

# Feature selectivity in area 21a of the cat

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We compared the feature tuning of neuronal activity in area 21a with the tuning in areas 17/18. Local field potentials and multi-unit activity recorded in alert animals showed similar selectivity to orientation in both areas, higher selectivity to spatial frequencies in areas 17/18 and higher selectivity and tuning significance to temporal frequencies in areas 17/18. In addition, only at sites in areas 17/18 did the local field potential exhibit locking to a horizontal motion

pattern extracted from a natural movie. These results suggest that area 21a is concerned with the analysis of spatial features but lacks a faithful representation of temporal features. Hence, they foster the hypothesis that cortical area 21a is part of a ventral form pathway. *NeuroReport* 17:809–812 © 2006 Lippincott Williams & Wilkins.

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## Introduction

The processing of visual information is organized into a number of cortical areas, most of which can be grouped into separate functional streams. In the primate, a ventral 'what' pathway, concerned with object structure, has been distinguished from a dorsal 'where' pathway, concerned with spatial localization [1]. In other model systems for vision, such as the cat, there is good evidence that the processing is organized into similar functional streams [2,3].

In the cat, neuronal activity in the early visual areas A17, A18 and the motion area PMLS (postero-medial part of the lateral suprasylvian cortex) has been well characterized (see e.g. [4,5]). Other areas around the suprasylvian sulcus, such as area 21a, are much less investigated. Several studies reported that individual neurons recorded in area 21a of anaesthetized animals are selective to both spatial and temporal properties of a stimulus but that selectivity to spatial properties was more prominent than that for temporal features [6–13]. Hence, it was suggested that area 21a is part of a form processing pathway and a possible homologue of the primate area V4 [3].

In this study, we quantified the selectivity of local population responses, local field potentials (LFPs) and multi-unit activity (MUA) recorded from area 21a of alert animals. LFPs characterize the ongoing processing around the electrode, are complementary to spiking activity and can be compared to data obtained from functional imaging studies [14,15]. Previous studies showed that LFPs recorded in alert animals can be used to study the selectivity to classical visual features in primary visual areas [16,17].

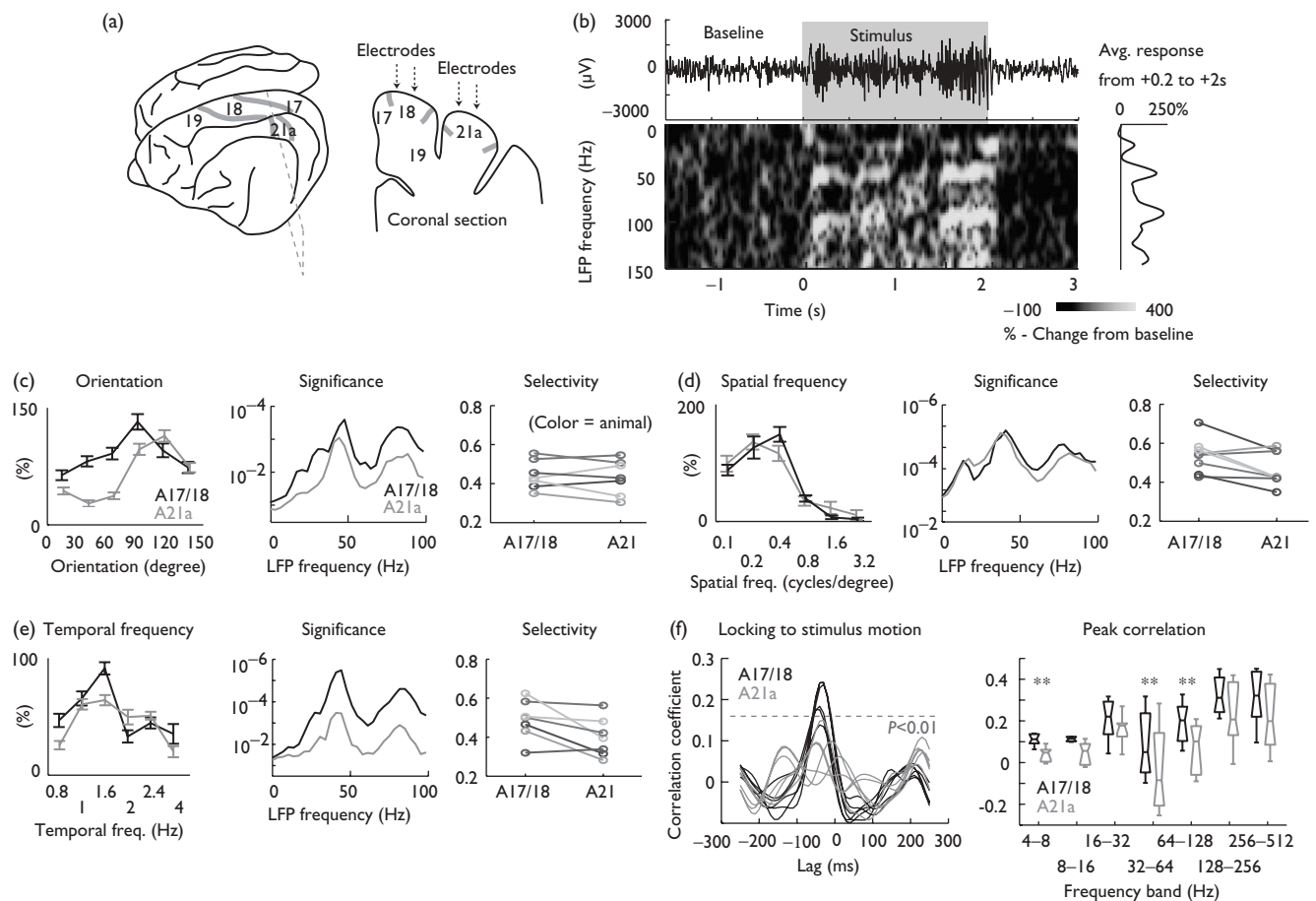
## Methods

### Recording procedures

Recordings were obtained from eight adult cats by using chronically implanted electrodes. Details of recording procedures have been described previously [17,18]. All procedures were in accordance with the Zürich cantonal guidelines and conformed to the Society for Neuroscience regulations.

Surgical manipulations were carried out under general anaesthesia (0.8–1.5% isoflurane in 30% O<sub>2</sub>/70% N<sub>2</sub>O) and sterile conditions. Electrodes were placed in areas 17/18 and 21a of the same hemisphere according to stereotaxic coordinates (A17/18: –2P/–2L and A21a: –2P/8L, cf. Fig. 1a) and cortical landmarks [19,20]. The placement of the electrodes within the desired areas was later verified using standard histological techniques. In three animals, floating electrode bundles [16] featuring six electrodes per cortical area were used (split in two bundles of three electrodes with different depth relative to the surface); in the remaining animals, small microdrives featuring two movable electrodes per cortical area were implanted [18]. Recording sessions were only begun after the animals had fully recovered.

For recordings, the animals were head-restrained and placed in front of a monitor (19" Hitachi, 120 Hz refresh, 8-bit grey scale, 57 cm in front of the animal, covering 40 × 30° of visual angle, mean luminance 30 cd/m<sup>2</sup>). Eye movements were recorded using a Dual Purkinje Imaging system (Fourward Optical Technologies Inc., Buena Vista, Virginia, USA). Signals from the electrodes were pre-amplified



**Fig. 1** (a) Sketch of cat visual cortical areas and electrode placement. (b) Single trial local field potential (LFP) data. Raw data (upper panel) and time-resolved frequency analysis (units of signal change, lower panel). The lower right graph shows the average signal change used for tuning analysis (averaged from +0.2 to +2 s). (c–e) Feature tuning of the LFP. Example tuning curves (mean and SEM, in units of signal change, right panel), average tuning significance as a function of LFP frequency (middle panel) and average tuning selectivity for each animal (right panel). Tuning selectivity was averaged across all sites from the same animal and cortical area. Colour code refers to cortical area (left and middle panels) and animal (right panel). All example tuning curves are from the same two recording sites. (f) Locking to stimulus motion. Cross-correlation between stimulus motion and LFP response for each recording site averaged across frequency bands (left panel). Negative lags of the correlation indicate that the stimulus precedes the response and the dashed line indicates the  $P < 0.01$  level (see Methods). Distribution of peak correlation across animals for individual frequency bands (right panel). Boxes indicate median and upper and lower quartiles. Results of a t-test between areas: \* $P < 0.05$ , \*\* $P < 0.01$ .

(Neurotrack Ltd, Budapest, Hungary) and digitized at 20 000 Hz using a Synamp system (Neuroscan Ltd, El Paso, Texas, USA) using a 5-Hz analogue high-pass filter. The state of alertness was controlled by inspection of eye movements and the low-frequency components of the LFP. Recording sessions with signs of decreased vigilance (fewer eye movements, increased low-frequency electroencephalogram power) were discarded. Importantly, for the present study, the data from areas 17/18 and 21a were acquired simultaneously.

### Visual stimuli

Smoothly drifting sine-wave gratings were used [temporal frequency (tf), spatial frequency (sf)]. *Sf-tuning*: vertical gratings including both directions of drift, tf: 2 Hz, sf: 0.1, 0.2, 0.4, 0.8, 1.6, 3.2 cycles per degree. *Tf-tuning*: vertical gratings including both directions of drift, tf: 0.8, 1, 1.6, 2, 2.5, 4 Hz, sf: 0.2 cycles per degree. *Orientation*: 12 equally spaced directions of drift between 0 and 360 degrees, sf: 0.2 cycles per degree, tf: 2 Hz. *Locking to stimulus motion*: vertical sine-wave grating, sf: 0.33 cycles per degree, moving in

horizontal directions according to a predefined motion pattern. The motion pattern had been extracted from a natural movie (see [18]) and describes the horizontal component of the motion on a frame-by-frame basis. All stimuli had the same mean luminance and root mean square contrast, were shown at least 20 times in a pseudorandom sequence, lasted 2 s and were separated by blank screens of the same mean luminance also lasting 2 s.

### Data analysis

The LFP was extracted by low-pass filtering the raw data at 500 Hz using a third-order Butterworth filter. A time-averaged Fourier spectrum was computed using a frequency resolution of 4 Hz. The initial 200 ms following stimulus onset was dominated by the evoked potential arising from stimulus onset and was discarded. The power in individual frequency bands was converted to units of percentage signal change compared with baseline (Fig. 1b).

Tuning curves were computed for each recording site and LFP frequency separately by pooling all trials of a given direction with those of the opposite direction of drift.

Tuning selectivity was quantified by computing an index, also known as sparseness [21]:

$$\text{selectivity} = \frac{1 - [(\sum_{k=1}^n \langle r_k \rangle)^2 / n(\sum_{k=1}^n \langle r_k \rangle^2)]}{1 - (1/n)}$$

Here,  $r_k$  denotes the response on trial  $k$ ,  $\langle r_k \rangle$  denotes the trial-averaged response and  $n$  is the number of values that a feature can take (e.g. the number of frequencies). The selectivity assumes a value of 0, if the response is unselective and a value of 1 if a response occurs for only one feature value.

The significance of each tuning curve was assessed using a Wilcoxon rank-sum test comparing individual repeats of the optimal stimulus with repeats of the null stimulus; this yielded one  $P$ -value for each LFP frequency and recording site (Fig. 1c–e). Overall tuning significance was compared using the negative logarithm (base 10) of this  $P$ -value, averaged across LFP frequencies. The tuning selectivity was then compared using the tuning curves from those LFP frequencies that yielded the highest significance. This frequency was established for each condition and recording site individually, but all maxima were in the lower  $\gamma$  band (30–50 Hz). The peak tuning frequencies in the LFP were  $0.27 \pm 0.15$  and  $0.45 \pm 0.21$  cycles per degree and  $1.9 \pm 0.3$  and  $2.4 \pm 0.7$  Hz. These frequencies are comparable to numbers previously reported for spiking activity [4,9,22]. Furthermore, all tuning curves for temporal frequency and 83% of the tuning curves for spatial frequency had a band-pass shape (in the latter case, 12% had low-pass type shapes and 5% high-pass type shapes).

The relationship between stimulus motion and LFP response was computed as the cross-correlation of the amplitude of stimulus motion and the response (Fig. 1f, see [17] for more details). The significance of these correlations was established using a bootstrap method (random shifts of the data, 500 repeats, 99% confidence interval).

Multi-unit spiking activity was extracted using a high-pass filter (1000 Hz) and a threshold (3 standard deviations of the signal). MUA responses were converted to percentage signal change and quantified as described for the LFP above.

For statistical analysis, all recording sites of the same area in the same animal were averaged; hence, Fig. 1c–d (left panels) shows as many data points as animals. A  $t$ -test was then used to compare areas 17/18 with area 21a across animals.

The animals were freely viewing the stimuli. Hence, a systematic bias of eye movements could theoretically influence the observed tuning properties. Measurements of eye movements, however, showed that these were not related to the stimulus (see Fig. 1 and Discussion in [17]).

## Results

### Orientation tuning

Tuning in the LFP was assessed at 40 recording sites in areas 17/18 and at 32 sites in area 21a of seven animals. Example tuning curves and the frequency dependence of the tuning significance are shown in Fig. 1c. Tuning was prominent around 30–50 Hz and between 70 and 90 Hz. Statistically, there was no difference between areas concerning tuning significance ( $3.4 \pm 1.5$  and  $2.8 \pm 0.9$  for A17/18 and A21a, mean  $\pm$  SD across animals;  $t$ -test:  $P=0.08$ ). Similarly, tuning selectivity was not different either ( $0.44 \pm 0.07$  and

$0.43 \pm 0.09$ ;  $P=0.46$ ). In addition, in the MUA (21 and 12 sites from three animals), neither tuning significance ( $5.6 \pm 2.0$  and  $4.6 \pm 1.9$ ,  $P=0.07$ ) nor tuning selectivity ( $0.47 \pm 0.02$  and  $0.42 \pm 0.02$ ,  $P=0.48$ ) was different. Hence, tuning to orientation is similarly prominent in areas 17/18 and 21a.

### Spatial frequency tuning

Tuning in the LFP was assessed at 40 sites in both areas from eight animals (Fig. 1d). Significance of tuning was the same in both areas ( $4.1 \pm 1.8$  and  $4.2 \pm 2.9$ ;  $P=0.59$ ), but tuning selectivity was stronger in areas 17/18 ( $0.53 \pm 0.08$  and  $0.46 \pm 0.08$ ;  $P=0.03$ ). Hence, spatial frequency tuning is similarly expressed, but more selective in areas 17/18.

### Temporal frequency tuning

Tuning in the LFP was assessed at 35 sites in area 17/18 and 26 sites in area 21a of seven animals (Fig. 1e). Significance of tuning was significantly more prominent in areas 17/18 ( $3.9 \pm 1.6$  and  $2.9 \pm 0.9$ ;  $P=0.04$ ) as was the tuning selectivity ( $0.49 \pm 0.1$  and  $0.39 \pm 0.09$ ;  $P=0.036$ ). In the MUA (21 and 12 sites from three animals), tuning significance ( $3.54 \pm 1.8$  and  $1.43 \pm 0.81$ ,  $P<0.01$ ) and selectivity ( $0.47 \pm 0.13$  and  $0.32 \pm 0.11$ ,  $P<0.05$ ) were significantly higher in areas 17/18. Hence, tuning to temporal frequency is expressed more in the primary visual cortex than in area 21a.

### Locking to the temporal stimulus profile

We previously showed that LFP responses within the primary visual cortex lock to the temporal profile of complex visual stimuli: the responses are correlated to the velocity profile of a natural movie or of a grating moving horizontally according to an irregular profile [17,18]. We here compared whether the strength of this locking was comparable in areas 17/18 (35 recording sites) and area 21a (26 sites) of seven animals (Fig. 1f). The correlation between LFP power and stimulus motion amplitude was higher in area 17/18. Especially, only for sites within areas 17/18 did the locking reach significance (based on a randomization test,  $P<0.01$ ). Across animals, the correlation strength was significantly different between areas for LFP frequencies between 4–16 and 32–128 Hz (individual significances are given in Fig. 1f). We conclude that only activity in the primary visual cortex, but not in area 21a, represents the temporal profile of the stimulus.

## Discussion

Previous studies examining neuronal activity in area 21a mostly recorded the spiking activity of individual neurons in anaesthetized animals [6–13]. In contrast to this, the present study quantified the stimulus selectivity in LFP and MUA recorded in areas 17/18 and area 21a of alert cats. The LFP is a continuous signal that characterizes the local processing near the tip of the electrode and represents a distance weighted average of mainly dendritic and somatic currents [14,15]. Hence, the LFP is thought to reflect more the input and intrinsic processing within an area, while the spiking activity, especially that of the often recorded pyramidal neurons, represents the output that is sent to the further processing stages. The LFP is complementary to the spiking activity and shares response properties with the signals from functional imaging. It will be interesting to

compare the present results with that of emerging studies of area 21a using optical imaging [23]. Nevertheless, one should keep in mind that the LFP is a spatially smoothed signal. Hence, the present comparison assumes that the typical column size is similar within both areas.

In both visual areas, the LFP was clearly selective to spatial and temporal attributes of drifting gratings and this selectivity was most prominent in the  $\gamma$  band. This is in agreement with previous reports (see [16] or [17] and references therein) and suggests that both the primary visual cortex and area 21a are similarly involved in the analysis of visual features. In addition, the present results show that tuning to orientation (significance and selectivity) and tuning to spatial frequency (significance) were similar in both areas. In contrast, tuning to temporal frequency (significance and selectivity) and locking to stimulus motion were significantly more prominent in the primary visual cortex and weaker in area 21a. Especially the latter was only observed in the primary visual cortex. These results suggest that the local processing in area 21a is more concerned with spatial properties of a stimulus but lacks a faithful representation of the stimulus' temporal profile. Hence, area 21a seems to be more involved in the analysis of spatial stimulus properties. This finding is in agreement with previous suggestions that area 21a is part of a ventral, form processing, pathway and a functional homologue to the area V4 in primates.

### Conclusion

Our results show that local population responses in areas 17/18 are better tuned to temporal features of a stimulus than are responses in area 21a, suggesting that the area 21a is part of a form processing pathway.

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