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RESEARCH REPORT

RESPONSE VARIABILITY AND STIMULUS DISCRIMINATION CAPACITY OF NEURONS IN MONKEY INFERIOR TEMPORAL CORTEX

KOVÁCS, GY., BENEDEK, GY. and SÁRY, GY.

Department of Physiology, Albert Szent-Györgyi Medical University, Szeged, Hungary

Summary: Single neurons (n=73) were recorded from the inferior temporal cortex (IT) of an awake macaque monkey, while performing a visual fixation task. Shape stimuli that elicited different responses of the IT neurons, were found to result in different response variances. The response variance vs. mean response relationship of the IT neurons could be described by an analogous function to those found in previous studies of A17 in cats and of V1 in macaques. A comparison of the stimulus discrimination capacities of the individual neurons revealed that neurons which exhibit lower variances can discriminate their preferred and non-preferred shape stimuli more reliably than neurons with higher variances.

Key words: inferior temporal cortex, response variability, shape selectivity, vision

INTRODUCTION

The response variability (SD^2) of single neurons in the primary visual cortex of anesthetized cats (Dean, 1981; Bradley et al. 1987) and of awake macaques (Vogels et al. 1989; Vogels and Orban 1991; Gur et al. 1997) is proportional to the intensity of the mean neural response (MR). The variability of the firing is understood to limit the stimulus discrimination

Correspondence should be addressed to:
Dr. Gy. Kovács
Department of Physiology, Albert Szent-Györgyi Medical University
H-6720 Szeged, Dóm sqr 10, Hungary

capacity of the neurons. Indeed, several investigators have found that the orientation discrimination capacity of the striate cortical neurons is a function of SD^2 in cats (Bradley et al. 1987; Scobey et al. 1989) and in anesthetized (Schiller et al. 1976) and in awake monkeys (Vogels and Orban 1991).

However, no data are available as concerns the relationship of SD^2 and MR in higher visual cortical areas, such as the inferior temporal cortex (IT) of awake macaques, and it is not known how the shape discrimination capacity of IT neurons is related to the neural SD^2.

The responses of the IT neurons is associated with presentation of simple or complex shapes, and there is a strong shape selectivity (for reviews, see e.g. Gross, 1992; Logothetis and Sheinberg 1996; Tanaka, 1996); this may underlie the human shape recognition ability. In the present experiments, we recorded the activities of single IT neurons from an awake, actively fixating monkey in response to complex colored pictures. We measured quantitatively SD and MR for single IT neurons and found that SD^2 is proportional to MR across a population of neurons firing differently in response to their preferred stimuli, as well as within each IT neuron, responding differently to the preferred and to the less effective shapes. Further, the shape discrimination capacity of IT neurons could be predicted from SD^2.

MATERIALS AND METHODS

An adult male rhesus monkey (Macaca mullata; weight=9 kg) served as subject. During the experiments, access to water was limited, but had dry food ad libitum, as well as supplementary fruits and vegetables. The procedures of Judge et al. (1980) were used to implant a scleral search coil into the eye contralateral to the recording site. A stainless steel plug was cemented to the skull to allow head fixation. The single cell recordings were performed through a circular recording chamber (diameter 20 mm) implanted over the IT (center: AP 18, LM 24), which allowed vertical approach to the area. All surgical steps were performed under full anesthesia (initiated with Ketamine (4 mg/kg) / Xylazine (0.7 mg/kg) and maintained with Ketamine (8 mg/kg/hour)), under aseptic conditions. The heart rate, O_2 saturation, blood pressure and respiration were monitored during the operation, and the body temperature was maintained constant. Antibiotics (300 mg Rocephin) and analgetics were administered postoperatively.

After full recovery, the animal was trained daily in the fixation paradigm. The animal was seated in a primate chair with its head fixed, allowing measurements of eye movement and neural activity. A fixation spot first appeared in the center of the screen (distance 57 cm, frame rate 72 Hz). When the animal fixated the target, a static background noise pattern was shown (18 × 13 deg; 16.4 cd/m^2) for 500 msec. Next, the stimulus shape appeared on the background for another 500 msec of fixation. The animal was required to maintain fixation throughout the trial in a 0.8 × 0.8 deg square window centered around the fixation spot. A small amount of water was administered to the animal as a reward, immediately after shape offset. To associate the presentation of the stimulus shape and not that of the fixation spot with the reward, the fixation spot remained on-screen for a random period (100 – 300 msec). The animal usually consumed 150-300 ml of water in a session of 2-3 hours, completing 2000-2500 trials a day, 5 days a week. The behavior of the animal was controlled by a 486 PC (sampling rate 200 Hz). Another PC controlled the presentation of the fixation spot and stimuli, and a third PC recorded and displayed, as raster and peristimulus time histograms, the neural activity and the stimulus and behavioral events (temporal resolution 1000 Hz). Single cell recordings were made with parylene and kapton coated tungsten microelectrodes, positioned by a Narishige microdrive. The neural signal was amplified and filtered and single neurons were isolated by means of an amplitude window discriminator. All procedures conformed to the guidelines of the NIH for the care and use of laboratory animals.

The stimuli were 20 geometrical shapes with different textures and colors, and complex colored pictures of everyday objects occupying a similar area (ca. 30 deg^2) and having a similar luminance (4.3 ± 0.73 cd/m^2, mean ± standard deviation).

During recording, we first searched for shape selective neurons, using our standard set of stimuli. Once a cell was found to be responsive to at least one of the 20 stimuli, determined by auditory and visual examination of the signal, we selected 4 stimuli for further analysis. In order to have a wide range of the selectivity tuning of the neuron, we generally selected 2 shapes evoking large responses and two shapes with less vigorous responses. These 4 stimuli were then presented to the animal in a semi-random fashion at least 10 times. The single cell recordings serving as the basis of the present study were performed as part of another, larger study (Kovács et al. 1998).

MR was calculated by measuring the total number of spikes, generated in one trial in a 400 msec time window, starting at 50 msec after stimulus onset.

The mean net firing rate was calculated by subtracting the neural activity during a fixation period of 400 msec preceding shape onset (baseline activity) from the activity obtained during stimulation. For each neuron and for each shape, we calculated MR, the standard deviation (SD), SD^2 and the coefficient of variation (CV = SD / MR). The responsivity and shape selectivity of the neurons were tested by analysis of variance (ANOVA, Kirk, 1968). The neural shape discrimination capacity (SDC) was expressed as 100 $\times$ (MR_{best}- MRw_{orst}) / MR_{best}, where MR_{best} and MR_{worst} are the mean net responses for the most preferred shapes (Best)* and for the least preferred shapes (Worst; Oram and Perrett, 1992), respectively.

RESULTS

Here we report data on 73 shape selective IT neurons. Since the animal is still engaged in recording experiments, no detailed anatomical description is available as concerns the correct location of the neurons. However, MRI and CT images of the brain and skull of the animal, taken in a costume-built stereotaxic device and correlated with the depth of the recordings, suggest that the recordings originate from area TE, and presumably TEO. Figure 1 shows the lateral surface of the macaque brain, reconstructed after the MRI images. Gray shadowing shows the presumed location of the recordings.

Neural responses were analysed in detail for all recorded units. Figure 2A shows SD^2 as a function of MR. There is a correlation between the two parameters ($r=0.66$, $p<0.05$); similarly as in earlier studies, this is best described by the function

$$SD^2 = a \times MR^b$$

* Please note that the terms "Best/Worst" or "Preferred/Non-preferred" refer only to the relative amplitude of the response elicited by our limited set of stimuli. In the present study, no attempt was made to determine the preferred object features, e.g. by the reduction process of Tanaka (1996); only a small set of stimuli, eliciting different firing rates and leading to shape selective responses, was necessary.

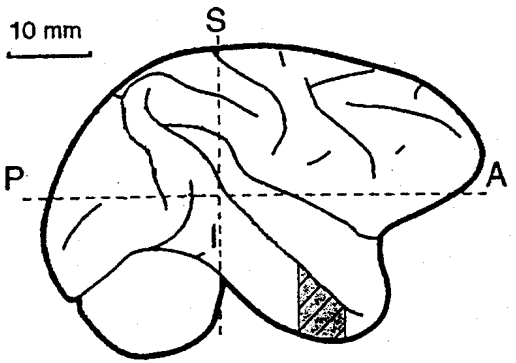
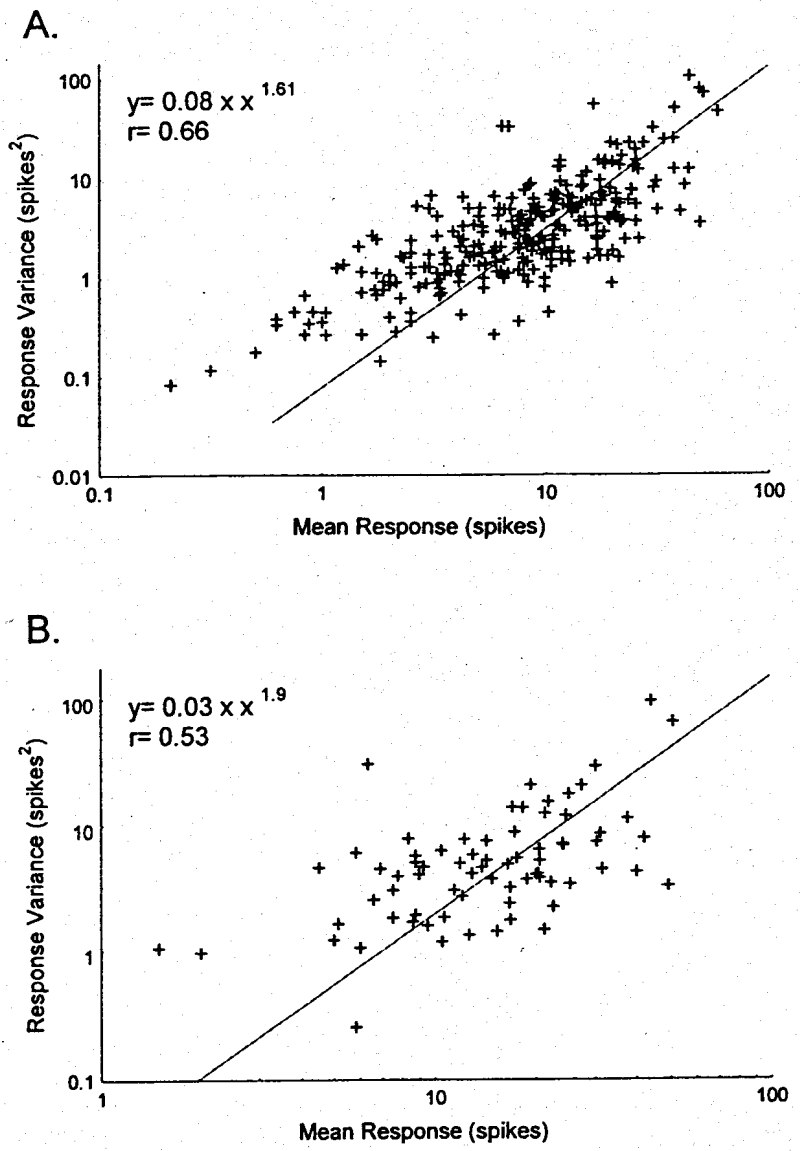


Fig. 1. Lateral view of the macaque brain, reconstructed after the MRI images of the animal. Gray shadowing shows the presumed area of recordings in the anterior part of inferior temporal cortex

Calculation of the SD^2 across the 73 neurons and 4 shape presentations (n=292), led to an the intercept a close to zero (0.08), and a slope b of 1.61. This variability in firing can stem from two independent sources. First, different neurons respond to their preferred stimuli with different firing rates. Thus, we tested the correlation of SD^2 and MR across the neurons (n=73) only for the stimulus evoking the largest neural activity (preferred shape; Fig. B). A similar correlation was found across the neurons for the preferred shapes (a=0.03, b=1.9, r=0.53, p~0.05) as for the whole sample. Second, shape selective neurons obviously respond differently to different shapes. To test whether SD^2 is proportional to the mean firing rate within the neurons as well, we calculated CV for the individual neurons for each shape separately. Figure lC depicts MR, SD^2 and CV as functions of shapes, ranked according to the mean net firing rates. It is obvious that, the smaller MR, the smaller SD^2, but the larger CV. This suggests dependence of SD^2 on MR.

To test the prediction that SD^2 is an important factor in determining neuronal shape selectivity we first calculated CV for the preferred, or Best shapes (n=73, mean=0.19, lower quartile: 0.14, higher quartile: 0.34). Next, the shape discrimination capacity index (SDC) was calculated separately for neurons having CV larger than the third quartile of the distribution (>0.34; i.e. for neurons in which the response intensity varies for repeated presentations of the same stimulus) and for neurons having CV smaller than the lower quartile (<0.14; i.e. for neurons in which the response intensity



does not vary so much for repeated stimulus presentations). The SDCs of the neurons with low CV (mean=89.38) were significantly higher (t-test with separate variance estimates: $t=2.5$, $p<0.017$), than those of the neurons with high CV (mean=58.37)

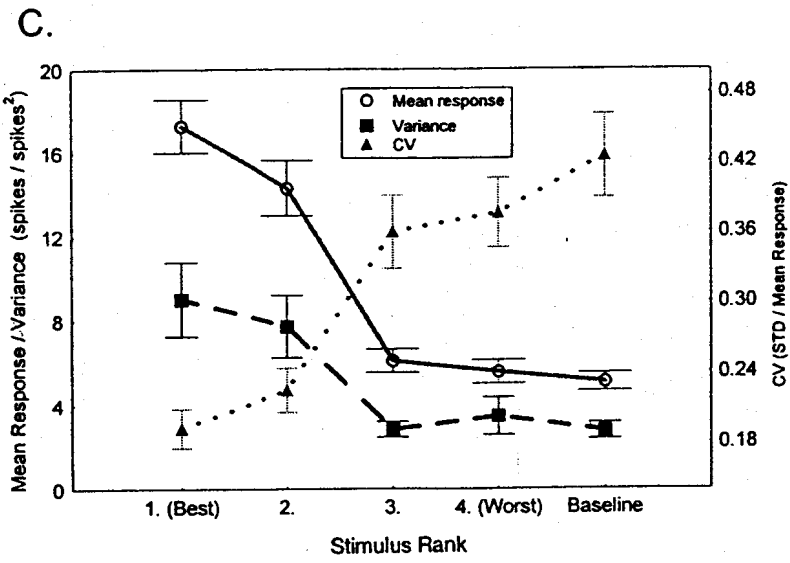


Fig. 2. Relationship between mean response strength and response variance of inferior temporal neurons. Response variance as a function of the mean response level for all recorded neurons and stimuli (A), and as a function of the mean response level only for the preferred shapes of the neurons (B). C depicts the mean response rate (MR), variance (SD^2) and coefficient of variation (CV) as a function of the stimulus rank. Shaded stripes show the mean (+ standard error) baseline firing rate (vertical stripes) and the response variance of the recorded neurons (obique stripes). The lines connecting the dots in the Figure serve only demonstrative purposes

DISCUSSION

The response variance of IT neurons was measured and correlated to the neuronal response in an awake, fixating monkey. CV for IT neurons was 0.19, which is similar to that found in V1 of awake monkeys (0.18; Gur et al. 1997), suggesting similar response variances in the striatal and extrastriatal visual areas. We observed that the variance in the IT neural responses was proportional to the intensity of the response. This is in agreement with previous studies of primary visual cortical neurons in cats (Dean, 1981; Bradley et al. 1987) and in monkeys (Vogels et al. 1989; Vogels and Orban 1991; Gur et al. 1997). An analogous relationship was found by Snowden et al. (1992) in MT/V5, an area involved in visual motion perception. As in all previous studies, we could describe this relationship by a power function. The

slope of the function was similar for IT (1.6) to those found for V1 and MT/V5 (1.1-1.2). This suggests that the decrease in neural response variance during information processing within the neocortex is lower than suggested by the continuous cortical convergence of the inputs, assuming uncorrelated noise across the neurons. However, the intercept for IT (0.08) was lower than the intercept for V1 (0.2 to 2.12; Vogels et al. 1989; Snowden et al. 1992, Gur et al. 1997) and for MT (1.37, Snowden et al. 1992). This can be attributed in part to our smaller fixation window, with consequently a lower of eye movements during recordings (Gur et al. 1997). Additionally, a lower modulation of the IT neural responses by slight positional changes of the image in the receptive field (i.e. positional invariance; Schwartz et al. 1983) can explain the lower effects of eye movements on the response variance. The lower intercept for IT (i.e. the better signal to noise ratio) can also be explained by assuming some degree of input convergence that is not totally counterbalanced by the correlated firing of the IT neurons (Gawne and Richmond, 1993).

The origin of this neural response variance is twofold. First, each neuron fires differently in response to its preferred stimuli, leading to different variances (Fig. 1B) across the neurons.

Second, variation of the shape of the stimulus results in different response rates in a given neuron. We found that the response variance of the individual neurons follows the mean response. This correlation of response and variance within neurons, however, is weak, as suggested by the significant decrease in CV with increasing response rate (Fig 2C). A similar weak response vs. variance correlation was found by Gur et al. (1997) for the stimulus contrast and stimulus orientation sensitivity of V 1 neurons.

The response variability is a major factor limiting the neuronal input sensitivity. The higher the variance of the firing, the less sensitive is the system to the same physical differences (Bradley et al. 1987, Shadlen and Newsome, 1994). Indeed, the orientation discrimination capacity of the primary visual cortical neurons depends on the response variability both in cats (Scobey and Gabor, 1989) and in monkeys (Vogels and Orban, 1990).

Here we have demonstrated that the input discrimination capacity of an extrastriate visual area, i.e. the shape discrimination capacity of the IT neurons, also depends on the degree of neural response variability. We measured the capacity of single IT neurons to discriminate preferred and non-preferred shapes. SDC proved significantly worse for neurons in which CV is higher (suggesting a higher modulation of the response for repetitions of the

same stimulus) than for neurons in which CV is lower (exhibiting lower changes in response intensity for repeated stimulations). This shows in a quantitative way that the neural response variance is a major limiting factor of neural stimulus discrimination not only in the striatal cortex (Scobey and Gabor, 1989), but also in a ventral stream extrastriate area such as the inferior temporal cortex.

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