequency band $f_0$. The coefficients were calculated from the data obtained during the initial period from the main electrode in V4. A scaling factor $\Gamma = 1$ indicates no change in the mean power coefficients (dashed black line). The inset shows the relative change in classification performance through attention for each of the 6 different shapes.](image)

In order to quantify the information content of different frequency bands, we selected the electrode in
V4 with highest performance. We then selected subsets of the wavelet coefficients restricted to specific frequency ranges and compared their classification performances (Fig. 2). Almost all stimulus-specific information was concentrated in the frequency range from 30 to 100 Hz.

In spike recordings, attention was found to increase the signal-to-noise ratios (SNRs) of neural activities and thereby to improve the discrimination performance of visual stimuli [1]. Here we checked if the observed attention effect on the LFPs can also be explained from increased SNRs. For this purpose we computed the wavelet coefficient SNRs in the attended and non-attended condition for all shapes and all frequencies. In fact, it turned out that the SNRs do not change between the two conditions. Accordingly, there must be a different mechanism for improving classification performance under attention.

Computing the mean wavelet coefficients for each initial shape \( c \) and each frequency band \( f_0 \), we found that attention scales the coefficients differently depending on shape and frequency (Fig. 3). Even subtle changes in the corresponding scaling factors \( \Gamma_c(f_0) \), as e.g. between the patterns 2 and 3 in Fig. 3, apparently lead to pronounced increases in classification performance (see inset in Fig. 3). These results lead us to the hypothesis that attention improves classification by selectively shifting the activities in different frequency bands for different shapes. We tested this hypothesis by transforming the non-attended data set into a pseudo-‘attended’ data set via pattern-specific scaling with the coefficients \( \Gamma_c(f_0) \) extracted from Fig. 3. This procedure kept the SNRs exactly constant. It turned out that the SVM performance on this pseudo-attended data set reached and sometimes even exceeded the performance on the original attended data set, thereby explaining the full attentional gain shown in Fig. 1, and confirming our hypothesis.

Discussion

Our results show that attention improves discriminability of visual stimuli in gamma-band neuronal activity. In contrast to enhancements of the signal-to-noise ratios seen in spike recordings we here found that encoding improvement in the LFPs is specifically linked to shifts in spectral content, without increases of the SNRs. This indicates the presence of a novel population effect of attention which improves the discriminability of object representations. The high classification performance on objects and direction of attention suggests that LFP signals also from visual cortex could be useful for brain machine interfaces.

Currently, we are investigating if information in the wavelet coefficients is modulated according to the direction of attention when the monkeys made attention-related errors (error analysis). There are several questions remaining on which we will work in the near future. First, which neuronal mechanism is responsible for the pattern-specific scaling under attention? Second, is there a similar improvement in classification performance if more than only a small number of stimulus categories have to be discriminated? Finally, it is important to clarify whether learning is a prerequisite for the attentional gain in information, or if attention improves the representation regardless whether a stimulus is familiar, or viewed for the first time.

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References


