

# MONOCHROMATIC AND POLYCHROMATIC VISUAL BACKGROUNDS INFLUENCE THE RESPONSE OF AREA 17 AND 18 NEURONS AFTER STIMULATION WITH STATIONARY AND MOVING LIGHT BARS

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(With 4 figures)

## ABSTRACT

The role of colour vision in night-active cats has not been elucidated completely hitherto. In order to assess the colour sensitivity in cat cortical neurons we used large isoluminant computer-generated monochromatic and polychromatic background stimuli which were superimposed on moving and stationary (on/off) light bars. Background stimuli were moved at different speeds either inphase or antiphase. The modulatory effect of the visual noise on the neuronal bar was the primary objective of the study. The maximum amplitudes of some 40% of the neurons tested was influenced by both moving and stationary bars. About two thirds of amplitude-sensitive cells showed also altered direction selectivity. Latencies and field widths, on the other hand, turned out to be rather stable. The retino-cortical conduction time was not influenced either. In conclusion, a large portion of cat cortical visual neurons is remarkably sensitive to the spectral composition of the visual noise process surrounding the stimulating light bar.

*Key words:* colour vision, cat, monochromatic and polychromatic visual noise.

## RESUMO

### **Fundos visuais monocromáticos e policromáticos influenciam a resposta de área de 17 e 18 neurônios após simulação com barreiras de luz estacionárias e móveis**

O papel da visão cromática nos gatos ativos à noite ainda não foi completamente elucidada. Para avaliar a sensibilidade cromática nos neurônios corticais do gato usamos grandes estímulos de fundos monocromáticos e policromáticos de igual luminância criados por computador, que foram sobrepostos em barreiras de luz (ligadas/desligadas) estacionárias e móveis. O efeito modulatório do ruído visual sobre a barreira neuronal foi o primeiro objetivo do estudo. As amplitudes máximas de cerca de 40% dos neurônios testados foram influenciadas tanto pelas barreiras móveis como pelas estacionárias. Aproximadamente dois terços das células sensíveis à amplitude também demonstraram seletividade da direção alterada. Estados latentes e larguras de campo, por outro lado, se revelaram bastante estáveis. O tempo de condução retino-cortical também não foi influenciado. Em conclusão, uma grande porção dos neurônios visuais do gato é notavelmente sensível à composição espectral do processo de ruído visual em redor da barreira de luz estimulante.

*Palavras-chave:* visão cromática, gato, ruído visual monocromático e policromático.

## INTRODUCTION

The capability of cats to discriminate colours has been debated for more than five decades. Nowadays, neurophysiologists have generally accepted that cats possess blue-sensitive (455 nm) and green-sensitive (560 nm) cones (Hammond, 1978). However, existence of a third cone-type, being sensitive around 500 nm or 600 nm, remains an issue of discussion (Zrenner & Wienrich, 1981; Ringo *et al.*, 1977). It has been also argued that the visual angle of the deterministic stimulus is decisively influencing the spectral sensitivity of cats (Loop & Bruce, 1978).

Effects of coloured visual backgrounds on the response profile of area 17 and 18 neurons following stimulation of receptive fields with moving and stationary white light bars has not been intensively investigated yet. Gouras (1985) emphasizes the important role of the contrast of an object, whether of brightness or of spectral distribution compared to background. Apparently, both form and colour contribute to visual information processing. In general, interaction between deterministic stimulus and visual background substantially characterizes the neuronal response of visual cells (Dinse, 1988). It is therefore possible that neuronal responses are modulated by either mono- or polychromatic visual noise processes.

## OBJECTIVE

This study should provide evidence that not only structure of visual noise but also colour of visual noise processes may have influence on responses of feline area 17 and 18 neurons following stimulation with stationary and moving light bars.

## METHODS

### *Animals and anaesthesia*

Anesthesia in 5 adult cats (*Felis domestica*, 2-4 kg body weight) was induced with ketamine and xylazine (0.25 ml Ketalar<sup>R</sup> i.m., 0.25 ml Rompun<sup>R</sup> i.m.) and atropine (1 mg i.m.). The animals were then anaesthetized with nitrous oxide (70% N<sub>2</sub>O:30% O<sub>2</sub>) and aliquots of barbiturates (Nembutal<sup>R</sup> approx. 1 mg/kg/h). In addition, a local anaesthetic (Xylocaine<sup>R</sup> 2%) was administered

during preparation. Muscle relaxation was achieved with gallamine (Flaxedil<sup>R</sup> 20 mg initially, then 10 mg/kg/h). Nutrition and fluids were given via an indwelling venous catheter (vena salvatella). Respiratory data were adapted by controlling end-expiratory CO<sub>2</sub>. ECG, body temperature and an EEG of the frontal cortex were continuously recorded during the experiment. The animal was put into a stereotactic apparatus and the head of the animal was fixed. The bone above areas 17 and 18 the dura mater was carefully removed and the brain protected with agar. All animals were sacrificed after approximately 3 days (Nembutal<sup>R</sup> 1000 mg i.v.) and the brain was removed for histological verification of electrode positions using current-induced lesions.

### *Data acquisition and analysis*

Single units were recorded from cat's visual cortex using an array with up to 8 independent (extracellular) microelectrodes (4 to 10 Mohm), which allowed to assess the occurrence of action potentials of 8 units (for theoretical considerations on extracellular recordings cf. Delgado, 1964). The array was fixed to a microelectrode manipulator (Microdrive 50-11-5) and adjusted to an anterior-posterior direction above areas 17 and 18. The positions of the electrodes were determined using the topographic atlas of Reinoso-Suarez (1961).

Each receptive field was plotted by hand on a tangential screen and their positions were delineated on a screen. Light bars were moved forward and backward or flashed on/off (stationary) by means of an automatic system of mirrors. Trajectories of the light bars, which were also drawn on the screen, were adjusted in order to stimulate each neuron subsequently. Visual field representations extended up to 30 degrees of visual angle.

Computer-generated isoluminant monochromatic and polychromatic visual background stimuli of 50°×50° visual angle were added. They were superimposed on moving light bars at different speeds either stationary, inphase or antiphase. As a rule, we measured the modulatory effect of coloured background compared to the monochromatic noise process. A difference of 20%, when the activities with mono- and polychromatic background were compared, was considered as relevant. The geometric arrangement of both the

neuronal stimulation and the data acquisition system was maintained constant during a series of recordings.

Action potentials were separated and digitalized using a window discriminator (Window discriminator WPI 120) and a Schmidt-trigger. The data were stored on an IBM compatible personal computer. The data were then analysed off-line and presented descriptively on the basis of the PSTHs (Peri-Stimulus-Time-Histogram) for both half-cycles, i.e. either for forward/backward motion or on/off stimulation. The key parameter was the maximum amplitude of the corresponding psth peak at a constant bin width of 20 ms. Further characteristics of neuronal response were latency (onset of psth peak), field width (width of psth peak) and direction selectivity index according to Orban (1984).

## RESULTS

After stimulation with moving light bars the maximum amplitude of about 40%-50% of the visual cells either increased or decreased following exchange of the monochromatic by the coloured visual noise. The relative motion of the background referred to the stimulus, i.e. either in- or antiphase motion, did not show a substantial effect. When the light bar was flashed on, amplitudes did change in approximately 50% of the neurons after addition of the polychromatic background. The off-responses were constant in about 60%-80% of the cells (Fig. 1). As a rule, we observed more marked alterations of the maximum amplitudes when stationary backgrounds were applied during on/off-stimulation.

The direction selectivity index characterizes the symmetry of the maximum amplitudes following application of light bars moved forward and backward. We allocated the cells to two groups whether the maximum amplitudes were changed or not by adding a coloured background instead of a monochromatic one. Approximately two thirds of these neurons, which had shown altered amplitudes, showed altered DI-values depending on the spectral distribution of the background (Fig. 2). On the other hand, the neurons with invariant amplitudes, with regard to the coloured background, revealed almost resistant DI-

values after exchange of the noise process. Only about 10% to 20% of these cells showed altered direction selectivities due to different backgrounds.

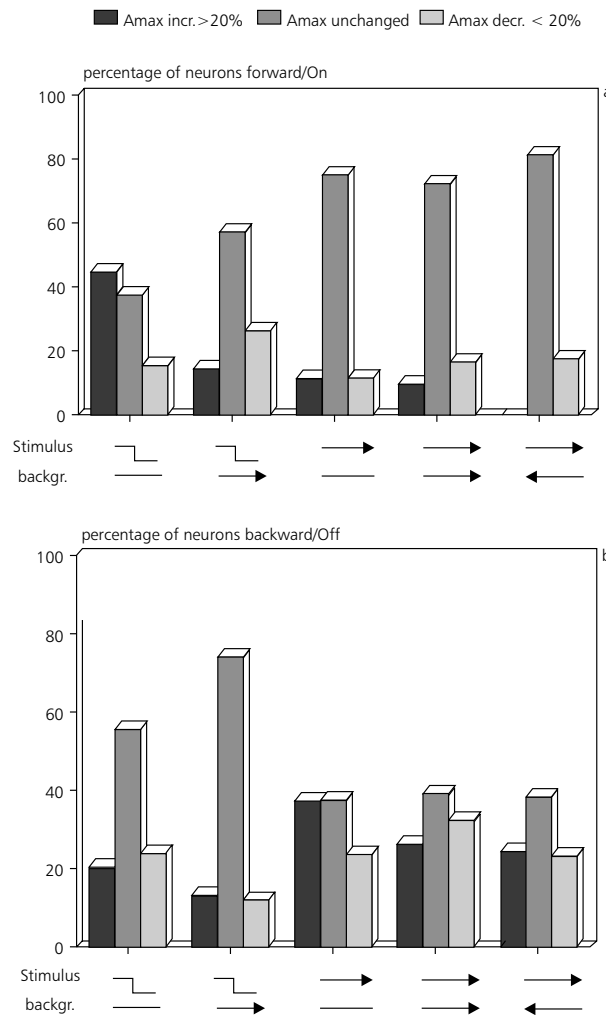
The latency following stimulation with moving light bars was not essentially affected by the polychromatic visual background (Fig. 3). 80% to 90% of the neurons did not show any change of the latency. Corresponding to the latency, the receptive field width also turned out to be rather constant. The latencies following stimulation with bars flashed on/off were not influenced systematically by the polychromatic visual noise process. Therefore, the retino-cortical conduction time is obviously stable in an order of 40 to 50 ms and not subject to modulating mono-/polychromatic visual noise processes.

The Fig. 4 shows an original psth of a visual neuron following stimulation with a moving light bar and inphase moved visual background. Although the maximum amplitude of the forward motion remained largely stable, the direction index changed from -17% to +12.6%, when the monochromatic background was exchanged by a polychromatic noise process.

## DISCUSSION

We have investigated the influence of the spectral properties of visual noise processes on the response characteristics of area 17/18 neurons. Obviously, the polychromatic noise process could alter maximum amplitudes of the psth in 1/3 to 1/2 of the visual neurons after stimulation with moving bars. The direction index of most of these sensitive cells was also markedly influenced. On the contrary, latency and field width appeared to be almost invariant referred to the spectral distribution of the background.

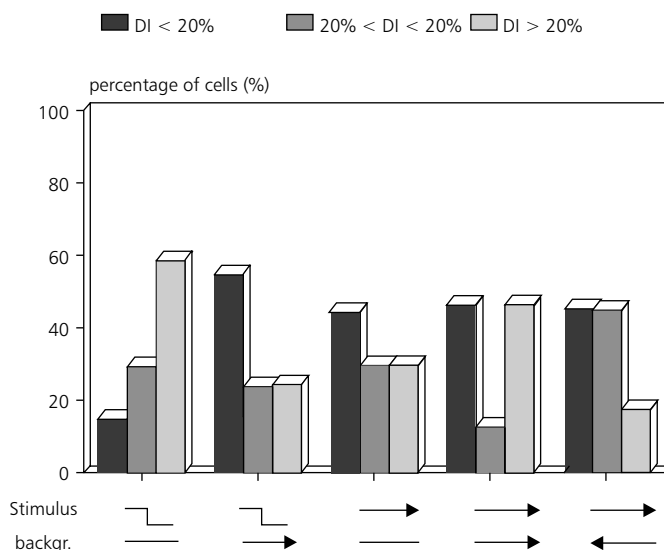
In addition, retino-cortical conduction time was not dependent of the spectral contrast. On the contrary, the response maximum was remarkably altered by polychromatic background following application of stationary bars flashed on/off. Although neuronal responses in cat visual cortex showed a striking variability (Dinse, 1988), the results support the view that both amplitude and consecutively direction sensitivity of a large portion of visual neurons is affected by the spectral composition of the background.



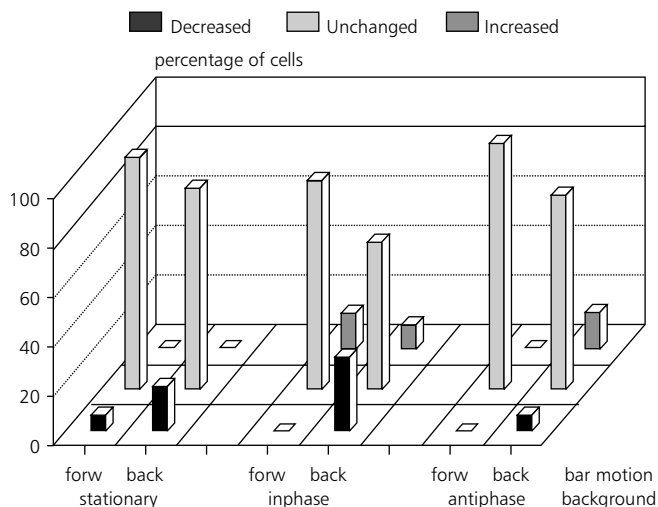
**Fig. 1a, 1b** — Change of maximum amplitudes (psth) following forward/On-stimulation (a) or backward/Off-stimulation (b). A total of 26 neurons were stimulated with deterministic stationary light bars (On/Off) and 17 neurons with deterministic moving bars (forward/backward motion). The change of amplitudes after switching from a monochromatic to a polychromatic background is presented. The background was either held stationary or moved in-/ antiphase, respectively.

Jacobs *et al.* (1991) investigated retinal colour sensitivity in rodents with flickered stationary stimuli. They found that house mice, in addition to the known sensitivity at 510 nm, possess a distinct sensitivity in the ultraviolet region. Although we did not record spectral functions with light bars flashed on/off, the changes response strength in some 50% of the tested cortical visual neurons after application of a polychromatic isoluminant background suggests that colour sensitive mechanisms exist in rodents which are independent of stimulus contrast. Psychophysical

experiments in man could show that the perception of colour is not only a function of the spectral composition of the deterministic stimulus but also depends on the spectral distribution of the environment (Brenner & Cornelissen, 1991). The perceived colour was shifted towards the complementary hue by coloured surroundings. In contrast to the findings in cat (Loop & Bruce, 1978) the target size had only a slight influence on perception. Furthermore, the interaction between rods and cones may improve the colour sensitivity of the visual system of man (Reitner *et al.*, 1991).



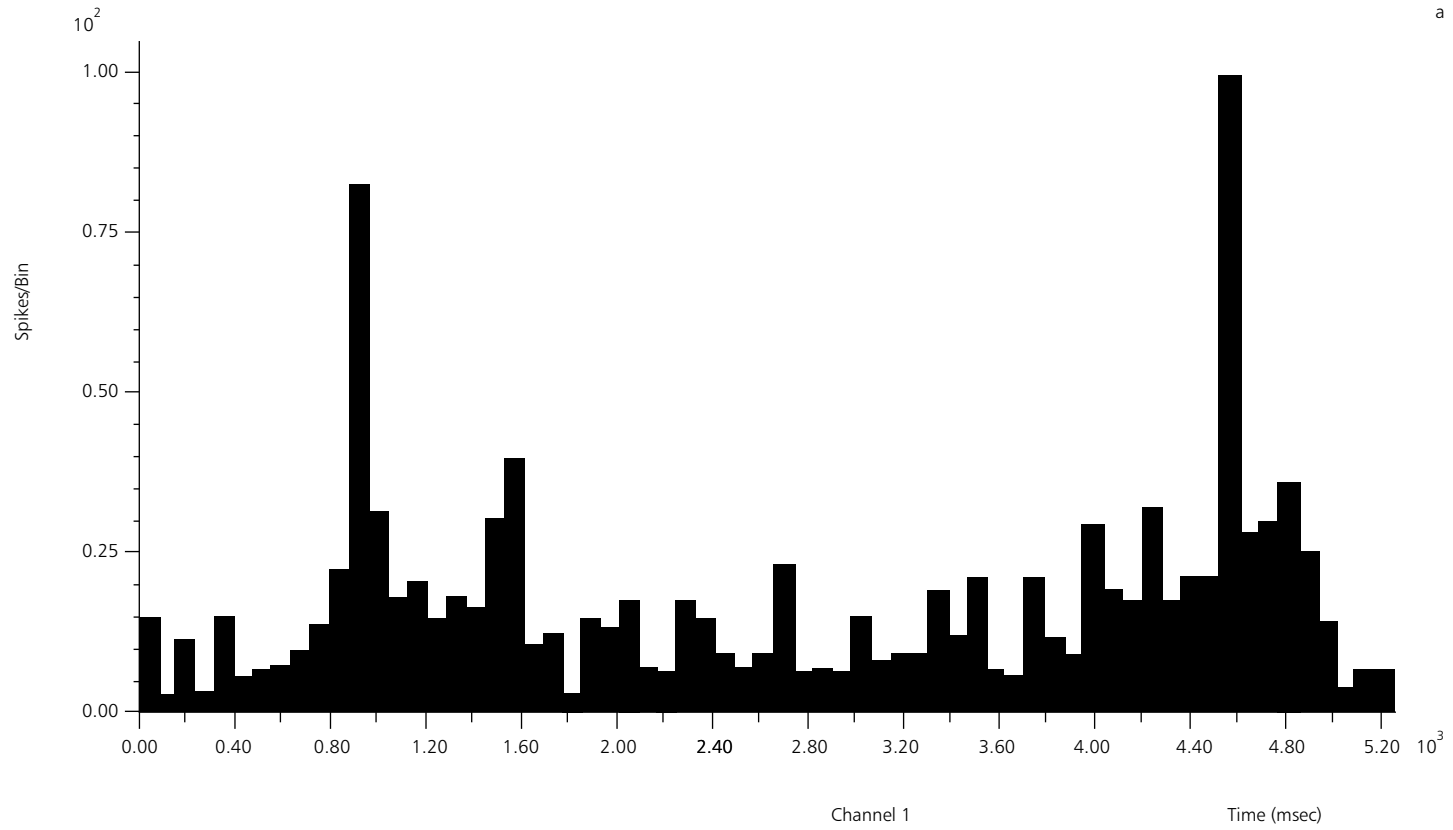
**Fig. 2** — Change of direction index acc. to Orban (1984) after switching from a monochromatic to a polychromatic background. Only cells which showed a change of amplitude of more than 20% were taken into consideration.



**Fig. 3** — Change of latencies of 17 visual neurons after switching from a monochromatic to a polychromatic background for both forward and backward motion of the deterministic light bar. Backgrounds were moved either in-/ antiphase or held stationary.

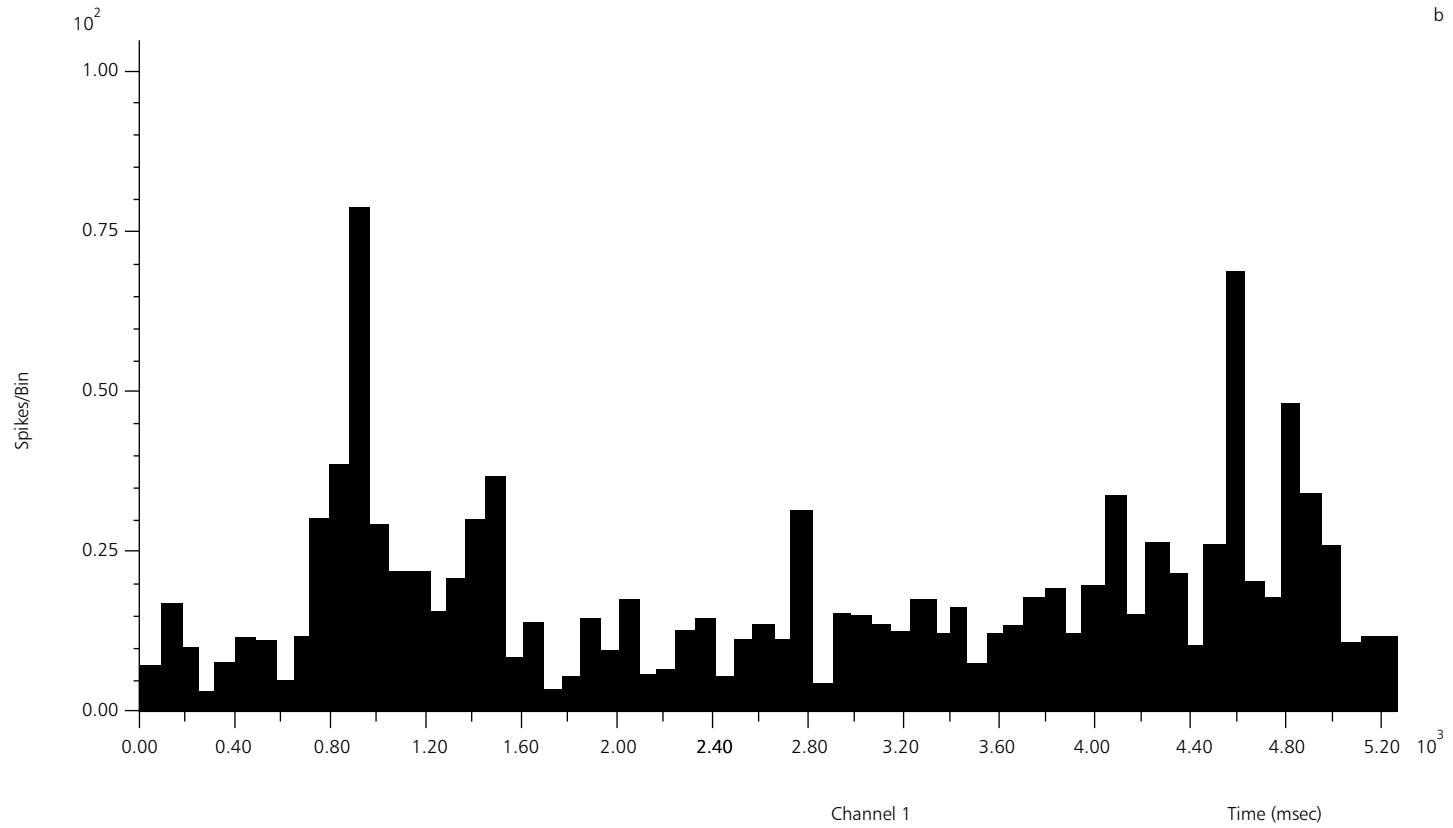
These modulating effects are important in dichromats when the function of the cones is impaired. Physiologically, trichromats can become functional tetrachromats when the target field includes the parafoveal retina. As cats are active in twilight, such mechanisms may be hypothetically possible and improve functional colour vision. The

result that polychromatic backgrounds altered the response maximums of visual neurons in area 17/18 cells is therefore not very much surprising in this context. Our most striking finding was that the direction selectivity is affected in a relevant portion of the neurons. Direction and velocity specify motion of an object in space (Orban, 1984).



a

**Fig. 4** — Original psth recording of a visual neuron following stimulation with a moving light bar (speed: 14 deg/sec). The monochromatic (Fig. 4a) and polychromatic (Fig. 4b) visual background was moved inphase with regard to the deterministic stimulus.



**Fig. 4 (continued)** — Original psth recording of a visual neuron following stimulation with a moving light bar (speed: 14 deg/sec). The monochromatic (Fig. 4a) and polychromatic (Fig. 4b) visual background was moved inphase with regard to the deterministic stimulus.

These results suppose that colour detection and motion detection cannot be completely separated although colour does obviously not play a major role in cat vision. On the contrary, in humans this separation appeared to be almost definite in the investigations of Ramachandran & Gregory (1978), who found that motion detection disappeared when the background dot patterns reached isoluminance. Cavanagh *et al.* (1984) revealed that moving equiluminous red-green chromatic sine-wave gratings altered perceived motion in volunteers, particularly at slow drift rates.

It is therefore questionable, if different qualities, such as colour, form or velocity, are analysed in completely separated channels as proposed by Livingstone (1988). The present results favour the view that, at least in cats, the spectral composition of the visual surrounding influences both response maximum and direction selectivity of visual neurons following stimulation with moving white light bars.

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