# Ocular following responses of monkeys to the competing motions of two sinusoidal gratings

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## Abstract

Ocular following responses (OFRs) were elicited in monkeys at short latencies ($\sim$50 ms) by applying motion in the form of successive 1/4-wavelength steps to each of two overlapping vertical sine-wave gratings that had different spatial frequencies. In the first experiment, the two sine waves had spatial frequencies in the ratio 3:5 and moved in opposite directions. The initial OFRs showed a highly nonlinear dependence on the relative contrasts of the competing sine waves. On average, when the contrast of one was less than a third of that of the other then the one with the lower contrast became ineffective – as though suppressed – and the OFR was entirely determined by the sine wave of higher contrast: winner-take-all. In a second experiment, the two sine waves had spatial frequencies in the ratio 3:7 and moved in the same direction (though at different speeds). The initial OFRs again showed a highly nonlinear dependence on the relative contrasts of the competing sine waves, with a winner-take-all outcome when the contrasts of the two sine waves were sufficiently different. In both experiments, the nonlinear dependence on the relative contrasts of the competing sine waves was well described by a contrast-weighted-average model with just two free parameters. These findings were very similar to those of [Sheliga, B.M., Kodaka, Y., FitzGibbon, E.J., Miles, F.A., 2006c. Human ocular following initiated by competing image motions: evidence for a winner-take-all mechanism. Vision Res. 46, 2041–2060] on the human OFR, indicating that the monkey is a good animal model for studying the nonlinear interactions that emerge when competing motions are used.
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## 1. Introduction

In primates, sudden movements of the visual scene elicit ocular following responses with ultra-short latencies: <75 ms in humans (Gellman et al., 1990; Sheliga et al., 2005a,b) and <60 ms in monkeys (Miles et al., 1986; Miura et al., 2006). It is generally believed that there are at least two different neural mechanisms by which primates analyze visual motion: one utilizes low-level motion detectors that are sensitive to first-order luminance modulation and the other(s) utilizes higher level mechanisms that are sensitive to features (Cavanagh and Mather, 1989). Recent findings strongly suggest that the initial OFRs of humans (Chen et al., 2005; Sheliga et al., 2005a, 2006a,c) and monkeys (Miura et al., 2006) are mediated by the low-level mechanism. Much of the initial evidence for this came from studies using a special broadband stimulus, the so-called missing fundamental (*mf*), which indicated that the initial OFRs depended critically on the Fourier composition of the motion stimulus (Sheliga et al., 2005a, 2006c; Miura et al., 2006). The *mf* stimulus is a square wave that lacks the fundamental, so that in the frequency domain it consists of summed odd harmonics, the largest being the 3rd and the *i*th harmonic having an amplitude proportional to 1/*i*. A special property of this stimulus, first recognized by Adelson (1982), is that when shifted 1/4 of its wavelength, all of its harmonics each shift 1/4 of their respective wavelengths, the 4*n* + 1 harmonics (where *n* is an integer) shifting in the direction of the actual image motion (i.e., forwards, along with the entire pattern and

its features), whereas the $4n - 1$ harmonics (which include the principal Fourier component, the 3rd harmonic) shift in the opposite direction (i.e., backwards).[1] The initial OFRs that were elicited when motion was applied to the *mf* stimulus in the form of successive 1/4-wavelength shifts of the pattern were always in the backward direction in both humans and monkeys, and this was attributed to the 1/4-wavelength (backward) shifts of the principal Fourier component (i.e., the 3rd harmonic).

This apparent dominance by the principal Fourier component suggested to Sheliga et al. (2006c) that there might be nonlinear interactions between the neural mechanisms sensing the conflicting motions of the various harmonics of this special broadband stimulus. In one test of this idea Sheliga et al. used moving stimuli with just two competing sine waves equivalent to the 3rd and 5th harmonics of the *mf* stimulus (the *3f5f* stimulus) that move in *opposite* directions, and found that the critical factor was the ratio of their two contrasts: when of similar contrast both were effective (vector sum/averaging), but when the contrast of one was less than about 1/2 that of the other then the one with the higher contrast became dominant and the one with the lower contrast was rendered ineffective: winner-take-all. In another experiment, Sheliga et al. (2006c) restricted the moving stimuli to two competing sine waves equivalent to the 3rd and 7th harmonics of the *mf* stimulus (the *3f7f* stimulus) that move in the *same* direction (but at different speeds). Again, they found that when the contrast of one was less than about 1/2 that of the other then the one with the higher contrast was dominant. Other studies on humans involving another short-latency oculomotor reflex, the disparity vergence response (DVR), indicated that it too depends on first-order energy mechanisms (Sheliga et al., 2006b) and shows nonlinear interactions, including winner-take-all behavior, when confronted with sine-wave gratings with competing binocular disparities that could have the same or opposite sign (Sheliga et al., 2007). These nonlinear interactions in the OFR and DVR were attributed to mutual inhibition between the neural channels sensing the motion (or the disparity) of the two competing sine waves. Thus, the nonlinear interactions here were assumed to result entirely from the intrinsic properties of the sensory pathways: *bottom-up processes*.

Previous studies on the initial OFR (for review, see Miles, 1998) have suggested that the monkey provides a good animal model of the human, and the present study was undertaken to determine if the monkey's initial OFR shows evidence of nonlinear interactions when confronted with competing motion stimuli like those used in the study of Sheliga et al. (2006c) on humans. In Experiment 1 we used the *3f5f* stimulus (see Fig. 1A–C), whose two component sine waves moved in opposite directions when the entire pattern shifted in 1/4-wavelength steps, and in Experiment 2 we used the *3f7f*

stimulus (see Fig. 1D–F), whose two component sine waves moved in the same direction when the pattern shifted in 1/4-wavelength steps. We report that the monkey's initial OFRs to these competing stimuli showed evidence of nonlinearities similar to those reported for humans.

## 2. Experiment 1: the initial OFR to the *3f5f* stimulus and its dependence on the relative contrasts of the two components

In this experiment we used two superimposed vertical sine-wave gratings whose spatial frequencies were in the ratio 3:5 and recorded the initial OFRs that were elicited when the pattern underwent successive 1/4-wavelength shifts of the fundamental frequency. As shown in Fig. 1A–C, this meant that each of the components underwent successive 1/4-wavelength shifts of opposite sign. The dependent variable was the relative contrast of the two gratings and we report that when the contrast of one exceeded that of the other, on average, by a factor of 3.3 then the responses to the grating of lower contrast were almost totally suppressed.

### 2.1. Methods

Data were collected from three rhesus monkeys (*Macaca mulata*). All procedures were approved by the Animal Care and Use Committee of Kyoto University. Many of the general procedures were the same as those used in previous studies of ocular tracking in monkeys (Kawano et al., 1994; Kodaka et al., 2004; Miura et al., 2006) and humans (Sheliga et al., 2005a, 2006c).

#### 2.1.1. Animal preparations

The monkeys were previously trained to fixate a small spot. Under pentobarbital sodium anesthesia and aseptic conditions, each monkey was implanted with a head holder, to allow the head to be fixed in the standard stereotaxic position during the experiments, and a scleral search coil to allow measurement of the position of the right eye (Judge et al., 1980).

#### 2.1.2. Visual display and stimuli

The animals faced a 19 in. CRT monitor (Eizo T766, driven by a PC Radeon 9800 Pro video card), which was 50 cm in front of the eyes, in a dark room. Visual stimuli were presented on the monitor (resolution, $1280 \times 1024$ pixels; vertical refresh rate, 100 Hz). The RGB signals from the video card were converted to black and white images with 11-bit grayscale resolution through an attenuator (Pelli, 1997), exactly as described by Sheliga et al. (2005a). Briefly, a luminance look-up table with 256 equally spaced luminance levels ranging from 0.3 cd/m² to 77.1 cd/m² was created by direct luminance measurements (LS-100 photometer; Konica-Minolta, Japan) under software control. This table was then expanded to 2048 equally spaced levels by interpolation.

The visual stimuli used in our experiments were almost identical to those used by Sheliga et al. (2006c) and so will be described only in brief. The visual images consisted of one-dimensional vertical grating patterns that could have one of three horizontal luminance profiles in any given trial: (1) a sum of two sine waves with spatial frequencies in the ratio 3:5, creating a pattern with fundamental frequency, *f* (termed the "*3f5f* stimulus"), (2) a pure sine wave with a spatial frequency identical to that of the 3*f* component of the *3f5f* stimulus (the "*3f* stimulus"); (3) a pure sine wave with a spatial frequency identical to that of the 5*f* component of the *3f5f* stimulus (the "*5f* stimulus"). Each image extended 360 mm horizontally (39.6°; 1280 pixels) and 270 mm vertically (30.2°; 1024 pixels) and had a mean luminance of 38.7 cd/m². The initial phase of a given grating was randomized from trial to trial at intervals of 1/4-wavelength. Motion was created by substituting a new image every frame (i.e., every 10 ms) for a total of 15 frames (i.e., stimulus duration, 150 ms), each new image being identical to the previous one except phase shifted horizontally

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[1] Of course, a 3/4-wavelength *forward* shift of a pure sine wave is exactly equivalent to a 1/4-wavelength *backward* shift (spatial aliasing), and it is the latter that determines the direction of both the perceived motion and any associated OFRs because the brain gives greatest weight to the nearest-neighbor matches (Sheliga et al., 2005a; Miura et al., 2006).