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Effects of contrast, spatial frequency, and stimulus duration on reaction time in rats

Daniel D. Kurylo [a,*], Caroline Chung [a], Sowmya Yeturo [a], Joseph Lanza [a], Arina Gorskaya [a], Farhan Bukhari [b]

[a] *Department of Psychology, Brooklyn College CUNY, Brooklyn, NY 11210, United States*
[b] *Department of Computer Science, The Graduate Center CUNY, New York, NY 10016, United States*

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ABSTRACT

Early visual processing in rats is mediated by several pre-cortical pathways as well as multiple retinal ganglion cell types that vary in response characteristics. Discrete processing is thereby optimized for select ranges of stimulus parameters. In order to explore variation in response characteristics at a perceptual level, visual detection in rats was measured across a range of contrasts, spatial frequencies, and durations. Rats responded to the onset of Gabor patches. Onset time occurred after a random delay, and reaction time (RT) frequency distribution served to index target visibility. It was found that lower spatial frequency produced shorter RTs, as well as increased RT equivalent of contrast gain. Brief stimulus presentation reduced target visibility, slowed RTs, and reduced contrast gain at higher spatial frequencies. However, brief stimuli shortened RTs at low contrasts and low spatial frequencies, suggesting transient stimuli are more efficiently processed under these conditions. Collectively, perceptual characteristics appear to reflect distinctions in neural responses at early stages of processing. The RT characteristics found here may thereby reflect the contribution of multiple channels, and suggest a progressive shift in relative involvement across parameter levels.

1. Introduction

Reaction time (RT) to stimulus onset includes the processing of basic stimulus components. The time scale of stimulus processing reflects physiological properties of neurons, such as stimulus sensitivity, response time, and conduction velocity. Change in RT characteristics across levels of stimulus parameters may therefore be used to explore mechanisms mediating early stimulus processing.

In humans, RT differences across contrast, spatial frequency, and stimulus duration correspond to response properties of primate pre-cortical channels. Low spatial frequency, low contrast, transient stimuli, which are associated with magnocellular processing, are distinguished from higher spatial frequency, higher contrast, sustained stimuli, for which parvocellular processing plays an increasing role. Examining RT across spatial frequency in humans, Felipe, Buades, and Artigas (1993) found that RT operates differently near contrast threshold than at higher contrasts. Results suggest a transformation between two mechanisms, one for transient, low spatial frequency stimuli, and another for sustained, higher spatial frequency stimuli. Consistent with this distinction, the use of shorter-duration, more transient stimuli, had little effect on RT at low spatial frequency, but increased RT with higher spatial frequency, low contrast stimuli (Murray & Plainis, 2003).

In addition, RT characteristics across contrast parallel gain properties in early visual processing. Murray and Plainis and Murray (2000), Murray and Plainis (2003) and Plainis and Murray (2000) derived a RT equivalent of contrast gain, in terms of change in RT across the reciprocal of contrast. At low spatial frequency, the reciprocal contrast function possessed shallow slopes (reflect high contrast gain, as seen with magnocellular processing), whereas slopes were steeper at higher spatial frequencies (reflecting lower gain, as seen with parvocellular processing). Across contrast, a discontinuity existed in the reciprocal contrast function, which is consistent with the operation of two mechanisms, one for low contrast, high gain, and another for higher contrast, lower gain.

Whereas RT across stimulus parameters in humans is consistent with properties of pre-cortical channels in primates, less is known about the functional capacities of early visual processing in rats. Rats possess multiple retinal ganglion cell types, as well as several pre-cortical pathways that relay through superior colliculus and thalamic nuclei. Stimulus components conveyed by each pathway, and their association with perceptual capacities, are less understood.

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[*] Corresponding author at: Psychology Department, Brooklyn College CUNY, 2900 Bedford Avenue, Brooklyn, NY 11210, United States. Fax: +1 718 951 4814.
E-mail address: dkurylo@brooklyn.cuny.edu (D.D. Kurylo).

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Several types of retinal ganglion cells are described in rats, distinguished by morphological as well as electrophysiological properties, including conduction velocity (Hale & Sefton, 1978). Some comparisons may be drawn between rat retinal ganglion subtypes and cat X-, Y-, and W-cell properties, although significant differences exist between species (Heine & Passaglia, 2011; Sefton & Dreher, 1985). In rats, retinal ganglion cells include large axon, fast conducting Class I cells (Ni & Dreher, 1981; Perry, 1979), which share some properties with cat Y-cells. A second category is medium size Class IIa cells (Ni & Dreher, 1981). A third group is comprised of thin and medium size axon Type IIb, IIIa, and IIIb cells (Ni & Dreher, 1981), which share some characteristics with W-cells. Recording from optic chiasm and optic tract, Heine and Passaglia (2011) examined receptive field properties of rat retinal ganglion cells. In addition to a small percentage of cells with slower response rates and larger receptive fields, response properties distinguished cells with fast response rates that possessed either non-linear (Y-like) or linear (X-like) spatial summation, although unlike Y- and X-cell distinction in cats, both cell types had similar receptive field sizes.

In rats, retinal ganglion cells project along several pathways, including those to (1) superior colliculus, (2) ventral lateral geniculate nucleus of the thalamus (vLGN), and (3) dorsal lateral geniculate nucleus (dLGN). The pathway to superior colliculus continues on to the lateral posterior nucleus of the thalamus (LPN), then to extrastriate and other cortical areas (Dean, 1981; Hughes, 1977). The vLGN pathways play a role in oculomotor control (Brauer & Schober, 1982), pupillary reflex (Young & Lund, 1998) and circadian rhythm (Harrington, 1997). A third visual pathway passes to dLGN, then on to primary visual cortex (Dean, 1981; Hale & Sefton, 1978; Ribak & Peters, 1975; Zarrinpar and Callaway, 2006). Retinal ganglion cells examined at the level of dLGN mainly display Y- and W-cell characteristics (Fukuda et al., 1979; Hale, Sefton, & Dreher, 1979; Lennie & Perry, 1981), and include cells with both non-linear and linear spatial summation (Lennie & Perry, 1981).

In sum, primates possess multiple pre-cortical channels that correspond to different ranges of temporal/spatial parameters. Further, this distinction is reflected by RT characteristics across parameter levels. For rodents, multiple processing systems are found at the level of retinal ganglion cells, as well as with pre-cortical and cortical pathways. The question addressed in the current study is whether RT to stimulus onset in rats also reflects a multi-channel system.

Animal psychophysics employs behavior as indirect measure of perceptual capacities. For rodents, operant responses on visual discrimination tasks have been used to determine perceptual thresholds. In measuring detection thresholds in mice, Busse et al. (2011) employed conditions that minimized choice bias and other non-perceptual strategies that may affect measurements. Stimuli appeared at one of two possible locations, and mice nose-poked a choice port associated with the location of the stimulus. Contrast sensitivity was determined across spatial frequency, and found to be similar to that found in rats. Histed, Carvalho, and Maunsell (2012) monitored lever press responses to a visual change detection task in head-fixed mice. It was found that contrast thresholds in mice were similar to those found in humans for eccentric viewing, where sampling density corresponds to that of mouse retina. Behavioral measurements of contrast sensitivity in rats have identified a sensitivity range of approximately 0.04–0.8 cycles/deg, with peak sensitivity at approximately 0.11 cycles/deg (Birch & Jacobs, 1979; Keller et al., 2000; Legg, 1984; Meier, Flister, & Reinagel, 2011). Contrast thresholds have been based upon behavioral responses, such as identifying the presence of sinusoidal gratings from multiple choice locations (Keller et al., 2000), or by indicating whether or not a grating had been presented (Meier, Flister, & Reinagel, 2011). These previous measurements have characterized the contrast response function in rats, and provide measures of relative sensitivity for the spatial frequencies used here.

The present study expands behavioral measurements in rats by examining visual detection across not only spatial frequency and contrast, but also stimulus duration. It was hypothesized that distinctions in early visual pathways in rats will be reflected by variation in RT across stimulus parameters. Specifically, it was predicted that low spatial frequency stimuli will produce faster RT and higher RT equivalent contrast gain, compared with higher spatial frequency. In addition, if higher spatial frequencies are processed by a slower responding system, then shortening stimulus duration should produce a disproportionate effect with higher spatial frequency, lower contrast stimuli. To test these predictions, RT measurements were examined in rats trained to respond to the onset of Gabor patches, which varied in contrast, spatial frequency, and duration.

2. Methods

Subjects: Five Long-Evans hooded rats served as subjects. Animals were water restricted and received water as reward during sessions, as well as ad lib for 1 h following sessions. Sessions occurred on four or five days each week, and animals were allowed water ad lib on remaining days. This study was conducted in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals, and approved by the Institutional Animal Care and Use Committee of Brooklyn College.

Apparatus: Behavioral measurements were made in an operant conditioning chamber (Fig. 1) in which a metal funnel extended 3 cm outside the front panel. Rats viewed stimuli through holes in the funnel positioned over each eye. Placement of the rat's head completely within the funnel was monitored with an infrared light beam positioned at the tip of the funnel. Stimuli were presented on a computer monitor (Trinitron CPD 4401) controlled by a graphics adaptor (NVidia GeForce FX5200) set to 1280 × 1024 pixel resolution and 60 Hz. Stimulus generation and data collection were controlled by customized computer software (Bukhari and Kurylo, 2008).

Stimulus conditions: Rats viewed stimuli at a distance of 24 cm and elevated by 10°. Stimuli consisted of Gabor patches on a gray background (22.3 cd/m^2). Luminance levels were linearized across a range of 2.9–42.2 cd/m^2.

Measurements were made at three separate spatial frequencies: 0.21 cpd, which corresponds to near peak sensitivity for Long-Evans rats, and 0.40 and 0.46 cpd, which correspond to the high-frequency limb of the rat CSF (Birch & Jacobs, 1979; Legg, 1984). Stimuli subtended a visual angle of 14.0°, in which approximately 2.5, 5.5, and 6.5 cycles were visible for the 0.21, 0.40, and 0.46 cpd stimuli, respectively.

In each session, five sequential contrasts levels were selected from Michelson contrasts of .16, .22, .28, .36, .52, .71, and .88. For higher spatial frequencies, higher ranges of contrasts were used. In addition, each session contained a no-stimulus condition. Contrast levels were presented in random order, with approximately 170 trials per session.

For all combinations of spatial frequency and contrast, measurements were made for stimulus durations of 33 and 1050 ms. Stimulus duration was linked to the monitor's vertical synchronization signal. Reaction time distributions were based upon approximately 90 trials, collected across multiple sessions. Measurements were made with a fully within-subjects design, in which each rat received all levels of contrast, spatial frequency, and duration.