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LONG ADAPTATION REVEALS MOSTLY ATTRACTIVE SHIFTS OF ORIENTATION TUNING IN CAT PRIMARY VISUAL CORTEX

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Abstract—In the adult brain, sensory cortical neurons undergo transient changes of their response properties following prolonged exposure to an appropriate stimulus (adaptation). In cat V1, orientation-selective cells shift their preferred orientation after being adapted to a non-preferred orientation. There are conflicting reports as to the direction of those shifts, towards (attractive) or away (repulsive) from the adapter. Moreover, the mechanisms underlying attractive shifts remain unexplained. In the present investigation we show that attractive shifts are the most frequent outcome of a 12 min adaptation. Overall, cells displaying selectivity for oblique orientations exhibit significantly larger shifts than cells tuned to cardinal orientations. In addition, cells selective to cardinal orientations had larger shift amplitudes when the absolute difference between the original preferred orientation and the adapting orientation increased. Conversely, cells tuned to oblique orientations exhibited larger shift amplitudes when this absolute orientation difference was narrower. Hence, neurons tuned to oblique contours appear to show more plasticity in response to small perturbations. Two different mechanisms appear to produce attractive and repulsive orientation shifts. Attractive shifts result from concurrent response depression on the non-adapted flank and selective response facilitation on the adapted flank of the orientation tuning curve. In contrast, repulsive shifts are caused solely by response depression on the adapted flank. We suggest that an early mechanism leads to repulsive shifts while attractive shifts engage a subsequent late facilitation. A potential role for attractive shifts may be improved stimulus discrimination around the adapting orientation.

Key words: vision, cortical plasticity, adaptation, orientation selectivity.

In feline 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). For contour orientation, preference appears in the primary visual cortex (V1) as an emergent property that is established early—before or at eye opening—and is considered relatively stable (Chiu and Weliki, 2003). After adult-like tuning levels are reached, a process that requires patterned visual experience (Crair et al., 1998), neurons display little variability in their orientation tuning properties through time (Mazer et al., 2002). On the other hand, visual history has long been known to affect perception (Gibson and Radner, 1937), prompting the search for adaptive processes in the visual system (e.g. Saul and Cynader, 1989).

At the neuronal level, repeated or prolonged exposure to a stimulus (adaptation) is classically known to reduce neurons' responsiveness to that same stimulus (Maffei et al., 1973). In recent years, this classical view of adaptation was challenged by several studies in which adaptation to a non-preferred orientation was shown to transiently modify neurons' preferred orientation (Müller et al., 1999; Dragoi et al., 2000, 2001a,b; Yao and Dan, 2001). In cat V1, following adaptation on one flank of the bell-shaped orientation tuning curve, neuronal responses to the adapting non-preferred orientation were reduced, while responses to orientations on the non-adapted flank remained similar or were enhanced (Dragoi et al., 2000). The resulting tuning curve appeared to slide away from the adapting flank, in what was described as a repulsive shift. Those shifts away from the adapter were the most frequent outcome of a 2 min adaptation. However, Dragoi et al. (2000) also reported a small number of attractive shifts which they considered peculiar. Moreover, in a study focused on synchrony, we recently reported attractive shifts of orientation tuning (Ghisovan et al., 2008a). In another series of papers, we investigated the effect of repeated adaptation on orientation and spatial frequency tuning (Bouchard et al., 2008; Ghisovan et al., 2008b). In both studies, a substantial proportion of attractive tuning shifts were observed. Yet, results from previous reports fail to disclose the conditions in which attractive orientation shifts occur, and the underlying mechanisms. Therefore, the present investigation examines the relationship between the original orientation bias and shift directions. Particularly what is the differential effect of adaptation on tuning curves of units exhibiting cardinal (vertical and horizontal) or oblique orientation preference? We specifically studied how the directions and the magnitude of the shifts depended on the cardinal or oblique orientations. In addition, we propose that the repulsive and attractive shifts may be attributed to two distinct mechanisms which could account for attractive or repulsive shifts respectively. Therefore, we suggest that orientation tuning displacements are attributed to two distinct putative mechanisms.

EXPERIMENTAL PROCEDURES

Animals, anaesthesia and surgical procedures

Twelve adult cats (2.5–3.5 kg, age 12–24 months) of either sex, sedated with acepromazine maleate (Atravet, Wyeth-Ayerst, Guelph, ON, Canada; 1 mg kg^{-1}, intramuscular) and atropine

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Abbreviations: GABA, γ-aminobutyric acid; LGN, lateral geniculate nucleus; MT, MEDIAL TEMPORAL AREA; OSI, orientation selectivity index; RF, multi-unit receptive field; SEM, standard error of the mean; V1, primary visual cortex.

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sulfate (ATRO-SA, Rafter, Calgary, AB, Canada; 0.04 mg kg^{-1}, intramuscular), were anaesthetized with ketamine hydrochloride (Rogarsetic, Pfizer, Kirkland, QC, Canada; 25 mg kg^{-1}, intramuscular). Lidocaine hydrochloride (Xylocaine, AstraZeneca, Mississauga, ON, Canada; 2%) 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 (Astra Pharma, Mississauga, ON, Canada; 5%) was applied on the pressure points. For the remaining preparations and recording, paralysis was induced with 40 mg and maintained with 10 mg kg^{-1} h^{-1} gallamine triethiodide (Flaxedil, Sigma Chemical, St. Louis, MO, USA; intravenous) 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 change 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 heated pad was used to maintain a body temperature of 37.5 °C. Tribrissen (Schering-Plough, Pointe-Claire, QC, Canada; 30 mg kg^{-1} per day, subcutaneous) and Duplocillin (Intervet, Withby, ON, Canada; 0.1 ml kg^{-1}, intramuscular) were administered to the animals to prevent bacterial infection. The pupils were dilated with atropine sulfate (Isopto-Atropine, Alcon, Mississauga, ON, Canada; 1%) and the nictitating membranes were retracted with phenylephrine hydrochloride (Mydfrin, Alcon, Mississauga, ON, Canada; 2.5%). The loci of the areae centrales 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) was performed over the primary visual cortex (area 17/18, Horsley-Clarke coordinates P0–P6; L0–L6). The underlying dura 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 anesthetized animal was administered a lethal dose of pentobarbital sodium (Somnotol, MTC Pharmaceuticals, Cambridge, ON, Canada; 100 mg kg^{-1}) by intravenous injection.

Ethical approval

Domestic cats (*Felis catus*) were prepared for electrophysiological recordings from 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.

Electrophysiological recordings

Multi-unit activity in the visual cortex was recorded by two sets of tungsten microelectrodes (Frederick Haer & Co, Bowdoinham, ME, USA; 2–10 MΩ at 1 kHz). 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, England; DataWave Technologies, Longmont, CO, USA in initial experiments). 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. Multi-unit 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). The stability of each cell's activity across conditions was verified qualitatively by visual control of the clusters disposition and of the waveforms shape.

Visual stimulation

Stimulation was monocular (dominant eye, the opposite eye was covered). After clearly detectable activity was obtained, the multi-unit 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, England) 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 drifting sine-wave grating patch (~2° to 5°) covering the excitatory RF (Maffei and Fiorentini, 1973).

Patches characteristics were set to evoke optimal responses: contrast at 80%, mean luminance at 40 $Cd.m^2$, optimal spatial and temporal frequencies set within the 0.1–0.5 cycles×deg^{-1} 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).

Protocol

After manual RF characterization, nine oriented stimuli centred on the preferred orientation were selected and used for the rest of the experiment. With a 22.5° interval between orientations, tuning curves covered 180°. Test orientations were presented in random order. Each oriented stimulus was presented in blocks of 25 trials lasting 4.1 s each, with a random inter-trial interval (1.0–3.0 s) during which no stimuli were presented. Thus, a recording session lasted for 25–30 min. Peri-stimulus time histograms were recorded.

Once control orientation tuning curves were characterized, an adapting stimulus was presented continuously for 12 min. The adapting stimulus was a drifting grating whose orientation was randomly selected in the range 22.5 to 67.5° off of the neuron's preferred orientation. It has been shown previously that larger gaps between optimal and adapting orientations are less efficient in inducing orientation shifts. All other stimulus parameters were kept constant, at control values, throughout the recordings. During this adaptation period no recordings were performed. Immediately after adaptation, orientation tuning curves were measured starting with the adapting and control preferred orientations, while the remaining orientations were recorded in random order. Following a recovery period of 60 to 90 min, another tuning curve measurement was performed.

Data analysis

Once single cells were sorted out off-line from multi-unit spike trains accumulated during data acquisition, orientation (θ) tuning