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CONTRAST ADAPTATION IS SPATIAL FREQUENCY SPECIFIC IN MOUSE PRIMARY VISUAL CORTEX

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Abstract—Contrast adaptation, generated by prolonged viewing of a high contrast spatial pattern, is known to reduce perceptual sensitivity to subsequently presented stimuli of similar spatial frequency (SF). Neural correlates of this pattern-specific contrast adaptation have been described in several classic studies in cat primary visual cortex (V1). These results have also recently been extended to mice, which is a genetically manipulable animal model. Here we attempt to parse the potential mechanisms contributing to this phenomenon by determining whether the SF specificity of contrast adaptation observed in mouse V1 neurons depends on the spike rate elicited by the adapting gratings. We found that adapting stimuli that drove a neuron more strongly generally produced more adaptation, implicating an intrinsic or fatigue-like process. Importantly, we also observed that slightly stronger contrast adaptation was produced when the adapting SF matched the test SF even when matched and nonmatched adapting gratings elicited similar spike rates indicating extrinsic or network processes contribute as well.

Key words: vision, sinusoidal gratings, spatial frequency, contrast adaptation, animal model, electrophysiology.

INTRODUCTION

In vision research, spatial contrast is defined as relative luminance across space. This stimulus attribute, henceforth referred to simply as contrast, is processed in the visual system as early as center-surround antagonism in the retina (Kaplan and Shapley, 1986). Contrast is critical for the detection of edges that can define object borders, textures, lighting conditions and shadows. There is perceptual and physiological evidence that the visual system possesses several self-calibration mechanisms to quickly adjust its sensitivity to contrast according to the recent stimulus history, and this is called contrast adaptation (see Kohn, 2007 for a recent review).

Perceptual studies of contrast adaptation show that prolonged viewing of a high-contrast adapting pattern can produce a perceived fading of the adapting stimulus and reduce sensitivity to subsequently presented low contrast test stimuli, but it can also improve discrimination around the adapting contrast (Blakemore and Campbell, 1969b; Greenlee and Heitger, 1988; Foley and Chen, 1997; Abbonizio et al., 2002). Of particular interest is the finding that contrast adaptation is strongest when the spatial frequency (SF) of the test stimulus matches that of the adapting stimulus (Blakemore and Campbell, 1969a,b; Blakemore and Nachmias, 1971; Blakemore et al., 1973; Snowden and Hammett, 1996). This pattern-specificity may provide clues about the possible mechanisms underlying contrast adaptation.

The neurophysiological correlates of perceptual adaptation have most frequently been studied in the primary visual cortex (V1) of cats and primates. V1 neurons have sigmoidal contrast response functions when the spike rate is plotted against stimulus contrast, and adaptation to a high contrast pattern causes this function to shift rightward and center the steepest part of the curve near the adapting contrast (Movshon and Lennie, 1979; Ohzawa et al., 1982, 1985; Sclar et al., 1989; Bonds, 1991; Ibbotson, 2005). As with psychophysical studies, the magnitude of adaptation shown by V1 neurons depends on the SF of the adapting and test stimuli (Movshon and Lennie, 1979; Ohzawa et al., 1985; Saul and Cynader, 1989), although this may not be the case for antecedent areas such as the dorsal lateral geniculate nucleus (dLGN; Duong and Freeman, 2007).

We recently explored pattern selectivity of contrast adaptation in mouse V1 with the aim of establishing similarities between a genetically tractable species and more traditional animal models of vision (LeDue et al., 2013). Neurons in mouse V1 share several properties with those described in cats and primates including retinotopic organization, orientation selectivity, and most important for this work, SF tuning and contrast adaptation (Kalatsky and Stryker, 2003; Niell and Stryker, 2008; Stroud et al., 2012). When mouse V1 neurons were tested at their preferred SF they adapted more when the adapting grating matched the test grating, which provides evidence of SF-specificity of contrast adaptation similar to what occurs in other species. Several explana-

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Abbreviations: AUC, area under the curve; cpd, cycles per degree; dLGN, dorsal lateral geniculate nucleus; F_0, mean time-averaged response; F_1, first Fourier coefficient of the response; M, matched adaptation; N.M., nonmatched adaptation; SDFs, spike density functions; SF, spatial frequency; TF, temporal frequency; V1, primary visual cortex.

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tions of how this specificity might occur have been raised in previous work in cats. The test stimuli of LeDue et al. (2013) were always presented at each neuron's peak SF, and matched adaptation (adapting SF = test SF) elicited higher spike rates than nonmatched adaptation (adapting SF ≠ test SF), so this specificity might reflect an intrinsic or fatigue-like process where higher firing rates elicited by preferred stimuli produce more adaptation (as proposed by Vautin and Berkley, 1977). Conversely, several examples of robust adaptation arising from stimuli that do not evoke strong responses indicate specificity need not be rooted in fatigue (e.g. Ohzawa et al., 1985; Crowder et al., 2006; Dhruv et al., 2011). In these cases adaptation is proposed to come from sources extrinsic to the recorded neuron, such as being inherited from broadly tuned afferents or implemented through local cortical networks.

In the present study we attempted to disambiguate possible mechanisms underlying contrast adaptation by examining SF-specificity of adaptation using adapting gratings that elicited approximately equal firing rates. For each mouse V1 neuron, two adapting SFs were selected that straddled the neuron's peak SF, and the test grating SF was matched to one of these stimuli. We found that when spike rates were equated between matched and nonmatched adaptation, thereby equalizing any potential intrinsic or fatigue-like processes, SF-specificity of contrast adaptation was still present but substantially weaker than previously reported.

EXPERIMENTAL PROCEDURES

Animals

Experiments were performed on male C57BL/6J mice, aged 2–7 months, weighing between 22 and 33 g (n = 14). All experimental procedures were conducted in accordance with the guidelines of the Canadian Council on Animal Care and were approved by the Dalhousie University Committee on Laboratory Animals.

Physiological preparation

Animals were pre-medicated with an injection of chlorprothixene (Sigma Aldrich, 5 mg/kg, i.p.), then placed in a custom face-mask and anesthetized with isoflurane in oxygen for the remainder of the experiment (2.5% isoflurane during induction, 1.5% during surgery and 0.5% during recording; Pharmaceutical Partners of Canada). Additional doses of chlorprothixene were given every four hours. Once anesthetized, mice were maintained at a body temperature of 37.5 °C using a heating pad, and their corneas were protected by frequent application of optically neutral silicone oil (30,000 cSt, Sigma Aldrich). Pupils were not dilated so there was presumably a large depth of focus, and paralysis was not induced because previous electrophysiological studies of mouse V1 have found eye movements under anesthesia are negligible (Wang and Burkhalter, 2007; Niell and Stryker, 2008; Gao et al., 2010).

To expose V1, the scalp was removed, a head post was secured using dental epoxy, then a craniotomy (~1 mm^2) was made 0.8 mm anterior and 2.3 mm lateral to lambda (Paxinos and Franklin, 2001). The craniotomy was filled with warm saline to prevent dehydration of the cortical surface. Extracellular recordings were made with glass micropipettes that were filled with 2 M NaCl and had a tip diameter of 2–3 μm. Signals from individual cells were isolated, amplified, filtered, and acquired with a CED 1401 interface and Spike2 software (Cambridge Electronic Designs, Cambridge, UK) sampled at 25 kHz. Online analyses were performed on the transistor–transistor logic (TTL) output from a window discriminator (Dagan, Minneapolis, MN, USA), but spike sorting and all subsequent analyses were performed offline.

Visual stimuli

Once a visually responsive neuron was isolated, the receptive field was mapped manually with bars and spots produced with an ophthalmoscope. Computer generated visual stimuli were programed in MATLAB (Math Works, Natick, MA, USA) using the Psychophysics Toolbox extension (Brainard, 1997; Pelli, 1997), and were presented on a calibrated CRT monitor (LG Flatron 915FT Plus 19 inch display, 100 Hz refresh, 1024 × 768 pixels, mean luminance = 30 cd/m^2) at a viewing distance of 15–30 cm. All stimuli were presented for 8–12 repetitions.

On-line tuning functions for orientation preference, receptive field size, and spatio-temporal tuning were calculated to select appropriate stimulus parameters for the adaptation protocol. Orientation selectivity was tested with square-wave gratings of 8 orientations presented in random order (22.5° spacing). For each orientation, the grating first appeared and remained stationary for 0.5 s, then drifted in one direction for 2 s, then paused for 0.5 s, then drifted in the opposite direction for 2 s, then paused for a final 0.5 s. Preferred stimulus size was tested in two ways: (1) with a circular aperture containing a sine-wave grating; and (2) with a full field grating with a circular aperture of gray in the center. Six different stimulus diameters were presented for 2 s each in random order (8°, 12°, 24°, 32°, 48°, 64°). In addition to testing size tuning, these stimuli served as a confirmation that the monitor was centered on the neuron's receptive field. The stimulus size used for subsequent tests was chosen as either the diameter where the size tuning function began to asymptote in neurons lacking surround suppression, or the peak of the function for neurons that showed surround suppression. Preferred spatial and temporal frequencies (TF) for each neuron were determined with sine-wave gratings of the preferred orientation and drift direction presented in an aperture of the preferred size. Thirty-six combinations of SFs (0.01, 0.02, 0.04, 0.08, 0.16, 0.32 cycles per degree (cpd)) and TFs (0.25, 0.50, 1, 2, 4, 8 Hz) were presented for 2 s each in random order. A gray of mean luminance was presented for 0.5 s between all grating stimuli used to generate on-line tuning functions.

A top-up contrast adaptation protocol was used to facilitate comparisons with previous mouse experiments, as well as original experiments performed in cats and primates (Movshon and Lennie, 1979; Duong and