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REPETITIVE ADAPTATION INDUCES PLASTICITY OF SPATIAL FREQUENCY TUNING IN CAT PRIMARY VISUAL CORTEX

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Abstract—Sensory neurons display transient changes in their response properties following prolonged exposure to an appropriate stimulus (adaptation). In adult cat primary visual cortex, spatial frequency-selective neurons shift their preferred spatial frequency (SF) after being adapted to a non-preferred SF. In anesthetized cats prepared for electrophysiological recordings in the visual cortex, we applied a non-preferred spatial frequency for two successive periods of adaptation (a recovery and interval of ~90 min separated both phases of adaptation) in order to determine if a first adaptation retained an influence on a second adaptation. The first application of a non-preferred SF shifted the tuning curve of the cell mainly in the direction of the imposed SF. The results showed that attractive shifts occurred more frequently (68%) than repulsive (12%) changes in cortical cells. The increase of responsivity was band-limited and occurred around the imposed SF, while flanked responses remained unmodified in all conditions. After a recovery period allowing neurons to restore their original SF tuning curves, we carried out a second adaptation which produced four major results: (1) a higher proportion of repulsive shifts (31%) compared to attractive shifts (49%), (2) an increase of the magnitude of the attractive shifts, (3) an additional enhancement of the evoked firing rate for the newly acquired SF, and (4) for the acquired SF the variability coefficient decreased following the second adaptation. The supplementary response changes suggest that neurons in area 17 keep a "memory" trace of the previous stimulus properties. It also highlights the dynamic nature of basic neuronal properties in adult cortex since repeated adaptations modified both the spatial frequency tuning selectivity and the response strength to the preferred spatial frequency. These enhanced neuronal responses suggest that the range of adaptation-induced plasticity available to the visual system is broader than anticipated.

Key words: visual cortex, spatial frequency selectivity, adaptation, plasticity, vision.

In cat and primate visual cortex, neurons are tuned to respond to visual scene features such as contour orientation, motion direction and speed (Hubel and Wiesel, 1959, 1968; Movshon, 1975). These tuning properties do not require visual experience and were considered unchangeable after birth (Hubel and Wiesel, 1963; Crair et al., 1998; Hensch, 2005). However, several authors reported that in the adult visual cortex of many mammals it is possible to modify preferred stimuli such as orientation and direction selectivities of targets that optimally excite neurons by applying a non-preferred adapting stimulus (Dragoi et al., 2000; Kohn and Movshon, 2003).

Several investigations reported modifications of original neuronal properties following adaptation. Specifically, in cats, at the single cell level, the repetitive exposure of a non-preferred orientation induces a decline of the response amplitude of V1 neurons to the control optimal orientation. In addition, discharges near the adapting orientation are also depressed while responses on the opposite flank of the tuning curve are enhanced. This dual effect resulted in a repulsive shift, that is, away from the adapting orientation, of the tuning curve to orientation (Dragoi et al., 2000, 2001, 2002; Sur et al., 2002). It has also been shown that in the macaque medial temporal (MT) area, adaptation to only one speed diminishes the neural response magnitude and reduces the width of speed tuning curves (Krekelberg et al., 2006). Neurons in area V4 acquire directional tuning after adaptation to motion while these cells lack direction selectivity prior to adaptation (Tolias et al., 2005). Also, adaptation to a near preferred direction causes tuning to shift toward the adapted direction (Kohn and Movshon, 2003; Clifford, 2002). The plasticity in adult cortex appears to develop in parallel with the reduction of intracortical inhibition (Maya Vetencourt et al., 2008).

Recently experiments carried out on cats' visual cortex have shown that the direction of orientation shifts may depend on the duration of the adaptation. Short adaptation produces mostly repulsive shifts while longer adaptation induces attractive shifts. Moreover, successive adaptations to orientation potentiate the responses to the adapter as if the neuron kept a memory trace of the adapter during the previous application (Ghisovan et al., 2008).

Spatial frequency (SF) tuning was the property investigated in this study. This feature exhibits some comparable characteristics to orientation, such as tuning curves leading to a preferred SF, but in addition, there are some dissimilar properties, such as an absence of clear clustering or columnar organization (Das, 2005; Issa et al., 2000; Movshon et al., 1978; Sirovich and Uglesich, 2004; Molotchnikoff et al., 2007). Thus, it is important to investigate how neurons react to two consecutive periods of adaptation, and how SF selectivity compares with orientation. In previous animal studies it was shown that following adaptation to a particular grating, the sensitivity of a single neuron to that grating is reduced more than its responsivity

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Abbreviations: Cyc./deg., cycles/degree; LGN, lateral geniculate nucleus; MT, medial temporal area; RF, receptive fields; SEM, standard error of the mean; SF, spatial frequency; V1, primary visual cortex.

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to other gratings, and particularly above and below the adapting frequency (Saul and Cynader, 1989; Movshon and Lennie, 1979). Earlier results have indicated that one period of adaptation to non-preferred SF induces both repulsive and attractive shifts (Bouchard et al., 2008). Human psychophysical analysis showed that adaptation to a sinusoidal grating raises threshold for detecting gratings of similar spatial frequency (Blakemore et al., 1970). In addition, frequent exposure to a single spatial frequency produces band-limited loss in contrast sensitivity centered at that particular spatial frequency (De Valois and De Valois, 1990). Globally then the sensitivity to SF varies depending on conditions with which the stimulus is presented.

The present investigation focused on the cat area 17 at the single cell level, and investigated the modifications of tuning curves for SF following two periods of adaptation. Particularly, as is the case for other properties, we asked if two periods of adaptation are applied, is it possible to increase the magnitude of shifts and the response amplitudes? That is, will the first adaptation leave a "memory" trace that leads to increased cellular responses?

EXPERIMENTAL PROCEDURES

Animals, anaesthesia, ethical approval and surgical procedures

Cats were prepared for electrophysiological recordings in the primary visual cortex. The animal preparation and recording procedures followed the guidelines of the Canadian Council on Animal Care and were approved by the Institutional Animal Care and Use Committee of the University of Montreal. Animals were supplied by the Division of Animal Resources of the University of Montreal.

Animals (2.5–3.5 kg, age 12–24 months) of either sex, sedated with 1 mg/kg intramuscular acepromazine maleate (Atravet, Wyeth-Ayerst, Guelph, ON, Canada) and 0.04 mg/kg intramuscular atropine sulfate (ATRO-SA, Rafter, Calgary, AB, Canada), were anaesthetized with 25 mg/kg intramuscular ketamine hydrochloride (Rogarsetic, Pfizer, Kirkland, QC, Canada). Lidocaine hydrochloride 2% (Xylocaine, AstraZeneca, Mississauga, ON, Canada) was injected subcutaneously as a local anaesthetic during surgery. A tracheotomy was performed for artificial ventilation, and one forelimb vein was cannulated. Animals were then placed in a stereotaxic apparatus. Xylocaine gel 5% (Astra Pharma, Mississauga, ON, Canada) was applied on the pressure points. For the remaining preparations and recording, paralysis was induced with 40 mg and maintained with 10 mg/kg/h gallamine triethiodide intravenous (Flaxedil, Sigma Chemical, St. Louis, MO, USA) administered in 5% dextrose lactated Ringer's nutritive solution. General anaesthesia was maintained by artificial ventilation with a mixture of N_2O/O_2 (70:30) supplemented with 0.5% isoflurane (AErrane, Baxter, Toronto, ON, Canada) for the duration of the experiment. Proper depth of anaesthesia was ensured throughout the experiment by (a) monitoring the EEG for changes in slow-wave and spindle activity and (b) monitoring the electrocardiogram and expired CO_2, for physiological changes associated with a decrease in depth of anaesthesia. In addition the heart rate remained unmodified after skin stimulation.

The end-tidal CO_2 partial pressure was kept constant between 25 and 30 mm Hg. A heating pad was used to maintain a body temperature of 37.5 °C. Tribrissen 30 mg/kg per day, subcutaneous (Schering-Plough, Pointe-Claire, QC, Canada) and 0.1 ml/kg intramuscular Duplocillin (Intervet, Withby, ON, Canada) were administered to the animals to prevent bacterial infection. The pupils were dilated with atropine sulfate 1% (Isopto-Atropine, Alcon, Mississauga, ON, Canada) and the nictitating membranes were retracted with phenylephrine hydrochloride 2.5% (Mydfrin, Alcon, Mississauga, ON, Canada). The loci of the areae centralis were inferred from the positions of the blind spots, which were ophthalmoscopically focused and back projected onto a translucent screen. In order to verify the stability of the eye this procedure was repeated at the end of tests. Plano contact lenses with artificial pupils (5 mm diameter) were placed on the cat's eyes to prevent the cornea from drying (University of Montréal, PQ, Canada).

A craniotomy (6×6 mm^2) was performed over the primary visual cortex (area 17/18, Horsley-Clarke coordinates P0–P6; L0–L6). The underlying dura mater was removed, and once the electrodes were positioned in area 17, the hole was covered with warm agar (3–4% in saline). Melted wax was poured over the agar to provide stability.

At the end of each experiment, which lasted ~48 h, the anaesthetized animal was administered a lethal dose of pentobarbital sodium 100 mg/kg (Somnotol, MTC Pharmaceuticals, Cambridge, ON, Canada) by intravenous injection.

Electrophysiological recordings

Multi-unit activity in the visual cortex was recorded by two sets of tungsten microelectrodes 2–10 MΩ at 1 kHz (Frederick Haer & Co, Bowdoinham, ME, USA). Each set, consisting of a four microelectrode linear array (inter-electrode spacing of 400 μm) enclosed in stainless steel tubing, was controlled by a separate micromanipulator. The signal from the microelectrodes was amplified, band-pass filtered (300 Hz–3 kHz), digitized and recorded with a 0.05 ms temporal resolution (Spike2, CED, Cambridge, UK). We recorded at cortical depths between 250 and 1500 μm (mean: 650 μm). Action potentials were sorted out using a window discriminator for further off-line analyses. Multiunit signals from one electrode usually included two (up to three) well-isolated single units. The spike sorting method was based on cluster classification in reduced space (Spike2, CED, Cambridge, UK). Only one site was tested a time. The stability of each cell's activity across conditions was verified qualitatively by visual control of the cluster's disposition and of the waveform's shape as described in Bouchard et al. (2008).

Visual stimulation

Stimulation was monocular for the dominant eye (the opposite eye was covered). After clearly detectable activity was obtained, the multiunit receptive fields (RF) were mapped as the minimum response fields (Barlow et al., 1967) by using a hand-held ophthalmoscope. RF edges were determined by moving a light bar from the periphery toward the centre until a response was elicited. Eye-screen distance was 57 cm. These preliminary tests revealed qualitative properties such as dimensions, velocity preference, orientation and directional selectivity. Visual stimuli were generated with a VSG 2/5 graphic board (Cambridge Research Systems, Rochester, UK) and displayed on a 21-in. monitor (Sony GDM-F520 Trinitron, Tokyo, Japan) placed 57 cm from the cat's eyes, with 1024×768 pixels, running at 100 Hz frame refresh. Stimuli were a drifting sine-wave grating patch (2° to 5°) covering the excitatory RF (Maffei and Fiorentini, 1973).

Patch characteristics were set to evoke optimal responses: contrast at 50%, mean luminance at 40 cd.m^2, optimal orientation and temporal frequencies were set within the 22.5–270° and 1.0–2.0 Hz range, respectively. The blank screen was uniformly gray (35 cd.m^2). In all cases the above parameters were chosen with the aim of evoking the maximal discharges. V1 neurons are known to respond well to sine wave drifting gratings (Bardy et al., 2006; Movshon et al., 1978).