Motion-defined contour processing in the early visual cortex

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Submitted 13 September 2011; accepted in final form 4 June 2012

Even though psychophysical studies have demonstrated the importance of relative motion cues in figure-ground segregation, the neural mechanism to detect these motion-defined boundaries is still unknown. Single-unit recording experiments by Hubel and Wiesel (1962) on cats showed that orientation selectivity for luminance edges first originates in brain areas as early as the primary visual cortex (V1). Simple cells in V1 have receptive fields with elongated excitatory and inhibitory areas lying adjacent and parallel to one another, which act as filters that perform linear summation of light intensity in their receptive fields. Hubel and Wiesel (1962) proposed a model in which receptive fields of simple cells are constructed by inputs from on-center and off-center lateral geniculate nucleus (LGN) cells arranged in alternating columns. A similar question could be asked in the case of motion-defined boundaries, i.e., where does orientation selectivity for these boundaries originate and what is the neural mechanism behind it?

Several single-unit studies have tried to locate the brain areas responsive to motion-defined boundaries and understand the underlying neural mechanism. Using temporal texture bars (dynamic random dot patterns moving on a stationary random dot background), Albright (1992) reported that most of the neurons in the area middle temporal (MT) of macaque monkeys were selective for the orientation of these bars, and Chaudhuri et al. (1997) found that more than half of the neurons in the V1 area of macaque monkeys were selective for the orientation of these bars. Marcar et al. (2000) also found a small fraction of neurons in macaque V1 and V2 that were selective for the orientations of motion-defined boundaries. In macaque V4, Mysore et al. (2006) reported a sizeable fraction of neurons (10–20%) that were selective for kinetic patterns. Both these studies (Marcar et al. 2000 and Mysore et al. 2006) used moving random dot texture patterns to generate motion-defined boundaries that were held stationary in the receptive field of a neuron. Zeki et al. (2003) found that the majority of neurons in macaque V3 and V3A were selective to the orientation of motion-defined bars made of random dot texture patterns. These studies suggest that motion-defined boundary selective neurons are present in different visual areas such as the V1, V2, V3, V3A, V4, and MT, with higher cortical areas containing a greater percentage of such cells. However, there is a potential problem with the random dot texture patterns used in all these studies, because such textures contain a broad range of spatial frequencies. Hence, these texture patterns will contain energy within the luminance passband of a neuron, and, therefore, the response of a neuron could be due to local luminance (first order) signals and not motion difference (second order) cues. Such luminance signals or artifacts can be avoided by using a sinusoidal grating as a texture pattern, with

NATURAL SCENES abundantly contain local variations in luminance that facilitate figure-ground segregation. However, these first-order cues often introduce ambiguities and make figure-ground segregation a difficult task (Marr 1982). For example, shadows introduce false luminance boundaries that do not correspond to objects’ boundaries in a visual scene. However, our visual system is able to distinguish these false boundaries from real ones using other cues, including second-order information such as texture, contrast, color, or motion differences between an object and its background. Particularly, relative motion is a powerful cue that can break camouflage when an object and its background have similar luminance, color, and texture. It can be sufficient to support perception of shape and size of three-dimensional surfaces and for depth ordering (Rogers and Graham 1979; Regan 1989; Regan and Hamstra 1992). This cue arises from motion parallax generated by an observer’s movement or from the exogenous movement of objects in a scene.
the spatial frequency higher than the neuron’s luminance resolution.

A neuroimaging study in human subjects (Reppas et al. 1997) found strong motion boundary-selective signals in early cortical areas (V1 and V2). However, it is unclear from neuroimaging studies whether the neurons in brain areas that respond to motion boundary stimuli are selective for the orientation of these boundaries, as neurons could be responding due to a center-surround antagonistic mechanism (Born and Tootell 1992; Born 2000; Shen et al. 2007) or just to the local motion of the carrier. However, a recent study (Larsson et al. 2010) was able to demonstrate orientation selectivity to motion boundaries in the human visual cortex using an event-related functional MRI adaptation technique. They showed that most of the motion boundary responsive visual areas, such as V2, V3, V3A, V3B, LO1, LO2, hV4, and V7, identified in previous neuroimaging studies (Dupont et al. 1997; Larsson and Heeger 2006; Tyler et al. 2006; Van Oostende et al. 1997; Zeki et al. 2003) are orientation selective. These results argue against the initial notion from neuroimaging studies (Dupont et al. 1997; Van Oostende et al. 1997) that motion boundaries are processed in a specialized “kinetic occipital” brain area (corresponding to LO1, LO2, and V3B).

Neuronal responses to contrast-defined (second order) boundaries have been extensively studied in cat area 18 using single-unit recordings (Zhou and Baker 1993, 1996; Mareschal and Baker 1998a, 1998a, 1999). The contrast-defined boundaries used in these studies were constructed by a coarse spatial scale contrast pattern (envelope), which modulates the contrast of a high spatial frequency sinusoidal grating (carrier; Fig. 1B). Around half of the neurons in area 18 responded to contrast-defined boundaries in a form-cue invariant manner, i.e., they were tuned to the same orientation and motion direction of luminance (first order; Fig. 1A) and contrast-defined (second order) boundaries. In these studies, carrier spatial frequency was constrained to lie outside a neuron’s spatial frequency passband (measured using luminance grating) to ensure that the response of a neuron was genuinely second order and not due to first-order luminance signals. Surprisingly, these neurons showed narrow band-pass tuning for carrier spatial frequency. Song and Baker (2007) subsequently showed that these contrast-defined boundary-responsive neurons also respond to texture-defined boundaries (second order) and again in a form-cue invariant manner. Texture-defined boundaries [illusory contours (ICs)], similar to contrast-defined boundaries, were constructed using high spatial frequency sinusoidal gratings as a carrier, whose phase was modulated by a square-wave envelope. Neurons showed narrow band-pass tuning for carrier spatial frequency of texture-defined boundaries and were selective for similar carrier spatial frequencies. These results suggest that these neurons would be functionally useful in mediating responses to boundaries regardless of the cue that defines them, and this cue invariance to different second-order boundaries might arise from a common nonlinear neuronal mechanism.

Fig. 1. The four types of grating stimuli used in this study and a model. A: luminance modulation (LM) sinusoidal grating with a vertical orientation. B: contrast modulation (CM) grating with a vertically oriented sinusoidal envelope that modulates the contrast of a horizontal high spatial frequency (SF) carrier grating. For unidirectional VM, the carrier in half of the envelope cycles is stationary and in the other half drifts with a specified temporal frequency (TF). D: “bidirectional” VM grating is constructed similarly to unidirectional VM except that the carrier in alternate half-cycles of the envelope drifts with equal speeds but in opposite directions. In the stimulus images here and in the following figures, carrier motion is indicated by thin white arrows, whereas envelope motion is depicted by thick gray arrows. E: schematic model for neuronal responses, in which first- and second-order responses are mediated by separate, parallel pathways. The top pathway is a coarse spatial scale linear filter (F0) that would be responsive to conventional LM gratings. The bottom pathway mediates nonlinear processing of CM and VM gratings. F: nonlinear filter-rectify-filter (FRF) model that responds selectively to CM and VM gratings. The first stage of the model consists of small scale filters (F1) that are selective for high SF carriers. The outputs of these F1 filters are rectified and pooled by a late coarse scale filter (F2), which would be selective for the envelope of CM and VM gratings and would have similar spatiotemporal properties as the F0 filter.
First- and second-order information are thought to be processed by two parallel pathways, based on results from both psychophysics (Ledgeway and Smith 1994; Mather and West 1993; Nishida et al. 1997; Scott-Samuel and Georgeson 1999; Allard and Faubert 2007) and neurophysiology (Zhou and Baker 1993) (for a review, see Baker and Mareschal 2001). First-order information can be detected by neurons acting as quasilinear spatiotemporal filters. To detect second-order information, neurophysiology experiments support a two-stage filter-rectify-filter (FRF) model (Mareschal and Baker 1999), involving early filtering, which is selective for local texture characteristics, followed by rectification, and second-stage coarse-scale spatiotemporal direction selective filtering (Chubb and Sperling 1988; Wilson 1999; Landy and Graham 2004). The second-stage filter has similar properties as the first-order filter, but it pools across a coarser spatial scale. These two parallel pathways converge onto a single neuron. This model has been supported by recent optical imaging (Zhan and Baker 2006) and single-unit neurophysiology (Song and Baker 2007).

In this study, we hypothesized that second-order-responsive neurons in area 18 might also respond selectively to motion-defined boundaries and that they might do so in a form-cue invariant manner. We used high spatial frequency sinusoidal gratings as texture (carrier) patterns and the relative motion between these textures to create motion-defined boundaries (Fig. 1, C and D). To ensure that responses were not simply due to the carrier motion, we carefully optimized the spatial frequency of the carrier grating for each neuron, such that it was well outside of the neuron’s conventional luminance grating resolution. A common motion-defined boundary occurs when an object moves in the visual field. In this case, the retinal image of the background is nearly stationary, but the image of the object moves; we mimicked this situation with a square-wave envelope in which alternate half-cycles contained either a moving or a stationary texture (carrier; Fig. 1C): a “unidirectional” motion boundary. We mimicked motion boundaries generated from motion parallax with a stimulus in which local motions are parallel to the edge, to avoid complexities of accretion-deletion cues (Sary et al. 1994). To assess form-cue invariance, we compared neurons’ responses to motion-defined boundaries with those to contrast- and luminance-defined boundaries. For all three types of boundaries, the envelope was drifting at a low temporal frequency. These comparisons also enabled inferences regarding similarity between underlying neural mechanisms for these different stimuli. In addition, we simulated a model of a generic area 18 neuron receiving inputs from two parallel pathways that separately process first- and second-order information, as described above, to see whether the selectivity of neurons to contrast- and motion-defined boundaries can be explained by a single such model.

We found that all contrast-defined boundary-responsive neurons also responded to unidirectional motion boundaries in a form-cue invariant manner and with similar carrier spatial frequency tuning. Some, but not all, contrast-defined boundary-responsive neurons also responded to bidirectional motion boundaries, typically with weaker responses than to unidirectional boundaries. The pattern of selectivity of these neurons matched well with the selectivity of the simulated model. This suggests that motion-defined boundaries are processed by the same nonlinear neural mechanism that processes contrast-defined boundaries.

MATERIALS AND METHODS

Animal preparation. All experimental procedures were reviewed and approved by the Animal Care Committee of McGill University. Cats were anesthetized using isoflurane-oxygen and maintained with isoflurane inhalation. Methylcellose gel (1%) was applied to protect the corneas, and a rectal thermistor inserted to monitor temperature during surgery. Intravenous cannulation was performed, and a loading dose of propofol (5 mg/kg) was delivered and then maintained at 6 mg·kg⁻¹·h⁻¹ for subsequent surgery. ECG leads were connected to monitor heart rate. Tracheal intubation was performed to provide a secure airway, and the animal was secured on a stereotaxic apparatus. A respirator (Ugo Basile) was connected to deliver a mixture of O₂-N₂O (30:70 ratio). End-tidal CO₂ was monitored with a capnometer (Hewlett-Packard) and maintained between 28 and 36 mmHg by adjusting the respirator stroke volume. A pulse-oximeter sensor (Ninon) measured blood oxygen. Eye drops [atropine (1%) and phenylephrine (2.5%)] were applied, and neutral contact lenses were inserted. A craniotomy was made to expose area 18 [Horseley-Clarke A3/L4 (Tusa et al. 1979)] as well as a duratomy when recordings were made with multielectrodes. The craniotomy was covered with 2% agarose followed by petroleum jelly. All surgical wounds were infused with bupivacaine (0.5%), and temperature was thermostatically regulated (Harvard Apparatus) at 37.5°C. The animal was anesthetized and paralyzed with a continuous infusion of propofol (5.3 mg·kg⁻¹·h⁻¹), fentanyl (7.4 μg·kg⁻¹·h⁻¹), and gallamine triethiodide (10 mg·kg⁻¹·h⁻¹). Glycopyrrolate (0.005 mg/kg) and dexamethasone (0.6 mg) were delivered intramuscularly every 12 h throughout the experiment. Artifical pupils were positioned, and the appropriate spectacle lenses were selected using a slit retinoscope to provide fraction at a viewing distance of 57 cm. The optic disk was back projected on a tangent screen (Fernald and Chase 1971) and used to estimate the location of the area centralis of each eye (Nikara et al. 1968).

Visual stimuli. Visual stimuli were generated by a Macintosh (Intel 4x2.66 GHz, 6GB, NVIDIA GeForce GT 120) using Matlab with Psychophysics Toolbox (Brainard 1997; Pelli 1997) and presented on a gamma-corrected 17-in. CRT monitor (resolution: 640 x 480 pixels, 10 mg·kg⁻¹·h⁻¹), phenylephrine (2.5%) were applied, and neutral contact lenses were inserted. A craniotomy was made to expose area 18 [Horseley-Clarke A3/L4 (Tusa et al. 1979)] as well as a duratomy when recordings were made with multielectrodes. The craniotomy was covered with 2% agarose followed by petroleum jelly. All surgical wounds were infused with bupivacaine (0.5%), and temperature was thermostatically regulated (Harvard Apparatus) at 37.5°C. The animal was anesthetized and paralyzed with a continuous infusion of propofol (5.3 mg·kg⁻¹·h⁻¹), fentanyl (7.4 μg·kg⁻¹·h⁻¹), and gallamine triethiodide (10 mg·kg⁻¹·h⁻¹). Glycopyrrolate (0.005 mg/kg) and dexamethasone (0.6 mg) were delivered intramuscularly every 12 h throughout the experiment. Artificial pupils were positioned, and the appropriate spectacle lenses were selected using a slit retinoscope to provide fraction at a viewing distance of 57 cm. Conventional luminance modulation (LM) sine-wave gratings (Fig. 1A) with a contrast of 30% were used to measure the luminance passband of a neuron (spatial frequency, orientation, and temporal frequency tuning). Contrast modulation (CM) gratings (Fig. 1B) were constructed by modulating the contrast of a carrier (pattern texture) by a low spatial frequency grating of 100% modulation depth (envelope). The CM grating was drifted with a temporal frequency slightly lower than the neuron’s optimum for LM gratings (Mareschal and Baker 1999). A high spatial frequency sinusoidal grating was used as a carrier, with a contrast of 70%. This carrier grating was held stationary except for measurements of carrier temporal frequency selectivity, in which it was drifted with varying temporal frequency. Motion-defined boundaries were generated using “velocity modulation” (VM) gratings, in which alternate half-cycles of the envelope contained a texture (carrier) moving with different velocities. This envelope was parallel to the motion direction of the carrier (shear), and it drifted in a direction perpendicular to the carrier motion with the same temporal frequency (between 1 and 4 Hz) used for CM gratings. In particular, we tested two types of velocity modulation gratings: unidirectional (Fig. 1C) and bidirectional (Fig. 1D). In unidirectional VM gratings, alternate half-cycles of the envelope contained a moving or stationary carrier. Bidirectional boundaries were created by oppositely moving carriers. For CM gratings, the envelope was sinusoidal, whereas for VM gratings it was a square wave. All stimuli were presented within a
raised cosine-tapered circular window against a gray background of the same mean luminance. On some trials, a uniform gray screen was presented to measure spontaneous activity.

**Extracellular recording.** Spikes from single neurons were recorded extracellularly with glass-coated platinum/iridium and parylene-coated tungsten single-channel microelectrodes (Frederick Haer) and 16 channel multielectrodes (Neuronexus). Spike times were collected through a lab interface (ITC-18, Instrutech) at 100-μs resolution, and, simultaneously, the raw data signals were also acquired with a Plexon recorder (filtered at 5 Hz to 8 kHz, sampled at 40 kHz) and streamed to hard disk for later analysis. Single units were isolated using a window discriminator (Frederick Haer) and displayed on a delay-triggered digital oscilloscope. When recordings with multielectrodes were made, spikes from one selected channel were analyzed online and used to guide the recording protocol (below). A photocell (TAOS, TSL12S) was used for the temporal registration of stimulus onset/offset timing and spike recordings.

A manually controlled bar-shaped stimulus was used to search for neural signals and to determine location of the receptive field, ocular dominance, eccentricity, and approximate optimal orientation. The CRT monitor was centered on the neuron’s receptive field, and the nondominant eye was occluded. Drifting sine-wave luminance gratings were used to measure the neuron’s luminance passband (spatial frequency, orientation, and temporal frequency tuning), with each stimulus condition randomly interleaved and repeatedly presented for 10–20 times. The neuron’s optimal LM grating was then presented in small circular patches in different locations on the screen to more accurately map the receptive field, and the screen was recentered if necessary. To measure the size of the receptive field and check for surround suppression, the optimal LM grating was presented in circular patches of varying sizes centered on the receptive field.

As an initial assessment of responsiveness to second-order stimuli, responses to drifting CM gratings were recorded with a stationary carrier, an envelope orientation at the neuron’s optimal luminance orientation, an envelope spatial frequency equal to or lower than the neuron’s optimal luminance spatial frequency, and an envelope temporal frequency slightly lower than the neuron’s optimal luminance temporal frequency (Zhou and Baker 1996; Mareschal and Baker 1999). A series of carrier spatial frequencies were tested, ranging from values near the screen resolution to the neuron’s luminance passband, to find the optimal carrier spatial frequency. We classified a neuron as second-order responsive if it gave significant responses compared with spontaneous activity (t-test) at relatively high carrier spatial frequencies that were well outside the luminance passband of the neuron and if this spatial frequency tuning was band pass. This condition of band-pass tuning ensured that the neuron’s response was genuinely second order and not due to a nonlinearity in the screen, which might give rise to a luminance signal at the envelope spatial frequency (Zhou and Baker 1994). If the neuron was classified as second-order responsive, then responses to VM gratings were recorded by testing a series of carrier spatial frequencies, with envelope orientation fixed to the neuron’s optimal luminance orientation. If a neuron responded significantly to VM gratings, then envelope orientation tuning was measured using the neuron’s optimal carrier spatial frequency, with carrier orientation always kept perpendicular to the envelope orientation. The temporal frequency of the drifting carriers in VM gratings was then varied to study carrier temporal tuning properties. The temporal frequency response for the carrier of CM gratings was also obtained for comparison with the VM results.

**Analysis.** Neurons were classified as either simple or complex type by measuring the ratio of modulated (first harmonic) to mean responses \([F_F/F_{peak} \text{ -- spontaneous}]\), or “alternating current-to-direct current ratio" to the neuron’s optimal LM grating. If the ratio was >1, the neuron was classified as a simple type cell; otherwise, it was classified as a complex cell (Skottum et al. 1991). Neuronal responses used in the formulas below had spontaneous activity subtracted from them.

Spatial frequency tuning curves were fit with a Gaussian function (DeAngelis et al. 1994) to obtain an estimated optimal spatial frequency, as follows:

\[
R(s_f) = ke^{-(sd - SF_{opt}/a)^2} + R_0
\]

where \(R(s_f)\) is the neuronal response at spatial frequency \(s_f\), and \(k, SF_{opt}, a,\) and \(R_0\) are free parameters. A bootstrap resampling method (Efron and Tibshirani 1993) was used to estimate 95% confidence intervals for the obtained optimal spatial frequency (\(R_{opt}\)) value.

For orientation tuning curves, circular variance (CV) was calculated as an index of tuning bandwidth (Marida 1972) as follows:

\[
CV = 1 - \frac{\sum_k R_k \exp(i2\theta_k)}{\sum_k R_k}
\]

where \(R_k\) represents the neuronal response at orientation \(\theta_k\). CV ranged from zero (sharp tuning) to unity (isotopic tuning). Optimal orientation (\(O_{opt}\)) was estimated as follows:

\[
O_{opt} = \arctan \left( \frac{\sum_k R_k \exp(i2\theta_k)}{\sum_k R_k} \right)
\]

where \(\arctan\) is the angular component of a complex number.

Motion direction selectivity of a neuron was measured by a direction selectivity index (DSI), as follows:

\[
DSI = \left( \frac{R_P - R_{N}}{R_P + R_{N}} \right) \times 100\%
\]

where \(R_P\) is the response of the neuron to its preferred direction of motion and \(R_N\) is the response to its nonpreferred direction. DSI ranged from 0% (nondirectional) to 100% (completely directional).

Neurons’ responses to a series of carrier temporal frequencies in both directions of motion were tested for CM and unidirectional VM gratings. The extent to which these data revealed direction selectivity to carrier motion was summarized by a symmetry index (SI), as follows:

\[
SI = 1 - \frac{\sum_k |R_k - R_{-k}|}{\sum_k |R_k + R_{-k}|}
\]

where \(R_k\) is the response of the neuron to VM or CM gratings with carrier drifting at \(k\) Hz and \(R_{-k}\) is the response to stimuli with carrier drifting at \(k\) Hz in the opposite direction. SI would be 0 if the neuron responds only to one direction of carrier motion and not to the other (direction selective), and it would be 1 if the neuron responds equally to both directions of carrier motion (nondirection selective).

The proportional decline in response of a neuron at high temporal frequency compared with its optimal response was given by the following falloff index (FI):

\[
FI = \frac{R_{14}}{R_{max}}
\]

where \(R_{14}\) is the response of a neuron at high temporal frequency and \(R_{max}\) is the maximal (optimal) response. FI was calculated for responses of a neuron to LM gratings as well as VM and CM gratings. In the case of LM gratings, \(R_{14}\) is the response to gratings drifting at 16 Hz and \(R_{max}\) is the response to the optimal temporal frequency. In the case of VM and CM gratings, \(R_{14}\) is the response to VM or CM gratings with carrier drifting at 16 Hz and \(R_{max}\) is the response to the same grating at its optimal carrier temporal frequency. FI ranged from 0 (response fell to spontaneous at 16 Hz) to 1 (optimal response at 16 Hz over the measured range of 0–16 Hz).

To evaluate whether a neuron exhibited a similar preference for the two kinds of gratings, Pearson’s correlation coefficient was calculated for scatterplots comparing optimal carrier spatial frequencies for CM and VM gratings and optimal orientations for LM gratings and the
envelope of VM gratings. In addition, nonparametric, paired comparisons (Wilcoxon signed-rank test) were performed.

For recordings with multielectrodes, spikes from only one channel were analyzed online to construct tuning curves. In the later offline analysis, spikes from other channels were detected and classified using Offline Sorter software (version 2.8.8, Plexon). Spikes were sorted using the “semiautomatic K-means” algorithm, and only clearly separable clusters of spikes were classified as single units. Isolated neurons from these channels were included in further analysis only if they showed very similar tuning to orientation and spatial frequency of LM gratings compared with the neuron recorded online. In some cases for recordings with single-channel electrodes, offline sorting of spikes was performed to correct misclassifications by the window discriminator and to isolate and assess spikes with lower amplitude.

Model. To explore to what extent the model scheme shown in Fig. 1, E and F, could provide an understanding of the general features of these neuronal responses, we constructed a computer simulation in Matlab. The architecture of the model (Fig. 1E) consisted of two parallel processing pathways, a linear filter F0 responding to luminance (first order) stimuli and a nonlinear pathway (F1-R-F2; Fig. 1F) processing nonluminance (second order) stimuli.

Filter F0 is a spatiotemporal filter constructed by taking a dot product of each frame of the stimulus with a gabor spatial filter to produce a temporal signal that is then convolved with the temporal filter (Adelson and Bergen 1985). Finally, this signal is half-wave rectified to give a simple cell-like modulated response.

\[ tfilt(t) = \frac{(k \times t)^ne^{-kxt}}{n!} - \frac{(k \times t)^2}{n + 2} \]

where \( tfilt \) is the temporal filter, \( t \) is time, \( k \) is a constant, and \( n = 2 \). \( k \) was calculated using the following equation:

\[ k = tmscl \times tfopt / 1,000 \]

where \( tmscl \) is a timescale factor defined as milliseconds/frame and \( tfopt \) is the optimal temporal frequency of the filter.

The first stage of the nonlinear pathway contained a pool of spatiotemporal filters (F1), which was implemented by convolving each spatial frame stimulus with a gabor spatial filter followed by temporal convolution with a monophasic temporal filter (Watson and Ahumada 1985), as follows:

\[ tfilt(t) = (k \times t)^ne^{-kxt} \]

where \( n = 0 \) and \( k \) is given by Eq. 8, where \( tfopt \) was set to 1 Hz.

Each of these temporal responses was then full-wave rectified and summed by a spatiotemporal filter (F2), which was constructed exactly the same as filter F0. The action of filter F2 on the rectified signals was also implemented as a dot product in the same manner as in the linear pathway, and the output of filter F2 was then half-wave rectified to give a simple cell-like modulated response.

Finally, the temporal output signals of these two pathways were summed to give the final output of the model. Note that the output of this model is an analog signal representing average spike frequency as a function of time rather than discrete spiking events.

We did not try to fit parameters of these filters to the data from individual neurons but instead used a generic model with fixed values of parameters, because our aim here was to explore to what extent the nonlinear FRF model that has been proposed to process second-order stimuli (Baker and Mareschal 2001) can provide some understanding of these data. Model responses were measured to the same stimuli used in the experimental recordings of the neuronal responses. The parameters of the model were as follows: for filter F0, the spatial frequency of the gabor was 0.08 cycles/° (cpd), the spatial bandwidth was 1.5 octaves, the aspect ratio (defined as the ratio of the filter’s axial length to cross-width) was 1, the orientation was 0°, and the optimal temporal frequency was 2 Hz. For filter F1, the spatial frequency of the gabor was 1.6 cpd, the spatial bandwidth was 1.5 octaves, the aspect ratio was 1, the orientation was 90°, and the parameters of the monophasic temporal filter were \( n = 0 \) and \( tfopt = 1 \) Hz, which were chosen to provide selectivity to the carrier temporal frequency of CM gratings roughly like those shown by neurons (see Fig. 8, C–H). The parameters for filter F2 were identical to those for filter F0.

RESULTS

For this study, we recorded from 115 area 18 neurons in 13 cats. Of these, 64 neurons (55%) were classified as second-order-responsive neurons, as they responded significantly to CM gratings and showed band-pass tuning to its carrier spatial frequency. These second-order-responsive neurons were further tested with VM gratings (motion defined) of two types: unidirectional and bidirectional. Carrier spatial frequency and envelope orientation tuning were also measured using unidirectional VM gratings, which gave stronger responses than bidirectional VM gratings.

Carrier spatial frequency selectivity. Previous studies have demonstrated that second-order-responsive neurons in area 18 show narrow band-pass tuning to carrier spatial frequency of CM gratings well outside their luminance passband (e.g., Zhou

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**Fig. 2.** Responses of a typical neuron to LM, CM, and VM gratings. Neuronal responses to LM gratings are shown as a function of SF measured at the grating’s optimal orientation. Snapshots of luminance gratings with two different SFs are shown at the top. Optimal luminance SF for this neuron was 0.08 cpd, and the neuronal response fell to spontaneous activity (dashed line) at 0.3 cpd. Responses of the same neuron were measured to CM and VM gratings as a function of carrier SF. Carrier SF tuning for both gratings was very similar, with peaks around 0.8 cpd, much greater than the optimal luminance grating SF of 0.08 cpd. Snapshots of CM and VM gratings with two different carrier SFs are shown at the bottom. cpd, cycles per degree.
Thus, we wanted to see if these neurons would also show similar selectivity to carrier spatial frequency of VM gratings. The neuron shown in Fig. 2 showed band-pass tuning to luminance gratings (0.02–0.2 cpd, with a peak response at 0.08 cpd). The CM gratings were tested with varying carrier spatial frequencies, with envelope orientation fixed at the neuron’s optimal luminance orientation. This neuron showed band-pass tuning to carrier spatial frequency with a response peak at 0.8 cpd. At this high spatial frequency range, the carrier signals were well beyond the neuron’s luminance resolution, and, hence, it was classified as a second-order-responsive neuron. This neuron was further tested with VM gratings for varying carrier spatial frequencies, with envelope orientation fixed at the neuron’s optimal luminance orientation. This neuron showed similar band-pass tuning to carrier spatial frequency as shown for CM gratings, again with a response peak at ~0.8 cpd. At this high spatial frequency range, the carrier signals were well beyond the neuron’s luminance resolution, and, hence, it was classified as a second-order-responsive neuron. This neuron was further tested with VM gratings for varying carrier spatial frequencies, with envelope orientation fixed at the neuron’s optimal luminance orientation. This neuron showed similar band-pass tuning to carrier spatial frequency as shown for CM gratings, again with a response peak at ~0.8 cpd. In this plot, the neuron’s responses are shown on different scales for carrier spatial frequency tuning and LM spatial frequency tuning, since this neuron’s LM grating response was much stronger than those to the CM and VM gratings.

The scatterplot shown in Fig. 3A shows a given neuron’s optimal carrier spatial frequency for VM gratings against that for CM gratings for 30 neurons (9 simple neurons and 21 complex neurons). Points on the scatterplot were highly correlated \( r = 0.7, P < 0.0001 \), and most of the points on the scatterplot were close to the equality line, indicating that carrier spatial frequency tuning was similar for both types of gratings. Only 1 neuron of the 30 total had significantly different optimal carrier spatial frequencies for 2 stimuli (bootstrap method, CI = 95%). Figure 3B shows a histogram plotted for ratios of optimal carrier spatial frequencies between CM and VM gratings, which was centered on one.

Envelope orientation selectivity. To assess form-cue invariance for luminance- and motion-defined boundaries, like that previously demonstrated for luminance- and contrast-defined boundaries (Mareschal and Baker 1998a), we measured the orientation selectivity of neurons to the envelope of unidirectional VM gratings for a comparison with that of LM gratings. Figure 4A shows responses of a typical neuron that was tuned to the orientation as well as motion direction of luminance gratings (\( \text{Ori}_{\text{opt}} = 97° \) and \( \text{DSI} = 0.94 \)). This neuron also showed similar orientation tuning for the envelope of VM gratings (\( \text{Ori}_{\text{opt}} = 91° \); Fig. 4B) and was also direction selective, although to a somewhat smaller degree (DSI: 0.55). We also measured envelope orientation tuning for CM gratings for this neuron.
was significantly greater than for LM gratings ($P$ were above the equality line, indicating broader tuning for VM gratings. Most of the points (23 of 26) were above the equality line, suggesting that neurons had weaker direction selectivity for VM compared with LM gratings.

Note that if a neuron was responding to the carrier motion, then the optimal envelope orientation for VM gratings would be orthogonal to that of LM gratings (since the carrier was always orthogonal to the envelope in these experiments), and it was not the case; instead, these results demonstrate that neurons’ VM grating responses are to the envelope and not to the local motion of the carrier and that they occur in a form-cue invariant manner.

**Carrier temporal frequency tuning.** A previous study (Marechal and Baker 1998b) demonstrated that most of the second-order-responsive neurons in cat area 18 showed band-pass tuning to the temporal frequency of drifting envelopes of CM gratings. Neurons were systematically selective for lower envelope temporal frequencies of CM gratings compared with LM gratings. Responses of these neurons usually fall off to spontaneous activity above an envelope temporal frequency of $\sim$10 Hz, whereas for luminance gratings, responses fall off around 16 Hz. To see if neurons show similar tuning properties to drifting carriers, we measured responses for CM and both unidirectional and bidirectional VM gratings for varying carrier temporal frequencies. Note that the envelopes of CM and both unidirectional and bidirectional VM gratings were drifted at a fixed temporal frequency that was slightly lower than the neuron’s optimal temporal frequency for LM gratings.

For unidirectional VM gratings, one carrier was always held stationary and the other drifted at varying temporal frequencies in both directions. For some neurons, the response decreased with increasing temporal frequency (Fig. 6C); the response of some neurons increased with temporal frequency (Fig. 6E), some neurons responded equally to all temporal frequencies (Fig. 6F), a few neurons showed band-pass tuning (Fig. 6D), and some neurons showed no such particular pattern (Fig. 6, G and H). Interestingly, almost all neurons showed symmetric tuning, i.e., a similar response pattern for both directions of carrier motion, indicated by SI values close to 1 in Fig. 6. The scatterplot shown in Fig. 9A shows a given neuron’s FI for unidirectional VM gratings against that for LM gratings. Most of the points (19 of 24) were above the equality line, suggesting that for unidirectional VM gratings, neuronal responses fall off at high temporal frequencies relatively less than for LM responses. FI values were significantly greater for VM gratings compared with LM gratings ($P = 0.0018$ by Wilcoxon signed-rank one-tailed test).

For bidirectional VM gratings, the carrier gratings drifted with equal and opposite velocities. Figure 7 shows carrier temporal frequency tuning for six neurons. The responses for most neurons in our sample decreased with increasing temporal frequency (e.g., Fig. 7C–G), except for one (Fig. 7H), which showed band-pass tuning. This was the only neuron that...
showed band-pass tuning in our sample of 19 neurons; all others gave low-pass responses.

In most previous single-unit studies using CM stimuli, the carrier grating was always held stationary while the envelope was drifting (Zhou and Baker 1993, 1994; Mareschal and Baker 1998a, 1999; Song and Baker 2007; Rosenberg and Issa 2010). In our present study, to measure the dynamic properties of early stages of a FRF model, we measured temporal frequency tuning for drifting carriers of CM gratings, similar to a recent study (Rosenberg and Issa 2011). Since we wanted to compare this CM carrier temporal frequency tuning with the carrier tuning for VM gratings, we maintained the carrier orientation perpendicular to the envelope orientation for CM gratings and varied carrier temporal frequency from 0 to 16 Hz (with 0 Hz corresponding to a stationary carrier). Figure 8 shows carrier temporal frequency tuning for six neurons.

Consistent with Rosenberg and Issa (2011), our sample neurons showed very diverse tuning, but most of them responded optimally to a stationary carrier, and the response decreased with increases in temporal frequency. Since the carrier of the CM gratings was stationary while we evaluated the neurons’ second-order responsivity, we might have inadvertently excluded in our sample any neurons that preferentially respond to CM gratings with drifting carriers (Rosenberg and Issa 2011). However, some neurons also responded quite well to very high temporal frequencies (Fig. 8, F and H). Similar to the results from unidirectional VM gratings, neurons usually showed symmetric tuning to carrier temporal frequency, i.e., the response pattern was similar to both directions of carrier motion (indicated by SI values close to 1 in Fig. 8). The scatterplot shown in Fig. 9B shows a given neuron’s FI for CM gratings against that for...
LM gratings. There was no systematic relationship between FIs for these two gratings, and FI values were not significantly different for CM and LM gratings ($P = 0.98$ by Wilcoxon signed-rank two-tailed test).

**Responsiveness to unidirectional and bidirectional gratings.** To assess how well CM-responsive neurons also responded to both uni- and bidirectional VM gratings, we compared response strengths for the two stimuli at their optimal carrier temporal frequencies. The scatterplot shown in Fig. 10A shows the response strength to bidirectional versus unidirectional VM gratings for 19 neurons (5 simple neurons and 14 complex neurons) from carrier temporal frequency data like those shown in Figs. 6 and 7. All the data points were on or below the equality line, indicating that neurons responded more strongly to unidirectional VM gratings; this difference was significant ($P < 0.0001$ by Wilcoxon signed rank one-tailed test). Even though all (19/19) of the second-order-responsive neurons responded significantly to unidirectional VM gratings, some neurons (9/19) failed to respond significantly (one-tailed $t$-test) to bidirectional gratings. The histogram (Fig. 10B) showing the ratio of response strength to uni- and bidirectional stimuli demonstrates that for all neurons, the ratio was less than or equal to unity and that for 16 of 19 neurons, the ratio was $<0.6$. The scatterplot and histogram show results only for those second-order-responsive neurons that were tested with both types of VM gratings.

**Envelope spatial frequency tuning.** Conceivably, VM gratings might be detected in two different ways: dynamic discontinuities between moving carriers (“edge-based” processing) or by relative speeds of the carriers (“region-based” processing).
We measured envelope spatial frequency tuning curves to uni- and bidirectional VM gratings and compared them with the tuning for ICs, which are thought to be detected by edge-based processing (Song and Baker 2007). Interestingly, neurons were tuned to higher envelope spatial frequencies of unidirectional VM gratings compared with bidirectional ones. Neurons showed similar envelope spatial frequency selectivity for ICs and bidirectional VM gratings (Fig. 11B). This similarity suggests that bidirectional boundaries are detected in a manner like ICs, i.e., by dynamic phase discontinuities of the carrier textures along the boundary. However, neurons were selective for higher envelope spatial frequencies of unidirectional VM gratings compared with ICs, approximately two times the peak envelope spatial frequency for ICs (Fig. 11A). Therefore, unidirectional boundaries may be detected primarily by differences in the speeds of textures between envelope half-cycles, i.e., region-based processing, with some additional contribution from dynamic discontinuities, i.e., edge-based processing.

Model simulation. We simulated an FRF model that has been previously proposed to explain the responses of area 18 neurons to CM gratings and ICs (Song and Baker 2007) to see how well it might also account for the responses of these neurons to VM gratings. The model parameters were not fit to a particular neuron’s data, but rather a generalized model was constructed to simulate the typical selectivity patterns of area 18 neurons for CM gratings, which was then tested to see how well it could predict selectivity patterns for VM gratings. Temporal parameters of the early filters were selected to mimic typical neurons’ responses to carrier temporal frequency of CM...
gratings, such that the model gave its best response to CM gratings with a stationary carrier and the response decreased with carrier temporal frequency (Fig. 8B), i.e., it gave a low-pass carrier temporal frequency response. These filters were not selective for the direction of carrier motion, in accordance with the neuronal responses (Fig. 8B) (Rosenberg and Issa 2011).

After the parameters of the model were fixed based on CM responses, we tested its selectivity to VM gratings and ICs. For unidirectional VM gratings, the response of the model increased with carrier temporal frequency (Fig. 6B). Although not all neurons’ responses were exactly like this response pattern, most of the neurons’ responses did remain significantly above spontaneous activity at high carrier temporal frequencies, as indicated by the FI shown in Fig. 9A. On the other hand, the model’s response decreased with carrier temporal frequency for bidirectional VM gratings (Fig. 7B), similar to the response pattern of nearly all the neurons in our sample. And also similar to the neurons’ responses, the model responded less strongly to bidirectional than to unidirectional VM gratings. Interestingly, the model showed similar envelope spatial frequency selectivity for ICs and bidirectional VM gratings (Fig. 11B), whereas it was selective for an envelope spatial frequency of unidirectional gratings that was twice that for ICs (Fig. 11A). These VM and IC envelope spatial frequency selectivity results were similar to those for neurons, thus supporting our hypothesis that bidirectional gratings are detected by edge-based processing, similar to ICs, whereas unidirectional gratings are detected predominantly by region-based processing.

**DISCUSSION**

This study demonstrated that neurons in the early visual cortex can respond to motion-defined contours. These neurons were selective to similar orientations of luminance- and motion-defined contours as well as similar directions of motion (form-cue invariance), although the strength of direction selectivity was weaker for motion-defined contours compared with luminance-defined contours. These neurons were also selective for the spatial frequency of the carrier gratings used for constructing motion-defined contours. This carrier selectivity was very similar to the selectivity shown for the carrier of contrast-defined contours. These findings suggest that both kinds of contours are detected by the same nonlinear neural mechanism. Responses to both contrast- and motion-defined boundaries often extended to quite high temporal frequencies of drifting carrier gratings to which most cortical neurons fail to respond when tested with luminance gratings. However, for a given neuron, tuning was similar for both directions of carrier motion.

**Sinusoidal grating carrier.** It might seem counterintuitive to use sinusoidal gratings as a carrier instead of the random dot texture patterns used in previous studies (Chaudhuri and Albright 1997; Mysore et al. 2006; Sary et al. 1993, 1995; Zeki et al. 2003), as these patterns look more similar to texture...
patterns present in the real world. However, a sinusoidal grating carrier with spatial frequency outside a neuron’s luminance passband provides powerful advantages in ruling out simple linear/luminance artifacts. First, it ensures that the responses are not mediated by the same linear filter thought to process luminance gratings. A random dot texture pattern, however, is broadband in spatial frequency, and some of its energy might fall within the luminance passband of a neuron, giving rise to a linear response. Second, these neurons show narrow carrier spatial frequency tuning, and this result rules out the possibility that their responses are mediated by early nonlinearities of the retina or CRT because such nonlinearities would not predict selectivity for carrier spatial frequencies.

However, VM stimuli with sinusoidal grating carriers introduce an ambiguity as to what the neuron is actually responding to. If a snapshot image of VM stimuli is taken at some moment in time (Fig. 1C), then it looks like an illusory contour with phase discontinuities between two carriers. But, by measuring envelope spatial frequency tuning to VM gratings as described below, we were able to disambiguate between responses to phase discontinuities and difference in speeds of carriers. Note that in natural scenes, shear motion between textures will give rise to both of these cues: phase discontinuities and relative speed.

Neural mechanism. A model consisting of two parallel signal-processing streams (Fig. 1E) has been proposed to explain the responses of cortical neurons to first- and second-order stimuli (Zhou and Baker 1993; Mareschal and Baker 1999; Song and Baker 2007). The first stream consists of a conventional coarse spatial scale linear filter \( F_0 \) selective for

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Fig. 11. Comparison of neurons’ and model’s envelope SF tuning to illusory contours (ICs) with that to VM gratings. A: comparison of responses to IC and unidirectional gratings. Responses from four neurons (bottom graphs) show that the preferred envelope SF for unidirectional VM gratings was two times higher than that for ICs, as predicted by the model (top right graph). B: comparison of responses to IC and bidirectional gratings. Responses from two neurons (bottom graphs) show that neurons’ preferred envelope SFs for bidirectional VM gratings and ICs were the same, as also predicted by the model (top right panel).
orientation, direction of motion, and spatial frequency of luminance gratings. The second stream consists of a nonlinear FRF model (Fig. 1F) that can explain the responses of neurons to second-order stimuli such as contrast- and texture-defined boundaries (Chubb and Sperling 1988; Wilson 1999; Landy and Graham 2004). This FRF model is composed of two linear filtering stages that are connected by a nonlinearity (e.g., rectification). The first stage consists of small-scale spatial filters (F₁) that are selective for high spatial frequencies of the carrier. The outputs of these early filters are rectified and pooled by a coarse spatial scale late filter (F₂), which is selective for envelope orientation, direction of motion, and spatial frequency. Filters F₁ and F₂ have similar preferences for orientation and direction of motion, but spatial frequency selectivity is coarser for F₂ compared with F₀. Here, we explored whether the FRF model proposed to explain responses to contrast- and texture-defined boundaries could also explain the responses of area 18 neurons to motion-defined boundaries.

If motion-defined boundaries are processed by a common FRF-like mechanism, then neurons should show similar tuning properties for carrier and envelope of motion- and contrast-defined boundaries. In the processing of motion-defined boundaries by an FRF model, filter F₁ could act as local motion defined boundaries. The outputs of these early filters are rectified and pooled by a coarse spatial scale late filter (F₂), which is selective for envelope orientation, direction of motion, and spatial frequency. Filters F₁ and F₂ have similar preferences for orientation and direction of motion, but spatial frequency selectivity is coarser for F₂ compared with F₀. Here, we explored whether the FRF model proposed to explain responses to contrast- and texture-defined boundaries could also explain the responses of area 18 neurons to motion-defined boundaries.

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a mixture of both region-based and edge-based processing. In addition, our results (Fig. 10) showed that responses of neurons are stronger to unidirectional than to bidirectional gratings; this could be because unidirectional gratings are simultaneously detected by both region-based and edge-based processing, whereas bidirectional gratings are detected by edge-based processing only.

The results from our model simulations also predicted that neurons’ FIs for carrier temporal frequency to uni- and bidirectional gratings would be different (Figs. 7B and 8B), which was demonstrated by the neurons’ responses in Figs. 7 and 8. However, it should be noted that this model was not accurate in explaining all the details of individual neuron’s responses, particularly the diversity of temporal responses (Figs. 6–8); to do so would require a more elaborate model architecture and additional model parameters, whose estimation would be beyond the aims and scope of this study. The purpose of this model was just to demonstrate, in a general way, how a simple FRF model could produce patterns of selectivity to different second-order stimuli that are similar to the neuronal data, particularly different carrier temporal frequency FIs to different stimuli and differing envelope spatial frequency selectivities.

The neural substrates for the elements of the FRF model are not known with certainty. It has been previously proposed that area 17 neurons could be the basis for the early filters (F1) due to their selectivity for high spatial frequency and the orientation selectivity shown for the carrier of CM gratings, which seemed to rule out a subcortical substrate (Mareschal and Baker 1998). However, a recent study (Rosenberg et al. 2010) showed that LGN Y cells also respond selectively to CM gratings; most interestingly, the nonlinear subunits of Y cells exhibited carrier orientation tuning similar to that seen in area 18 neurons. These results suggest that nonlinear subunits of Y cells could provide the early filters (F1), with subsequent cortical summation of Y cell afferents providing the envelope orientation and spatial frequency tuning (F2) observed in area 18 neurons. Also consistent with this idea are the very good responses to quite high carrier temporal frequencies in both LGN Y cells (Rosenberg et al. 2010) and area 18 neurons (Fig. 8) (Rosenberg and Issa 2011), whereas area 17 neurons failed to respond at high temporal frequencies (Movshon et al. 1978). On the other hand, carrier spatial frequency tuning bandwidth is very broad in LGN Y cells compared with that in area 18 neurons (Rosenberg et al. 2010), so it is not yet clear to what extent the early filtering (F1) might be accounted for at the geniculate level.

In summary, our results are consistent with the idea that these VM grating responses can be understood in terms of the same FRF model previously proposed for responses to CM and IC stimuli, suggesting a common neural mechanism for all these second-order stimuli.

Cue invariance. For the visual system to perform figure-ground segregation, it should be able to delineate an object from a background, which might be the same with respect to all cues except one, e.g., color. However, that object should also stand out if it appears against a different background with the same color but a different texture. To perform this task, information about presence of a particular cue is not important, but rather the contrast between cues that distinguish an object from its background is of primary importance, regardless of the nature of the cues. Thus, the visual system should be able to combine information across different cues to perform figure-ground segregation, i.e., the segmentation mechanism should be form-cue invariant (Albright 1992). This strategy of form-cue invariance is computationally economical and can help resolve perceptual ambiguities when multiple cues are present. In addition, it might be important for shape recognition and shape constancy.

Neurons in the early visual cortex have been previously shown to respond in a form-cue invariant manner to stimulus attributes such as orientation and motion direction of boundaries. Neurons in cat area 17 (Zhou and Baker 1993, 1996), cat area 18 (Zhou and Baker 1993, 1996; Mareschal and Baker 1998a, 1998b; Leventhal et al. 1998; Zhou et al. 2001; Song and Baker 2006, 2007; Tanaka and Ohzawa 2006), primates V1 (Chaudhuri and Albright 1997), and primate V2 (e.g., von der Heydt et al. 1984; von der Heydt and Peterhans 1989; Leventhal et al. 1998; Lui et al. 2005) have been shown to respond in a form-cue invariant manner to the orientation of luminance and nonluminance boundaries.

A long-standing concern has been the possibility that second-order responses might be mediated by simple early nonlinearities in the display device or the photoreceptors, or by luminance signals in the stimuli, without any implication of a specialized mechanism (e.g., FRF) to explain the form-cue invariance. However, the demonstration of carrier-tuned responses to stimuli with sine-wave grating carriers in previous studies (e.g., Zhou and Baker 1994; Mareschal and Baker 1998) as well as in the present study (Fig. 2) make such explanations seem very unlikely. One group failed to find carrier-tuned second-order-responsive neurons in cat area 18 and primate V2 (El-Shamayleh and Movshon 2011), but other laboratories have consistently replicated such tuned responses in cat area 18 (Rosenberg et al. 2010; Tanaka and Ohzawa 2006) and recently also in primate V2 (Li et al. 2011).

In this study, we demonstrated that neurons previously shown to selectively respond to luminance-, texture-, and contrast-defined boundaries can also display form-cue invariant responses to motion-defined boundaries. These neurons showed similar orientation selectivity for luminance- and motion-defined boundaries, but direction selectivity was weaker to motion-defined boundaries, similar to what has been previously found for contrast- and texture-defined boundaries (Song and Baker 2006, 2007). This form-cue invariant orientation tuning in the early visual cortex could be used by higher brain areas such as the MT, V4, and inferior temporal (IT) that have been reported to respond to motion-defined patterns in a form-cue invariant manner (Albright 1992; Mysore et al. 2006; Sary et al. 1993).

This study suggests that specific processing of motion-defined boundaries begins in early visual areas. Furthermore, it suggests that these boundaries are processed by a common nonlinear mechanism that also mediates response to other second-order stimuli, such as contrast-and texture-defined boundaries, and it could be the basis for form cue invariance to these stimuli.

ACKNOWLEDGMENTS

The authors thank Guangxing Li for providing the software for curve fitting and Plexon data file analysis. The authors also thank Guangxing Li, Vargha Talebi, and Lynda Domazet for assistance with the experiments.
MOTION-DEFINED CONTOUR PROCESSING

GRANTS
This work was supported by Canadian Institutes of Health Research Grants MA-9685 and MOP-119498 (to C. L. Baker).

DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS
Author contributions: A.G. and C.L.B. conception and design of research; A.G. performed experiments; A.G. analyzed data; A.G. and C.L.B. interpreted results of experiments; A.G. prepared figures; A.G. drafted manuscript; A.G. and C.L.B. edited and revised manuscript; A.G. and C.L.B. approved final version of manuscript.

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