2014 13th International Conference on Control, Automation, Robotics & Vision
Marina Bay Sands, Singapore, 10-12th December 2014 (ICARCV 2014)

Stimuli Design for Identification of Spatially Distributed Motion Detectors in Biological Vision Systems

Egi Hidayat*, Mojtaba Soltanalian*, Alexander Medvedev*, and Karin Nordström†
*Department of Information Technology
Uppsala University
Uppsala, Sweden
Email: {egi.hidayat, mojtaba.soltanalian, alexander.medvedev}@ it.uu.se
†Department of Neuroscience
Uppsala University
Uppsala, Sweden
Email: karin.nordstrom@neuro.uu.se

***Abstract*—Visual motion perception in biological vision systems is typically modeled via a set of elementary motion detectors (EMDs) forming a spatially distributed network. This paper addresses the problem of estimating the *weights* of such an EMD construct from a linear combination of their output signals. This challenge arises in e.g. mathematical modeling of animal motion perception. In particular, the spatial excitation properties of sinusoidal gratings are important since these basis signals are typically utilized as visual stimuli in biology. It is demonstrated that one cannot uniquely estimate the weights of more than three contributing EMDs with a single frequency sinusoidal grating as the visual stimulus. However, a higher spatial excitation order can be obtained with multi-frequency sinusoidal grating stimuli. Two approaches to the design of stimuli with a given spatial excitation order are presented. Several numerical examples are provided to examine the performance of the proposed stimuli design methods.**

I. Introduction

The concept of the correlator type elementary motion detector (EMD) in biological motion vision was introduced in the middle of the last century [5]. Today the mathematical EMD model is generally accepted as an explanation to visual responses to wide field motion in many different animals. Despite its wide support, nobody has directly measured the output of a single EMD so far, due to the fact that the associated neural circuitry cannot be located accurately. Nevertheless, recordings can be made in the fly optic ganglia, from lobula plate tangential cells (LPTCs) that are believed to spatially pool the output from many EMDs (see e.g. [3]). It is worth pointing out that hundreds of EMDs are expected to contribute to an experimentally measurable LPTC neural response [1].

In a previous paper on the identification of the EMD layer [7], a method for estimating the weights of the contributing identical EMDs has been proposed. The method yields a unique estimation of the weights, under the assumption that the visual stimulus provides *enough* excitation so that the outputs of the individual EMDs are distinguishable from each other.

This work was supported by European Research Council via the Advanced Grant 247035 (to EH, AM, SysTEAM), and the Swedish Research Council (to KN, VR 2012-4740).

The spatial excitation properties of stimuli in laboratory experiments have always made an important topic in different areas of biomedical research, such as in fat-water separation based on magnetic resonance imaging [8] or in the studies of the human visual system [4]. In this paper, a study of excitation properties of the sinusoidal grating stimuli for the identification of a layer of spatially distributed detectors from a linear combination of the output signals of the participating EMDs representing an LPTC response is reported. The class of sinusoidal gratings is selected due to their popularity with the biologists and the ease of implementation.

The paper is organized as follows. First, the EMD layer model is briefly summarized. Then the response of the EMD layer to both single and multiple frequency sinusoidal gratings is derived. Two approaches to sinusoidal grating stimulus design for higher spatial excitation orders are presented. Finally, simulation results are provided to illustrate the theoretical insights of the paper.

II. Identifiability properties of the EMD layer

The EMD model originally formulated in [5] can be summarized in mathematical terms as follows:

$$\begin{aligned} v^+(t) &= \int_0^t w^+(t-\theta)u^+(\theta)\ \mathrm{d}\theta, \\ v^-(t) &= \int_0^t w^-(t-\theta)u^-(\theta)\ \mathrm{d}\theta, \\ y(t) &= v^+u^- - v^-u^+, \end{aligned} \tag{1}$$

where u^+ and u^- are the scalar inputs of the EMD, y is the output, and w^+ and w^- are the impulse responses of the low-pass filters in the input channels. Both w^+ and w^- are here assumed to be finite-dimensional, to simplify calculations. This assumption is, however, not crucial for the forthcoming analysis and can be dropped with some additional analytical effort, see [7].

Notice that (1) is a Wiener system with a static bilinear output transformation. The EMD model considered in biology is typically symmetrical, i.e. w^+ and w^- are identical [2]. This construction is generally known as a symmetrical EMD model and is the focus of this paper. Despite the output nonlinearity, the frequency of a single-tone sinusoidal input is preserved in the steady-state response of a symmetric EMD model. However, this is not true when $w^+ \neq w^-$, see [7].

It is believed that the EMDs are uniformly spatially distributed in a flat layer and all possess identical dynamics. Under this assumption, the visual input to neighbouring EMDs has identical shape, but the inputs are shifted in time.

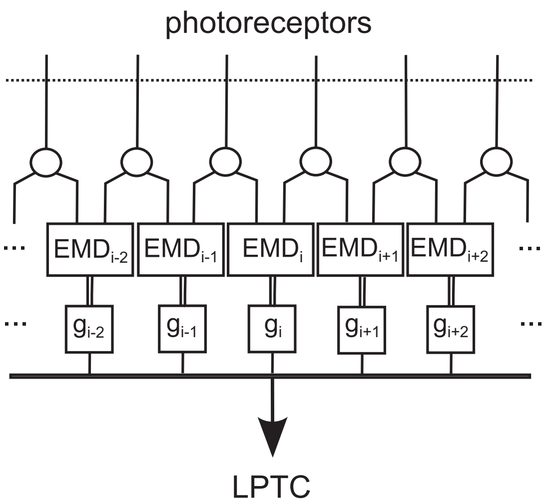

Fig. 1. Schematic illustration of an EMD layer. Abbreviations are explained in the main text.

Let $y(t,n)$ denote the output of the n-th EMD in the layer, then the measured signal of the EMD-layer output is modeled as

$$y_N(t) = \sum_{j=1}^{N} g_j y(t,j) = \sum_{j=1}^{N} g_j y(t-\tau_j), \tag{2}$$

where $g_j, \tau_j, j = 1, \ldots, N$ are unknown constants characterizing the individual contributions of the EMDs in the layer.

In order to obtain a unique solution for the EMD weights, $\gamma = \begin{bmatrix} g_1 & \ldots & g_N \end{bmatrix}^T$, N linearly independent EMD responses are required. In other words, the stimulus provided to the EMD layer has to possess the spatial excitation order of at least N.

EMD layer response to sinusoidal grating stimuli

A visual stimulus consisting of a sinusoidal grating exciting the two input channels of the n-th EMD in a layer results in the following input signal forms

$$u^+(t,n) = c_0 + c_1 \sin(\omega t + \phi + \tilde{n}\delta),$$
$$u^-(t,n) = c_0 + c_1 \sin(\omega t + \phi + n\delta),$$

where $\tilde{n} = n-1$. The signal form of the stimulus is thus parametrized in terms of the frequency ω and the phase shift ϕ. The weights c_0 and c_1 represent the mean luminance of the pattern and the pattern contrast of the grating in the laboratory experiments. The constant δ is the phase difference between the two input channels resulting from the temporal delay (and spatial separation) between the channels τ that is evaluated to

$$\delta = -\omega\tau.$$

Since the EMD dynamics are assumed to be known, a first-order linear block is treated, without loss of generality. Indeed, these simple dynamics alone capture the behavior of the biological data quite well [6]. For the symmetrical EMD model with the linear block transfer function

$$W(s) = \frac{K}{s+a},$$

the EMD output is given by

$$y(t,n) = y_t(t,n) + y_s(t,n),$$

where $y_t(t,n)$ and $y_s(t,n)$ represent the transient and the steady-state response, respectively. It can be shown by a straightforward calculation that the transient response is

$$\begin{aligned} y_t(t,n) = & \frac{2c_1 K \sin\left(\frac{\delta}{2}\right)}{a\sqrt{a^2+\omega^2}} \mathrm{e}^{-at}\Bigg[c_1 a \cos\left(\frac{\delta}{2}\right) \sin\left(\omega t + \tan^{-1}\left(\frac{\omega}{a}\right)\right) \\ & + c_0 \sin(n\delta)\Bigg(\sqrt{a^2+\omega^2} \sin\left(\omega t + \phi - \frac{\delta}{2}\right) \\ & + a \cos\left(\phi - \frac{\delta}{2} + \tan^{-1}\left(\frac{a}{\omega}\right)\right)\Bigg) \\ & + c_0 \cos(n\delta)\Bigg(-\sqrt{a^2+\omega^2} \cos\left(\omega t + \phi - \frac{\delta}{2}\right) \\ & + a \sin\left(\phi - \frac{\delta}{2} + \tan^{-1}\left(\frac{a}{\omega}\right)\right)\Bigg)\Bigg], \end{aligned} \tag{3}$$

while the steady-state response is given by

$$\begin{aligned} y_s(t,n) = & \frac{2c_1 K \sin\left(\frac{\delta}{2}\right)}{a\sqrt{a^2+\omega^2}} \Bigg[-\frac{c_1 a\omega \cos\left(\frac{\delta}{2}\right)}{\sqrt{a^2+\omega^2}} \\ & - c_0 \sin(n\delta) \sin\left(\omega t + \phi - \frac{\delta}{2} + \tan^{-1}\left(\frac{a}{\omega}\right)\right) \\ & + c_0 \cos(n\delta) \cos\left(\omega t + \phi - \frac{\delta}{2} + \tan^{-1}\left(\frac{a}{\omega}\right)\right)\Bigg]. \end{aligned} \tag{4}$$

From (3) and (4), it is seen that the response of n-th EMD to a sinusoidal grating comprises three linearly independent (as functions of n) terms. Since the decay rate of the transient EMD response is relatively high due to the fast linear dynamics, this identifiability analysis takes into account only the steady-state response part.

To simplify the computations, define $\tilde{y}_s(t,n)$ as a normalized version of (4) such that

$$\tilde{y}_s(t,n) = \tilde{c} - \sin(\omega t + \tilde{\phi}) \sin(n\delta) + \cos(\omega t + \tilde{\phi}) \cos(n\delta), \tag{5}$$

where

$$\begin{aligned} \tilde{y}_s(t,n) = & y_s(t,n) \frac{a\sqrt{a^2+\omega^2}}{2c_0 c_1 K\omega \sin\left(\frac{\delta}{2}\right)}, \\ \tilde{c} = & -\frac{a c_1 \cos\left(\frac{\delta}{2}\right)}{c_0\sqrt{a^2+\omega^2}}, \\ \tilde{\phi} = & \phi - \frac{\delta}{2} + \tan^{-1}\left(\frac{a}{\omega}\right). \end{aligned}$$

From (2) and (5), the normalized steady-state output of the EMD layer is

$$\tilde{y}_{N,s}(t) = \tilde{c}\sum_{n=1}^{N} g_n - \sin(\omega t + \tilde{\phi})\sum_{n=1}^{N} g_n \sin(n\delta) + \cos(\omega t + \tilde{\phi})\sum_{n=1}^{N} g_n \cos(n\delta).$$

The expression above can be represented in a matrix form as

$$\begin{aligned} Y &= \Xi\gamma, \\ \Xi &= \tilde{c}\mathbb{1}_{(M+1)\times N} - \tilde{f}_s \otimes z_s + \tilde{f}_c \otimes z_c, \end{aligned} \tag{6}$$

where $\mathbb{1}_{(M+1)\times N}$ is an $(M+1)\times N$ matrix of unit elements, $\otimes$ is the tensor product of vectors, and

$$\begin{aligned} \tilde{f}_s &= \begin{bmatrix} \sin(\tilde{\phi}) & \sin(\omega T + \tilde{\phi}) & \dots & \sin(M\omega T + \tilde{\phi}) \end{bmatrix}^T \\ \tilde{f}_c &= \begin{bmatrix} \cos(\tilde{\phi}) & \cos(\omega T + \tilde{\phi}) & \dots & \cos(M\omega T + \tilde{\phi}) \end{bmatrix}^T \\ z_s &= \begin{bmatrix} \sin(\delta) & \sin(2\delta) & \dots & \sin(N\delta) \end{bmatrix}^T \\ z_c &= \begin{bmatrix} \cos(\delta) & \cos(2\delta) & \dots & \cos(N\delta) \end{bmatrix}^T. \end{aligned}$$

The vector Y stands for the EMD layer steady-state output vector and the vector γ is comprised of the weights of the participating EMDs

$$\begin{aligned} Y &= \begin{bmatrix} \tilde{y}_{N,s}(0) & \tilde{y}_{N,s}(T) & \dots & \tilde{y}_{N,s}(MT) \end{bmatrix}^T, \\ \gamma &= \begin{bmatrix} g_1 & g_2 & \dots & g_N \end{bmatrix}^T. \end{aligned}$$

In (6), the rank of Ξ determines the largest number of EMD weights that can be uniquely estimated from Y. By inspection of the structure of the matrix Ξ in (6), it always holds that $\operatorname{rank}\Xi \le 3$ and one concludes that only three EMDs can be uniquely distinguished among by means of a one-frequency sinusoidal grating, i.e. $N \le 3$.

EMD layer response to multiple frequencies

In the previous section it was shown that a single-tone sinusoidal grating stimulus, as typically used in insect motion vision, is not sufficient for identifying more than three unique EMDs in a layer. At the same time, hundreds of EMDs are expected to contribute to the neural response recorded from LPTCs. Therefore, the stimuli have to possess a high spatial excitation order to enable an unambiguous estimation of the EMD layer. One feasible solution is to utilize a grating composed of a sum of sinusoids as stimulus. This is well in line with Fourier series as a means of representing bounded periodical signals.

For r sinusoidal grating, the input signals to n-th EMD are defined as follows:

$$\begin{aligned} u^+(t,n) &= c_0 + \sum_{i=1}^{r} c_i \sin(\omega_i t + \phi_i + \tilde{n}\delta_i), \\ u^-(t,n) &= c_0 + \sum_{i=1}^{r} c_i \sin(\omega_i t + \phi_i + n\delta_i). \end{aligned}$$

To avoid unnecessary cumbersome expressions, the derivation below is carried out for the case of $r = 2$ but it can be generalized in a straightforward manner to an arbitrary r by expanding the involved sums.

Similarly to the case of a single-tone sinusoidal grating stimulus, the EMD response to a sum of sinusoidal gratings comprises a transient and a steady-state component. The transient response can be written as

$$\begin{aligned} y_t(t,n) = {}& \frac{2\mathrm{e}^{-at}}{a}\sum_{i=1}^{2}\frac{c_i K \sin\left(\frac{\delta_i}{2}\right)}{\sqrt{a^2+\omega_i^2}}\Bigg[c_i a \cos\left(\frac{\delta_i}{2}\right) \\ & \times \sin\left(\omega_i t + \tan^{-1}\left(\frac{\omega_i}{a}\right)\right) \\ & + c_0 \sin(\tilde{n}\delta_i)\Bigg(\sqrt{a^2+\omega_i^2}\sin\left(\omega_i t + \phi_i + \frac{\delta_i}{2}\right) \\ & + a\cos\left(\phi_i + \frac{\delta_i}{2} + \tan^{-1}\left(\frac{a}{\omega_i}\right)\right)\Bigg) \\ & + c_0 \cos(\tilde{n}\delta_i)\Bigg(-\sqrt{a^2+\omega_i^2}\cos\left(\omega_i t + \phi_i + \frac{\delta_i}{2}\right) \\ & + a\sin\left(\phi_i + \frac{\delta_i}{2} + \tan^{-1}\left(\frac{a}{\omega_i}\right)\right)\Bigg)\Bigg] \\ & + \frac{c_1 c_2 K}{a^2+\omega_1^2}\mathrm{e}^{-at}\Bigg[\Big(\omega_1\cos(\phi_1+\tilde{n}\delta_1) - a\sin(\phi_1+\tilde{n}\delta_1)\Big) \\ & \times \sin(\omega_2 t + \phi_2 + n\delta_2) \\ & - \Big(\omega_1\cos(\phi_1+n\delta_1) - a\sin(\phi_1+n\delta_1)\Big) \\ & \times \sin(\omega_2 t + \phi_2 + \tilde{n}\delta_2)\Bigg] \\ & + \frac{c_1 c_2 K}{a^2+\omega_2^2}\mathrm{e}^{-at}\Bigg[\Big(\omega_2\cos(\phi_2+\tilde{n}\delta_2) - a\sin(\phi_2+\tilde{n}\delta_2)\Big) \\ & \times \sin(\omega_1 t + \phi_1 + n\delta_1) \\ & - \Big(\omega_2\cos(\phi_2+n\delta_2) - a\sin(\phi_2+n\delta_2)\Big) \\ & \times \sin(\omega_1 t + \phi_1 + \tilde{n}\delta_1)\Bigg], \end{aligned}$$

while the steady-state response reads as

$$\begin{aligned} y_s(t,n) = {}& \sum_{i=1}^{2}\frac{2c_i K \sin\left(\frac{\delta_i}{2}\right)}{a\sqrt{a^2+\omega_i^2}}\Bigg[-\frac{c_i a \omega_i \cos\left(\frac{\delta_i}{2}\right)}{\sqrt{a^2+\omega_i^2}} \\ & - c_0 \sin(n\delta_i)\sin\left(\omega_i t + \phi_i - \frac{\delta_i}{2} + \tan^{-1}\left(\frac{a}{\omega_i}\right)\right) \\ & + c_0 \cos(n\delta_i)\cos\left(\omega_i t + \phi_i - \frac{\delta_i}{2} + \tan^{-1}\left(\frac{a}{\omega_i}\right)\right)\Bigg] \\ & + \frac{c_1 c_2 K}{a^2+\omega_1^2}\Bigg[\Big(a\sin(\omega_1 t + \phi_1 + \tilde{n}\delta_1) \\ & - \omega_1\cos(\omega_1 t + \phi_1 + \tilde{n}\delta_1)\Big)\sin(\omega_2 t + \phi_2 + n\delta_2) \\ & - \Big(a\sin(\omega_1 t + \phi_1 + n\delta_1) - \omega_1\cos(\omega_1 t + \phi_1 + n\delta_1)\Big) \\ & \times \sin(\omega_2 t + \phi_2 + \tilde{n}\delta_2)\Bigg] \end{aligned}$$

$$+\frac{c_1c_2K}{a^2+\omega_2^2}\Bigg[\Bigg(a\sin(\omega_2 t+\phi_2+\tilde{n}\delta_2) - \omega_2\cos(\omega_2 t+\phi_2+\tilde{n}\delta_2)\Bigg)\sin(\omega_1 t+\phi_1+n\delta_1) - \Bigg(a\sin(\omega_2 t+\phi_2+n\delta_2)-\omega_2\cos(\omega_2 t+\phi_2+n\delta_2)\Bigg) \times\sin(\omega_1 t+\phi_1+\tilde{n}\delta_1)\Bigg]. \quad (7)$$

Once again, neglecting the transient component that vanishes at a high convergence rate, the main focus of the analysis is put on the sustained steady-state response of the EMD. Introduce the following notation

$$\begin{aligned}
\omega_{i,j}^+ &= \omega_i+\omega_j, \quad \delta_{i,j}^+=\delta_i+\delta_j,\\
\omega_{i,j}^- &= \omega_i-\omega_j, \quad \delta_{i,j}^-=\delta_i-\omega_j,\\
\tilde{c} &= -\sum_{i=1}^{r}\frac{c_i^2\omega_i K\sin(\delta_i)}{a^2+\omega_i^2}, \quad \tilde{c}_i=\frac{2c_0c_iK\sin(\frac{\delta_i}{2})}{a\sqrt{a^2+\omega_i^2}},\\
\tilde{\phi}_i &= \phi_i-\frac{\delta_i}{2}+\tan^{-1}\left(\frac{a}{\omega_i}\right)\\
\tilde{c}_{i,j}^+ &= \frac{c_ic_j\omega_{i,j}^-K\sin\left(\frac{\delta_{i,j}^-}{2}\right)}{\sqrt{(a^2+\omega_i^2)(a^2+\omega_j^2)}},\\
\tilde{\phi}_{i,j}^+ &= \phi_i+\phi_j-\frac{\delta_{i,j}^+}{2}+\tan^{-1}\left(\frac{a^2-\omega_i\omega_j}{a\omega_{i,j}^+}\right)\\
\tilde{c}_{i,j}^- &= -\frac{c_ic_j\omega_{i,j}^+K\sin\left(\frac{\delta_{i,j}^+}{2}\right)}{\sqrt{(a^2+\omega_i^2)(a^2+\omega_j^2)}},\\
\tilde{\phi}_{i,j}^- &= \phi_i-\phi_j-\frac{\delta_{i,j}^-}{2}+\tan^{-1}\left(\frac{a^2+\omega_i\omega_j}{a\omega_{i,j}^-}\right).
\end{aligned}$$

With the definitions above, the expression in (7) can be represented in a more compact form as follows

$$\begin{aligned}
y_s(t,n) =& \tilde{c}+\sum_{i=1}^{r}\tilde{c}_i\cos(\omega_i t+n\delta_i+\tilde{\phi}_i)\\
&+\sum_{i=1}^{r-1}\sum_{j=i+1}^{r}\Bigg(\tilde{c}_{i,j}^+\sin(\omega_{i,j}^+t+n\delta_{i,j}^++\tilde{\phi}_{i,j}^+)\\
&+\tilde{c}_{i,j}^-\sin(\omega_{i,j}^-t+n\delta_{i,j}^-+\tilde{\phi}_{i,j}^-)\Bigg), \quad (8)
\end{aligned}$$

where $r=2$. Equation (8) reveals the general structure of the steady state response of the n-th EMD to a sinusoidal grating with r distinct frequencies. The spatial excitation order corresponds to the number of linearly independent functions of n in (8), which quantity is easily seen to be at most $4\binom{r}{2}+2r+1=2r^2+1$.

From (2) and (8), the EMD-layer steady-state output is

$$\begin{aligned}
y_{N,s}(t) =& \tilde{c}\sum_{n=1}^{N}g_n+\sum_{n=1}^{N}\sum_{i=1}^{r}g_n\tilde{c}_i\cos\left(\omega_i t+n\delta_i+\tilde{\phi}_i\right)\\
&+\sum_{n=1}^{N}\sum_{i=1}^{r-1}\sum_{j=i+1}^{r}g_n\Big(\tilde{c}_{i,j}^+\sin\left(\omega_{i,j}^++n\delta_{i,j}^-+\phi_{i,j}^+\right)\\
&+\tilde{c}_{i,j}^-\sin\left(\omega_{i,j}^-+n\delta_{i,j}^-+\phi_{i,j}^-\right)\Big).
\end{aligned}$$

Similarly to the case of the single-tone sinusoidal grating stimulus, the steady-state output vector is described in a matrix form as $Y=\Xi\gamma$, where

$$\begin{aligned}
\Xi =& \tilde{c}\mathbb{1}_{(M+1)\times N}+\sum_{i=1}^{r}\tilde{c}_i\left(\tilde{f}_{c,i}\otimes z_{c,i}-\tilde{f}_{s,i}\otimes z_{s,i}\right)\\
&+\sum_{i=1}^{r-1}\sum_{j=i+1}^{r}\Big(\tilde{c}_{i,j}^+\left(\tilde{f}_{s,i,j}^+\otimes z_{c,i,j}^++\tilde{f}_{c,i,j}^+\otimes z_{s,i,j}^+\right)\\
&+\tilde{c}_{i,j}^-\left(\tilde{f}_{s,i,j}^-\otimes z_{c,i,j}^-+\tilde{f}_{c,i,j}^-\otimes z_{s,i,j}^-\right)\Big),
\end{aligned}$$

with

$$\tilde{f}_{c,i}=\begin{bmatrix}\cos(\tilde{\phi}_i)\\ \cos(\omega_iT+\tilde{\phi}_i)\\ \vdots\\ \cos(M\omega_iT+\tilde{\phi}_i)\end{bmatrix}, \tilde{f}_{s,i}=\begin{bmatrix}\sin(\tilde{\phi}_i)\\ \sin(\omega_iT+\tilde{\phi}_i)\\ \vdots\\ \sin(M\omega_iT+\tilde{\phi}_i)\end{bmatrix},$$

$$\tilde{f}_{c,i,j}^+=\begin{bmatrix}\cos(\tilde{\phi}_{i,j}^+)\\ \cos(\omega_{i,j}^+T+\tilde{\phi}_{i,j}^+)\\ \vdots\\ \cos(M\omega_{i,j}^+T+\tilde{\phi}_{i,j}^+)\end{bmatrix}, \tilde{f}_{s,i,j}^+=\begin{bmatrix}\sin(\tilde{\phi}_{i,j}^+)\\ \sin(\omega_{i,j}^+T+\tilde{\phi}_{i,j}^+)\\ \vdots\\ \sin(M\omega_{i,j}^+T+\tilde{\phi}_{i,j}^+)\end{bmatrix},$$

$$\tilde{f}_{c,i,j}^-=\begin{bmatrix}\cos(\tilde{\phi}_{i,j}^-)\\ \cos(\omega_{i,j}^-T+\tilde{\phi}_{i,j}^-)\\ \vdots\\ \cos(M\omega_{i,j}^-T+\tilde{\phi}_{i,j}^-)\end{bmatrix}, \tilde{f}_{s,i,j}^-=\begin{bmatrix}\sin(\tilde{\phi}_{i,j}^-)\\ \sin(\omega_{i,j}^-T+\tilde{\phi}_{i,j}^-)\\ \vdots\\ \sin(M\omega_{i,j}^-T+\tilde{\phi}_{i,j}^-)\end{bmatrix},$$

$$\begin{aligned}
z_{c,i} &= \left[\cos(\delta_i)\quad \cos(2\delta_i)\quad \ldots\quad \cos(N\delta_i)\right]^T,\\
z_{s,i} &= \left[\sin(\delta_i)\quad \sin(2\delta_i)\quad \ldots\quad \sin(N\delta_i)\right]^T,\\
z_{c,i,j}^+ &= \left[\cos(\delta_{i,j}^+)\quad \cos(2\delta_{i,j}^+)\quad \ldots\quad \cos(N\delta_{i,j}^+)\right]^T,\\
z_{s,i,j}^+ &= \left[\sin(\delta_{i,j}^+)\quad \sin(2\delta_{i,j}^+)\quad \ldots\quad \sin(N\delta_{i,j}^+)\right]^T,\\
z_{c,i,j}^- &= \left[\cos(\delta_{i,j}^-)\quad \cos(2\delta_{i,j}^-)\quad \ldots\quad \cos(N\delta_{i,j}^-)\right]^T,\\
z_{s,i,j}^- &= \left[\sin(\delta_{i,j}^-)\quad \sin(2\delta_{i,j}^-)\quad \ldots\quad \sin(N\delta_{i,j}^-)\right]^T.
\end{aligned}$$

III. Input design

In theory, it should be possible to generate a stimulus that comprises an infinite number of sinusoidal gratings. This is impossible to achieve in practice. The visual stimuli in biological research can be implemented as dynamical images on a cathode ray tube screen. The refresh rate of the screen determines the upper bound of the frequencies of the sinusoids, while the resolution and precision of the laboratory equipment would give the lower bound of the feasible frequency range. Here, it is assumed for design purposes that the frequencies are positive integer numbers.

Problem formulation

Given the feasible range for the stimulus frequency components

$$D = [\underline{m}, \overline{m}],$$

where $\underline{m}$ and $\overline{m}$ stand for the minimum and maximum frequencies, find a set of frequencies

$$\boldsymbol{\omega} = \{\omega_1, \dots, \omega_r\} \subseteq D$$

such that r is maximized and the number of distinct elements in the set S given by

$$S = \{\omega_k, \omega_k + \omega_l, \omega_k - \omega_l\}, \quad k, l \in \{1, \dots, r\}, k > l \quad (9)$$

is exactly r^2. Then the weights $g_i, i = 1, \dots, 2r^2 + 1$ can be uniquely estimated from the measurements $y_s(t, n)$ obtained by applying the sinusoidal grating with the frequencies in the set $\boldsymbol{\omega}$.

Constructive method

As the set S in (9) is constructed from the frequencies in $\boldsymbol{\omega}$, their pairwise differences and sums, a sensible solution is to use the power basis 3^k, that is for $D = [0, \overline{m}]$

$$\boldsymbol{\omega} = \{3^0, 3^1, \dots, 3^{r-1}\}, \quad 3^{r-1} \le \overline{m}.$$

From a number theory perspective, it is straightforward to verify that the set above satisfies the conditions indicated in the problem formulation. The number of excitation frequencies is then given by $r = 1 + \lfloor \log_3 \overline{m} \rfloor$ where $\lfloor \dots \rfloor$ denotes the floor operator. In addition, for the case when $\underline{m} \neq 0$, introduce the notation

$$\underline{r} = \lceil \log_3 \underline{m} \rceil, \quad \overline{r} = \lfloor \log_3 \overline{m} \rfloor,$$

where the symbol $\lceil \dots \rceil$ denotes the ceiling operator. Then the set $\boldsymbol{\omega}$ is given by

$$\boldsymbol{\omega} = \{3^{\underline{r}}, 3^{\underline{r}+1}, \dots, 3^{\overline{r}}\}, \quad 3^{\underline{r}} \ge \underline{m}, \quad 3^{\overline{r}} \le \overline{m},$$

which leads to

$$r = 1 + \overline{r} - \underline{r}.$$

It should be noted that the constructive solution above is prone to the curse of dimensionality, as the basis frequencies grow exponentially with r, which property can be viewed as a motivation for developing the algorithmic approach in the following.

Iterative method

Another solution to the stimuli design problem can be obtained through iteratively examining all integers in D and discarding those that are overtones of a frequency in the set, or those that result from pairwise summation and subtraction of the frequencies. Below is one possible realization of such an iterative method.

1) Initialize the frequency set $\boldsymbol{\omega}$ as all integers in the given interval D;
2) Set iteration counter $k = 1$, remove $2\omega_1$ from the set $\boldsymbol{\omega}$;
3) Start iteration:
   a) $k = k + 1$,
   b) Construct the auxiliary sets:
   $$S^\circ = \{\omega_l\}, \quad S^+ = \{\omega_k + \omega_l\},$$
   $$S^- = \{\omega_k - \omega_l\}, \quad l < k, \quad \omega_k, \omega_l \in \boldsymbol{\omega}$$
   c) Remove $2\omega_k, 2\omega_k + \omega_m, 2\omega_k - \omega_m, \omega_k + 2\omega_m$ from $\boldsymbol{\omega}$ where $\omega_m \in S^\circ$,
   d) Remove $\omega_n, \omega_n + \omega_k$ from $\boldsymbol{\omega}$ where $\omega_n \in (S^+ \cup S^-)$,
   e) Continue iteration as long as k less than the dimension of $\boldsymbol{\omega}$.

The solution obtained from the iterative method above is not necessarily the best one but it usually provides a better solution than the constructive method, i.e. it produces the frequency set $\boldsymbol{\omega}$ with a larger dimension r.

Estimate repeating frequency components at the output side

In the biological experiments, the set of possible frequencies for the stimulus is typically fixed. Hence, one might be interested to see how many weights can be uniquely estimated from a set of given frequency components.

The number of distinct frequency components of the EMD layer output response to a stimulus whose components characterized by ω can be obtained by computing the number of unique elements in the following matrix

$$\Omega = \begin{bmatrix} \omega_1 & \omega_1 + \omega_2 & \omega_1 + \omega_3 & \cdots & \omega_1 + \omega_r \\ \omega_2 - \omega_1 & \omega_2 & \omega_2 + \omega_3 & \dots & \omega_2 + \omega_r \\ \vdots & & \ddots & \ddots & \vdots \\ \vdots & & & \ddots & \vdots \\ \omega_r - \omega_1 & \omega_r - \omega_2 & \cdots & \cdots & \omega_r \end{bmatrix}.$$

The matrix Ω is made of three additive terms. The main diagonal consists of the frequencies in $\boldsymbol{\omega}$, the upper triangular part contains the sums of all pairs of frequencies in $\boldsymbol{\omega}$, and the lower triangular part is comprised of pairwise differences between the frequency components. A suitable representation of the matrix is given by

$$\Omega = \boldsymbol{\rho} \otimes \mathbb{1}_{1\times r} + \mathbf{U}(\mathbb{1}_{r\times 1} \otimes \boldsymbol{\rho}^T) - \mathbf{L}(\mathbb{1}_{r\times 1} \otimes \boldsymbol{\rho}^T),$$

where $\boldsymbol{\rho}$ is a vector containing all the elements in the set $\boldsymbol{\omega}$, while $\mathbf{U}(\cdot)$ and $\mathbf{L}(\cdot)$ represent projection operators extracting the upper and lower triangular part of a matrix, respectively.

Consider the case where there are only ν unique components in Ω, such that $\nu < r^2$, then the number of EMDs that can be uniquely distinguished is $N \le 2\nu + 1$.

Simulation example

Simulations were performed to show the improvement in the EMD layer weights estimation with a higher number of sinusoidal components in the multiple frequency gratings. The layer is constructed from 50 individual EMDs with randomly selected weight values. The EMDs are separated by $1°$. The estimation is performed from 1000 samples measured at a sampling rate of 10 kHz. The estimated weights are computed using the standard Matlab's least squares solver. It is shown in Fig. 2 that the correct estimation of weights is obtained when at least 5 sinusoidal waves are included in the stimulus. It is shown that the estimation error decreases with increasing number of sinusoidal waves in the stimulus. The frequency set for the stimulus used in the simulation is

$$\boldsymbol{\omega} = \{8, 13, 19, 28, 42\},$$

which results in

$$\Omega = \begin{bmatrix} 8 & 21 & 27 & 36 & 50 \\ 5 & 13 & 32 & 41 & 55 \\ 11 & 6 & 19 & 47 & 61 \\ 20 & 15 & 9 & 28 & 70 \\ 34 & 29 & 23 & 14 & 42 \end{bmatrix}.$$

Since all the elements in Ω are distinct, the set $\boldsymbol{\omega}$ with $r = 5$ achieves the maximal excitation order and $2r^2 + 1 = 51$ weights can be correctly estimated from the frequency components of the layer output.

Fig. 3 shows the performance of the estimation approach on data corrupted by measurement disturbance. The simulated disturbance is normal distributed white noise with zero mean and variance of 0.1. It can be seen that the stimulus requires a larger number of sinusoidal waves to yield good estimation of the EMD-layer weight values.

IV. Conclusions

In order to devise an effective identification of a flat EMD layer in biological vision systems, the spatial excitation properties of sinusoidal gratings are investigated, and their design is discussed. It is shown that the excitation of a single-tone sinusoidal grating stimulus, a typical stimulus used in motion vision research, cannot guarantee a unique solution for more than three participating EMDs. Estimation of the EMD weights in a realistic layer model requires input signals that have much higher spatial excitation order. To overcome the excitation deficiency, multiple sinusoidal grating stimuli can be used. Two input design methods are proposed that produce such stimuli of a given excitation order. Simulation results show that with a higher number of sinusoids in the stimulus, a more accurate estimation can be achieved.

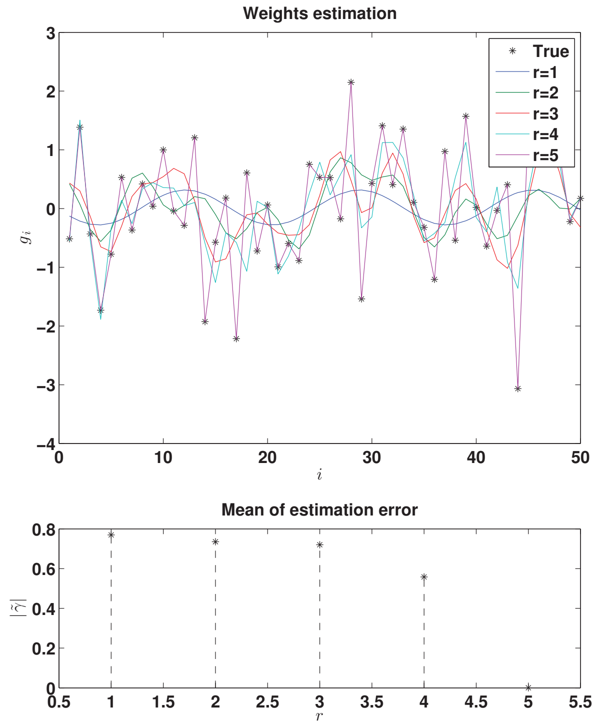

Fig. 2. Upper plot: weight estimation in a layer of 50 EMDs using different stimuli. The star symbols mark the true values of the weights. Increasing the number of sinusoidal waves in the stimulus improves the EMD-layer weights estimation. For 5 frequencies in the stimuli ($r = 5$), $2r^2 + 1 = 51$ weights can be correctly estimated. Lower plot: mean values of the weight estimation error.

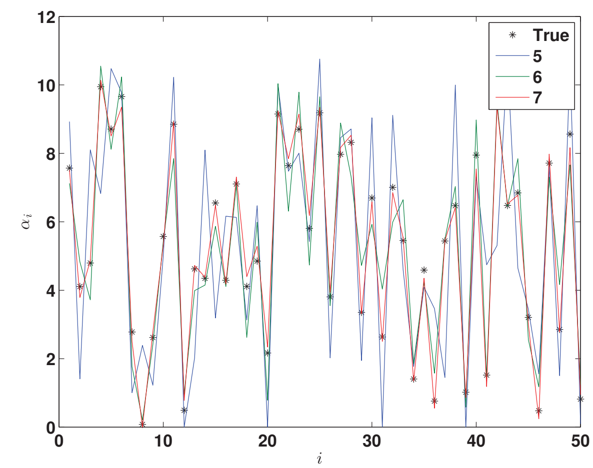

Fig. 3. Weight estimation performance under the influence of measurement disturbance. The star symbols mark the true values of the weights. A larger number of sinusoidal waves than 5 is required to obtain a good estimate of the weights.

References

[1] A. Borst, J. Haag, and D.F. Reiff. Fly motion vision. *Annual Review of Neuroscience*, 33:49–70, 2010.

[2] M. Egelhaaf, A. Borst, and W. Reichardt. Computational structure of a biological motion-detection system as revealed by local detector analysis in the fly's nervous system. *Vision Research*, 20:397–407, 1989.

[3] N. Franceschini, A. Riehle, and A. Le Nestour. Directionally selective motion detection by insect neurons. In Stavenga D.G. and Hardie R.C., editors, *Facets of Vision*, pages 360–390. Berlin Heidelberg: Springer Verlag, 1989.

[4] H.K. Hartline. The effects of spatial summation in the retina on the excitation of the fibers of the optic nerve. *American Journal of Physiology*, 130(4):700–711, 1940.

[5] B. Hassenstein and W. Reichardt. Systemtheoretische Analyse der Zeit, Reihenfolgen und Vorzeichenauswertung Bei der Bewegungsperzeption des Rüsselkäfers Chlorophanus. *Zeitschrift für Naturforschung*, 11:513–524, 1956.

[6] E. Hidayat, A. Medvedev, and K. Nordström. Laguerre domain identification of the elementary motion detector model in insect vision. In *Adaptation and Learning in Control and Signal Processing*, pages 623–628, 2013.

[7] E. Hidayat, A. Medvedev, and K. Nordström. On identification of Elementary Motion Detector. In *International Symposium on Computational Models for Life Sciences*, 2013.

[8] G. Morrell and A. Macovski. Three-dimensional spectral-spatial excitation. *Magnetic Resonance in Medicine*, 37(3):378–386, 1997.