Acta Physiologica Hungarica, Volume 87 (1), pp. 31–41 (2000)

Isoluminant monochromatic and polychromatic visual backgrounds alter response characteristics of cat visual neurons after stimulation with stationary and moving light bars

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Received: October 19, 1999
Accepted: February 7, 2000

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 PSTH peaks of some 40% of the neurons tested was influenced by both moving and stationary bars. About 2 thirds of maximum peak-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.

Keywords: colour vison, cat, monochromatic and polychromatic visual noise

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 [8]. However, existence of a third cone-type, being sensitive around 500 nm or 600 nm, remains an issue of

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discussion [7, 16, 17]. It has been also argued that the visual angle of the deterministic stimulus is decisively influencing the spectral sensitivity of cats [11].

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 [6] emphasizes the important role of the contrast of an object, whether of brigthness 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 [4]. It is therefore possible that neuronal response 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 reponse characteristics of feline area 17 and area 18 neurons following stimulation with stationary and moving light bars.

Materials and methods

Animals and anesthesia

Anesthesia in 5 adult cats (*Felis domestica*, 2–4 kg body weight) was induced with ketamine and xylazine (0.25 ml KetalarR i.m., 0.25 ml RompunR i.m.) and atropine (1 mg i.m.). The animals were then anaesthetized (Respirator Pump, Schuler and Braun, FRG) with nitrous oxide (70% N_2O:30%O_2) and aliquots of barbiturates (NembutalR, approx. 1 mg/kg/h). In addition, a local anaesthetic (XylocaineR 2%) was administered during preparation. Muscle relaxation was achieved with gallamine (FlaxedilR 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_2. ECG, body temperature and an EEG of the frontal cortex were continuously recorded during the experiment. The animal was put into a stereotactic apparatus (Narashige, Japan) and the head of the animal was fixed. The bone above areas 17 and 18 and the dura mater was carefully removed and the brain protected with agar. All animals were sacrificed after approximately 3 days (NembutalR 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 of 26 cells 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 [14].

Each receptive field was plotted by hand on a tangential screen (Marata glass 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 and prisms (Ingenieurbüro Ebenhoch and Schulze, Darmstadt, FRG). 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 (discrete Gaussian 1d spectra) stimuli of 50*50 degree visual angle were added. Mean contrasts (Fig. 1) between light bar or monochromatic background was 70.6% and with regard to polychromatic background 72.3% (Mavolux Spotmeter, Gossen, FRG). They were superimposed on moving light bars at different speeds either stationary, inphase or antiphase (Ingenieurbüro Ebenhoch and Schulze, Darmstadt, FRG). As a rule, the modulatory effect of coloured background compared to the mono-chromatic noise process was measured. A difference of 20%, when the activities with mono- and polychroma tic 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 amplified (WPI Differential PreAmplifier DAM 5, USA), separated and digitalized using a window discriminator (Window discriminator WPI 120; Oscilloscope, Tectronix R 5103 N, USA) 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.

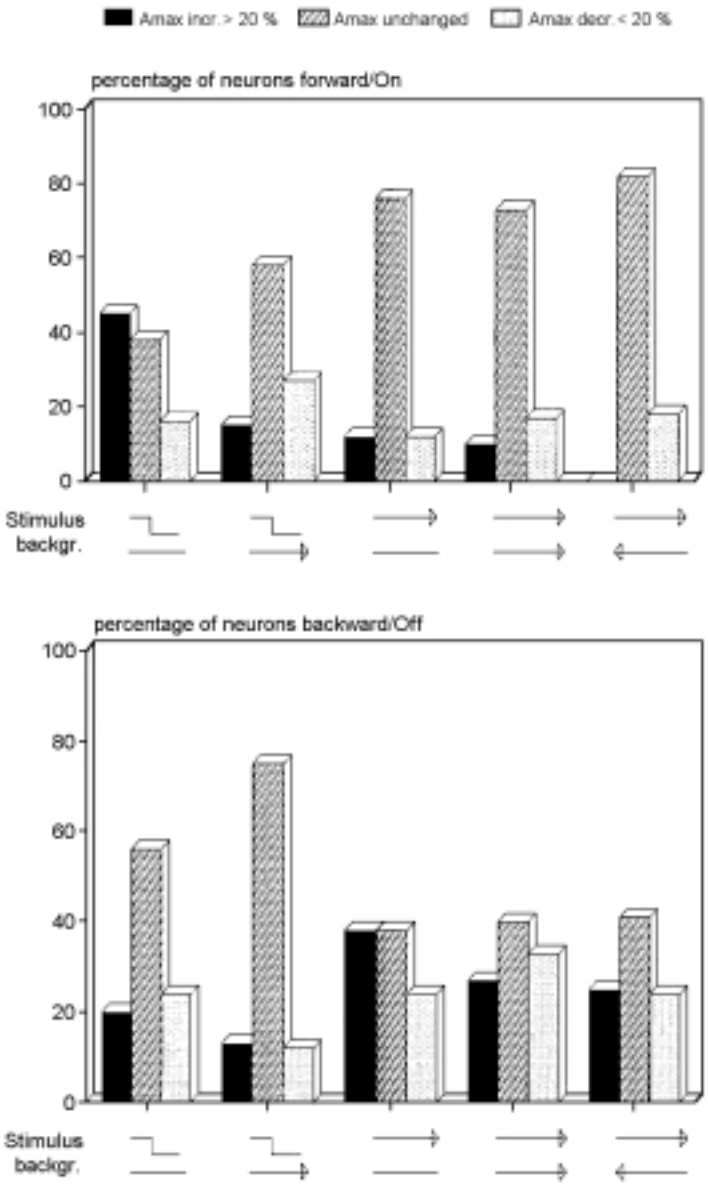

Fig. 1. Contrast of light bars with regard to monochromatic and polychromatic background, respectively. Luminance L [Stilb] was measured acc. to Orban (1984) : C = Lmax–Lmin/Lmax+Lmin * 100 [%]. The small figures represent the mean luminance of corresponding light bars or background. The large figures denote the respective calculated contrast values

The PSTH can be considered as the cross-correlogram between stimulus and neuronal response [5]. The key parameter was the maximum of the corresponding PSTH peak [spikes/bin] at a constant bin width of 20 ms and 16 repetitions of the identical stimulus in order to improve statistical evidence. Further characteristics of neuronal response were latency ([ms]; onset of PSTH peak above spontaneous activity), field width ([ms]; width of PSTH peak above spontaneous activity) and direction selectivity index (DI) according to Orban [12] on basis of maximum PSTH peaks of preferred (Pmaxpr) and non-preferred (Pmaxnpr) direction:

DI = (Pmaxpr-Pmaxnpr/Pmaxpr) * 100[%]. All data were represented descriptively using histograms.

Results

After stimulation with moving light bars the maximum 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 antiphasic motion, did not show a substantial effect. When the light ar was flashed on, maximum PSTH peaks 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. 2). As a rule, we observed more marked alterations of the maximum PSTH peaks when stationary backgounds were applied during on/off-stimulation.

The direction selectivity index characterizes the symmetry of the maximum peaks following application of light bars moved forward and backward. We allocated the cells to two groups whether the maximum PSTH peaks were changed or not by adding a coloured background instead of a monochromatic one. Approximately two-thirds of these neurons, which had shown altered maximum peaks, showed altered DI-values depending on the spectral distribution of the background (Fig. 3). On the other hand, neurons with invariant maximum peaks, 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.

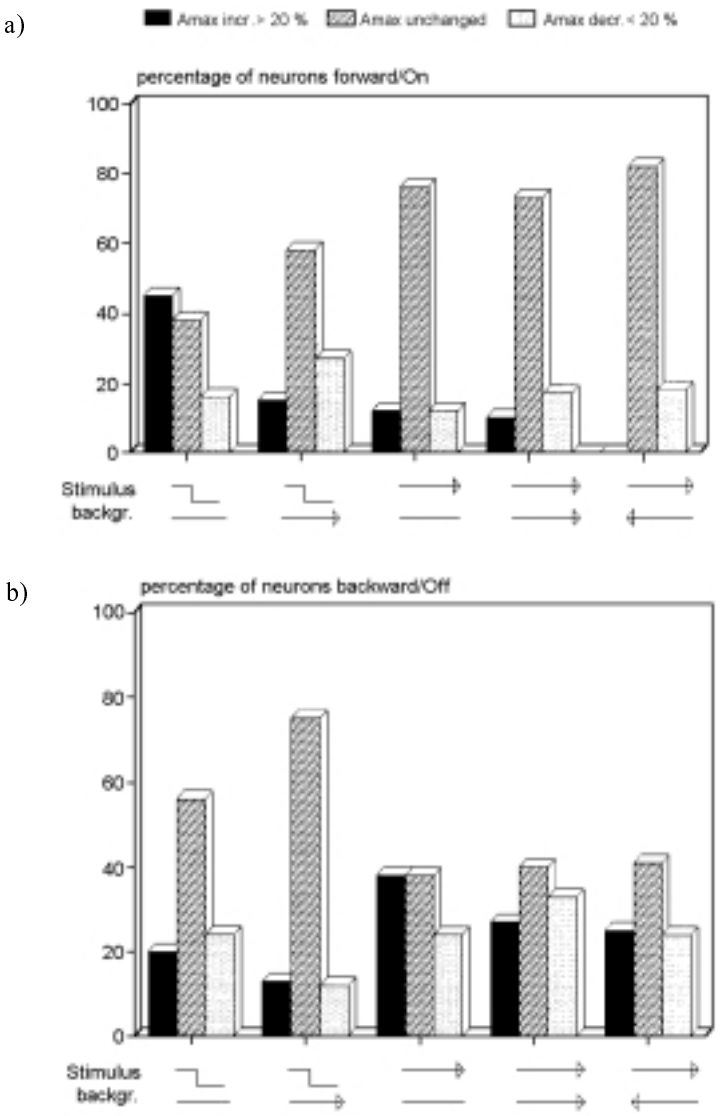

Fig. 2a, 2b. Change of maximum PSTH peaks following forward/On-stimulation (2a) or backward/Off-stimulation (2b). For each stimulus-background constellation 26 neurons were stimulated 16 times with identical deterministic stationary light bars (On/Off) and with deterministic moving bars (forward/backward motion). Relative frequencies (%) were calculated separately for each stimulus-backround constellation. The change of maximum peaks after switching from a monochromatic to a polychromatic background is presented. The background was either held stationary or moved in-/antiphase, respectively

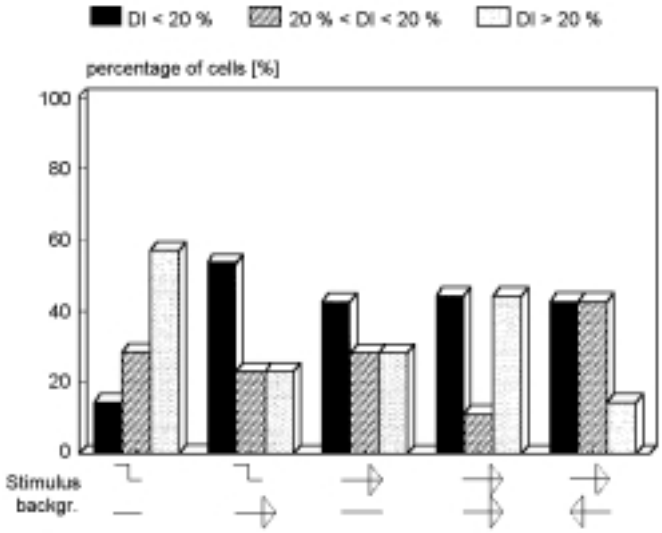

Fig. 3. Change of direction index acc. to Orban (1984) after switching from a monochromatic to a polychromatic background. In order to exclude non-responding neurons, only cells which showed a change of maximum PSTH peaks of more than 20% beforehand (N=17 for each stimulus-background constellation) were taken into consideration for analysis of the direction index. Relative frequencies (%) were calculated separately

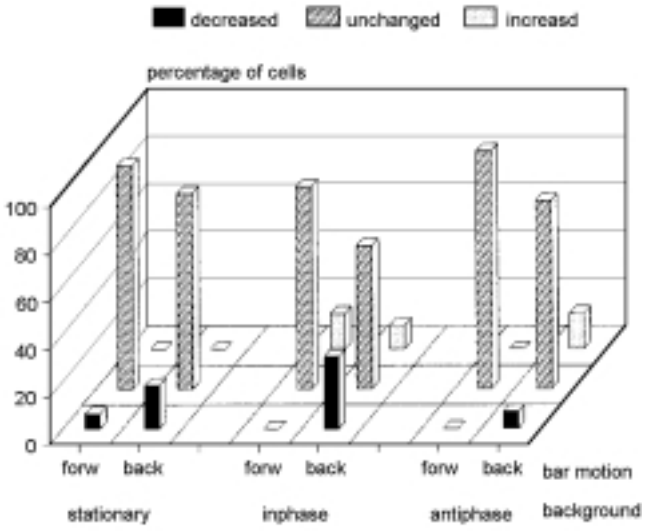

Fig. 4. Change of latencies of 26 visual neurons for each stimulus-background constellation after switching from a monochromatic to a polychromatic background for both 16 repeated forward and backward motions of the deterministic light bar. Relative frequencies (%) were calculated separately for each stimulus-background constellation. Backgrounds were moved either in-/antiphase or held stationary

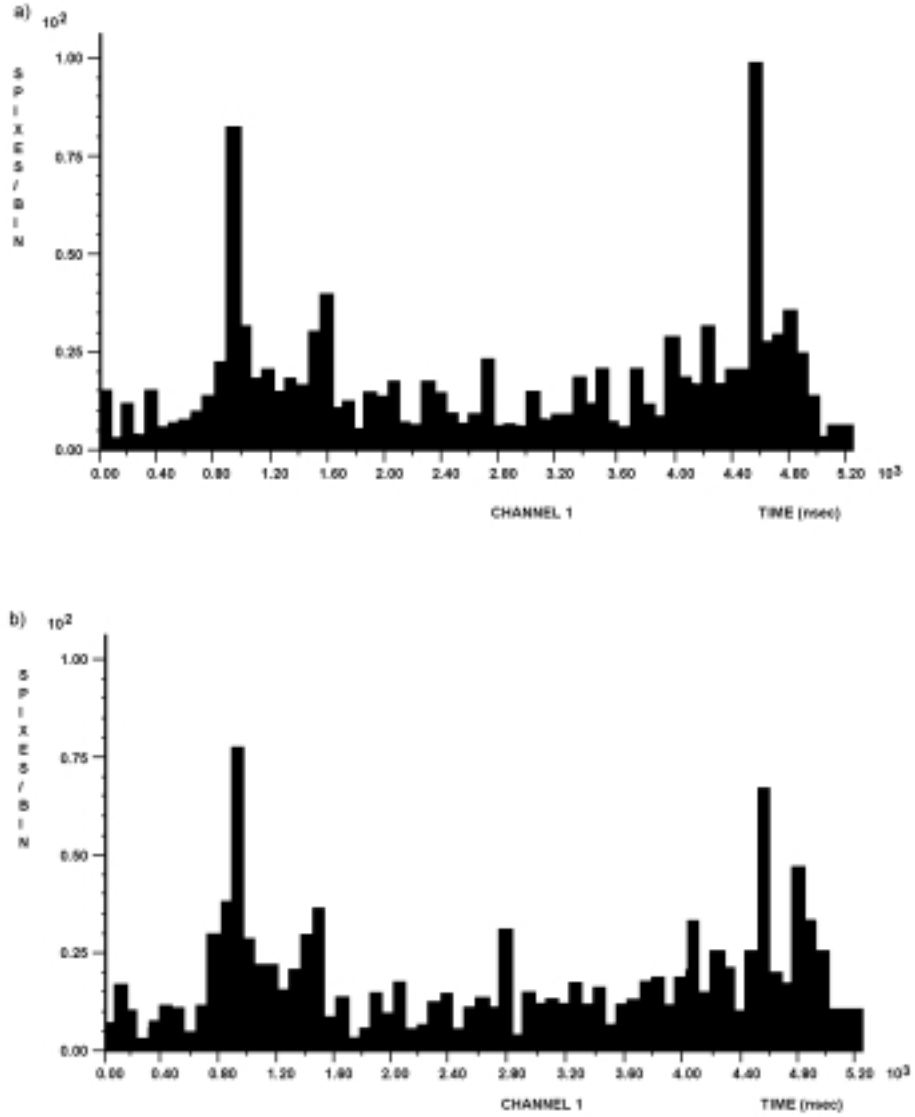

Fig. 5a, 5b. Original PSTH recording of a visual neuron following stimulation wtih a moving light bar (speed: 14 deg/sec, 16 repetitions). The monochromatic (Fig. 5a) and polychromatic (Fig. 5b) visual background was moved inphase with regard to the deterministic white stimulus

Latencies following stimulation with moving light bars was not essentially affected by the polychromatic visual background (Fig. 4). 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. 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.

Figure 5 shows an original PSTH of a visual neuron following stimulation with a moving light bar and inphase moved visual background. Although the maximum PSTH peaks 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 peaks 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 dependend of the spectral contrast. On the contrary, the response maximum was remarkably altered by polychromatic backgrounds following application of stationary bars flashed on/off. Although neuronal responses in cat visual cortex showed a striking variability [4], the results of this study support the view that both maximum peaks and consecutively direction sensitivity of a large portion of visual neurons is affected by the spectral composition of the background.

Jacobs et al. [9] 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 sensitivity functions with light bars flashed on/off, the changed 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 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 [1]. The percieved colour was shifted towards the complementary hue by coloured surroundings. In contrast to the findings in cat [11] 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 [15]. 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 twillight, 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.

The 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 [12]. 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 investigati ons of Ramachandran and Gregory [13], who found that motion dectection disappeared when the background dot patterns reached isoluminance. Cavanagh et al. [2] revealed that moving equiluminous red-green chromatic sine-wave gratings alte red 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 [10]. Recently, clinical investigations with patients suffering from striate cortical damage with regard to blindsight showed that additional thalamo-extrastriate neural pathways may be relevant colour vision [3]. 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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