Lie group Analyses to pattern formation of Gurken distribution in Drosophila oogenesis

Li-Mei Pai\textsuperscript{a}, Pei-Yu Wang\textsuperscript{a}, Ruo-Rung Huang\textsuperscript{b}, Wei-Chieh Lin\textsuperscript{b}, Jen-Cheng Wang\textsuperscript{b}, Chia-Hui Fang\textsuperscript{b}, and Tzer-En Nee\textsuperscript{b,*}

\textsuperscript{a} Department of Biochemistry, Chang Gung University, Kwei-Shan, Tao-Yuan 333, Taiwan, Republic of China.

\textsuperscript{b} Graduate Institute of Electro-Optical Engineering and Department of Electronic Engineering, Chang Gung University, Kwei-Shan, Tao-Yuan 333, Taiwan, Republic of China.

Abstract

We carried out a Lie group study of the micro-Raman tissue spectra of the Gurken gradients of \textit{Drosophila} oogenesis. (2×2) matrix representations resulting from the polarized Raman scattering were employed to assess the roles of the Dally-like protein (Dlp) in follicle cell. It was found that the Gurken expansion caused by over-expressing Dlp revealed a $X_1$ Lie point symmetry, while the Gurken distribution in the wild-type egg showed a $X_{23}$ Lie point symmetry. The correlation between the corresponding continuous symmetry operations and the observed Gurken localization were a corroboration of the significance of the Lie group analysis by means of the reaction-diffusion equation in a prolate spheroidal coordinate system.
These investigations suggested that the group-theoretical approach can be applied to characterize the fluctuating asymmetry and the developmental stability in a wide variety of organisms.

**Keywords:** Lie group, Raman spectra, Gurken, *Drosophila*

* Electronic mail of corresponding author: neete@mail.cgu.edu.tw
Introduction

Quantitative characterization of the morphogen gradients is vital for understanding their effects on the determination of cell-fate [1]. However, the detection of the extracellular diffusible molecules is still exceedingly difficult to determine experimentally. Polarized Raman microspectroscopy has been successfully employed with cell systems for the analysis of many biological processes [2], such as cell cycle dynamics [3-6], cell differentiation [7-9], and cell death [10-12]. In the fruit fly, Gurken is a transforming growth factor-α (TGF-α) related to morphogen that promotes different levels of epidermal growth factor receptor (Egfr) signaling in follicle cells along the dorsoventral axis of the Drosophila egg chambers. It was found that the Dally-like protein (Dlp) causes an expansion of the Gurken distribution, while Drosophila Casitas B-lineage lymphoma (D-Cbl) reduces the extent of the Gurken gradient [13-15]. In fact, the problem of how multicellular organisms regulate and control proliferation, differentiation, and cell survival during embryonic development is one of the biggest challenges facing science today [16]. In 1952, Alan Turing proposed simple but subtle reaction-diffusion equations to formulate the spatial homogeneity of biochemical reactions in developmental biology [17]. More recently, it has come to be recognized in a broad range of expertise that the solutions to this pressing question involve biology, chemistry, physics, and mathematics, rather than
just one of these disciplines [18]. In a wide variety of sciences and technologies, group theory has played a successful and especially ubiquitous role [19]. However, less work has been devoted to the principles of symmetry in morphogen gradients or even in biology-related research, due to the difficulty of its abstract perspective [20]. While it is true that most multicellular organisms considered in their entirety possess unsymmetry, many bio-molecules and tissues do have local symmetry intrinsically. In the present work, after observing the asymmetrically localized Gurken gradient in stage 10A egg chambers by confocal microscopy, (2×2) matrix representations resulting from the polarized micro-Raman measurement can be employed to assess the roles of Dlp in the follicle cell. We will focus in depth on group theoretical analysis of the Raman tissue spectra in the developmental stages of Drosophila oogenesis. In order to corroborate the significance of the group theoretical approach, the correlation between the corresponding Lie symmetry operations and the observed Gurken localization will be carried out by means of the reaction-diffusion equation in a prolate spheroidal coordinate system.

**Experiments**

Fly crosses were carried out using standard procedures at 25 °C. The following stocks were used: *GR1-Gal4* and *OreR* were found in the Bloomington stock center.
The total cell lysate from the H1299 cell was lysed with a lysis buffer (10 mM Tris, 1 mM EDTA, 1 mM EGTA, 50 mM NaCl, 50 mM NaF, 20 mM Na₂P₂O₇, 1mM Na₃VO₄, 1mM PMSF, 1 mM benzamidine, 0.5 μg/ml Leupeptin, 1% Triton-X 100, pH 7.4), then sonicated and add to a 6xsample buffer. Total cell lysates prepared from ovaries, dechorionated embryos, larvae and H1299 cells were separated by SDS-PAGE and blotted with anti-Egfr (1:500, Santa Cruz) or tubulin (1:500, Sigma). An ECL detection kit (Pierce) was used to develop signals. Ovaries were dissected in the 1 X PBS buffer and fixed in 200 μl 4% paraformaldehyde in PBS plus 600 μl heptane and 0.25% NP-40 for 20 minutes. For antibody staining, ovaries were blocked in PBST plus 1% BSA for one hour. To aid in visualization of the deoxyribonucleic acid (DNA), 0.5 μg/ml DAPI (Sigma) was added for 5 minutes at room temperature; to visualize action, 10 units of phalloidin (Molecular Probes) were added for 30 minutes. After incubation with a fluorescent secondary antibody (1:1000, Molecular Probes) for one hour and several washes, the ovaries were mounted in glycerol and examined by fluorescence microscopy.

Confocal Raman microspectroscopy is the combination of confocal microscopy with traditional Raman spectroscopy. Spectra were collected using a BX41 Olympus optical microscope, equipped with one air-cooled charge-coupled device (CCD) camera which is used for standard point spectroscopy. The attached microscope is a
BX41 Olympus optical microscope and is equipped with four objectives (×100/0.9 NA, ×50/0.75 NA, ×10/0.25 NA, and ×50/0.5 NA) and integrated with the Raman Spectrometer and a trinocular viewer that accommodates a video camera allowing direct viewing of the sample. This allows the collection of Raman spectra from different points on the sample, with a spatial resolution of a few micrometers. The spectrometer (iHR550 from HORIBA Jobin Yvon) has a focal length of 0.55 m, a Czerny-Turner design, stray light $1 \times 10^{-5}$ equipped with 1200 gr/mm and 2400 gr/mm gratings. The Rayleigh cutoff is less than 100 cm$^{-1}$ with a notch filter. The thermoelectric cooled CCD (Symphony, 1024 × 256, Front Illuminated Open Electrode, working temperature -130 °C) covers a wide spectral range (200-900 nm).

Sample excitation is achieved using an argon ion laser (CVI Melles Griot, New Mexico, U.S.A.) emitting at 488 nm and 25 mW. Calibration of the wavenumber axis is achieved by recording the Raman spectrum of silicon (one accumulation, 10 s) in both static and extended modes. If necessary, an offset correction is performed to ensure that the position of the silicon band is at 520.50 ± 0.10 cm$^{-1}$. Different sets of polarization input and output used in the polarized Raman measurements facilitate the characterization of the tissue spectra by the group-theoretical approach. The polarization configurations of polarized Raman spectra for the *Drosophila* oogenesis include the $Z(XX)\overline{Z}$, $Z(XY)\overline{Z}$, $Z(YX)\overline{Z}$, and $Z(YY)\overline{Z}$ scattering configurations.
The input/output polarizations are selected with a half-wave-plate and a polarizer, respectively.

We can represent the tissue optical characteristics by a transformation, i.e.,

\[
\begin{bmatrix}
S_{\perp\perp} & S_{\perp\parallel}
\end{bmatrix}
= \begin{bmatrix}
M_{11} & M_{12}
M_{21} & M_{22}
\end{bmatrix}
\begin{bmatrix}
I_{\perp}
0
0
I_{\parallel}
\end{bmatrix},
\]

where \(S_{\perp\perp}, S_{\perp\parallel}, S_{\parallel\perp}, \) and \(S_{\parallel\parallel}\) are the scattering intensities measured with a vertical linear analyzer and a horizontal linear analyzer, respectively; \(I_{\perp}\) and \(I_{\parallel}\) are the incident intensities polarized by a vertical linear polarizer and a horizontal linear polarizer, respectively; \(\begin{bmatrix}
M_{11} & M_{12}
M_{21} & M_{22}
\end{bmatrix}\) is a cell structure-dependent (2×2) matrix constructed by different polarizer and analyzer measurements. This unique matrix is expected to provide many valuable insights into developmental biology.

**Results and discussion**

Figures 1 (a) and (b) show the confocal images of the partial distribution of the Gurken gradient for stage 10A in the wild-type egg chambers and the partial distribution of the Gurken gradient obtained by over-expressing Dlp for stage 10A of the 1st filial generation egg chambers, respectively. The anterior of the egg chamber is oriented towards the left, and the dorsal side faces upwards. The Gurken gradient was detected by the anti-Gurken antibody shown in green, and the egg chamber
organization was revealed by phalloidin staining in red. It can be seen that there is a
detectable expansion of the Gurken gradient with overexpression of Dlp in the follicle
cells while the Gurken gradient remains unchanged. The average extension of the
Gurken protein in wild-type egg chambers was estimated to be about 69 μm, which is
equal to 10 follicle cells. Accordingly, when Dlp was overexpressed in the follicle
cells, it was found that the distribution of the Gurken spread to 13 follicle cells and
about 86 μm. Significantly, the overexpression of Dlp expanded the distribution of the
Gurken gradient. Meanwhile, as we have previously reported, overexpression of Dlp
also resulted in a weakly ventralized egg shell phenotype, in which the dorsal midline
cell fate was eliminated, not shown here [13, 21].

To examine in depth on these observations, we carried out a systematic study on
the Raman scattering intensity as a function of the incident light polarization. Figures
2 (a) and (b) show the polarized Raman spectra for the ventralized egg and the
wild-type egg, respectively. For purposes of comparison of the data collected by the
different optical probes, all the measured intensities are normalized relative to the
unpolarized forward scattering light. The observed Raman amide III band around
1300 cm⁻¹ is attributed to the coupled N–H/C–H deformations in the tissue [22-26].
Accordingly, the matrix representatives extracted from the normalized scattering
amplitudes for the ventralized egg and the wild-type egg are
$$X_{\text{ventralized}} = \begin{bmatrix} 0.3566 & 0.5043 \\ -0.2479 & -0.3610 \end{bmatrix} \quad \text{and} \quad X_{\text{wild-type}} = \begin{bmatrix} 0.0670 & 0.0324 \\ -0.0160 & 0.0217 \end{bmatrix},$$

respectively.

Interestingly, a multiplicative commutation relation between $X_{\text{ventralized}}$ and $X_{\text{wild-type}}$ is found as follows:

$$\begin{bmatrix} X_{\text{ventralized}} & X_{\text{wild-type}} \end{bmatrix} = X_{\text{ventralized}} X_{\text{wild-type}} - X_{\text{wild-type}} X_{\text{ventralized}} = \begin{bmatrix} -3.684 \times 10^{-5} & 4.055 \times 10^{-4} \\ 2.517 \times 10^{-4} & 3.684 \times 10^{-5} \end{bmatrix} \cong \begin{bmatrix} 0 & 0 \\ 0 & 0 \end{bmatrix}.$$ 

This result not only reveals the bioluminescent properties of the oogenesis but also is replete with symmetry-related characteristics in the developmental stages. Eleven-dimensional Lie algebra can be obtained from the prolongation structure of the reaction-diffusion equations proposed by Turing to describe the morphogen expansion. On careful inspection of the well-known Lie algebra commutation relations, as shown in the Appendix, Table 1, these two matrices are assigned to be the $X_1$ point symmetry and $X_{23}$ point symmetry for the ventralized egg and the wild-type egg, respectively [21]. Using group-theory formalism for the Gurken redistribution, our data suggest that overexpression of the Dlp causes a breaking of symmetry from $X_{23}$ point symmetry to $X_1$ point symmetry.

Several simple combinatorial codes defined in computer graphics have recently been successfully implemented to obtain the gene expression patterns in the follicle cells for the operations of union, difference, intersection, and addition [27].
Biophysical modeling, dimensional analyses are used to consider quantitative characterization of the transcriptional response to the morphogen for a number of genetic backgrounds. Quantitative characterization of the shape of the Gurken gradient was also achieved by looking at the value of the Thiele modulus [1]. Therefore, further examination is necessary to corroborate the symmetry-related characteristics of the matrix representation of Raman scattered radiation. It is essential to assess the correlation between the observed Gurken localization and the corresponding Lie group operations by means of the reaction-diffusion equation in a prolate spheroidal coordinate system [20]. The reaction-diffusion mechanism used here is mathematically equivalent to a second order differential equation or Laplace equation. The complete well-known Lie point symmetries are shown in the Appendix.

According to the Raman characterization we have obtained in the present work, the symmetry operations of $X_1$ and $X_{23}$ are the major concern, i.e.,

$$X_1 = \frac{1}{a \sqrt{\sinh^2 \xi + \sin^2 \eta}} \frac{\partial}{\partial \xi} \quad \text{and} \quad X_{23} = \frac{\cosh \xi \cdot \cos \eta}{\sqrt{\cosh^2 \xi - \cos^2 \eta}} \frac{\partial}{\partial \eta} - \sin \theta \frac{\partial}{\partial \theta}.$$

Under the steady state, the boundary value of the oocyte is set to zero, both inside and outside of the egg shell. Acting on the reaction-diffusion equation with these two infinitesimal generators, we can numerically find the total field solutions for the *Drosophila* oogenesis modeled as a hollow prolate spheroid with an anterior-posterior axis of 320 μm, a dorsal-ventral axis of 145 μm and an eggshell
thickness of 10 μm.

Fig. 3 (a) and (b) show the spatial distribution of the morphogen for the ventralized egg and the wild-type egg, respectively. Obviously, the results obtained from the infinitesimal symmetry group are in considerable agreement with the Gurken asymmetric distributions plotted in Fig. 1. As we know, there are four main types of symmetry for the reaction-diffusion equation, translation, rotation, inversion, and dilation [20]. The Gurken spreads for the wild-type egg and the ventralized egg exhibit rotation transformations and translation transformations, respectively, reflecting the developmentally regulated expression of Dlp. Compared with the bio-Raman observations, the pattern formations of the Gurken localizations fully corroborate the point-symmetry assignment for these two samples. The observed changes in the Gurken gradient and in the Raman spectra, both governed by the same Lie point symmetry operations, exhibit the inherent properties of the symmetry principle applied in developmental processes. In future, we hope to carry out further experimental work to extend our knowledge. D-Cbl may be the most informative protein to this end, since, as in our previous report, over-expression of D-Cbl significantly reduces the expansion of the Gurken distribution [15]. It is believed that the continuous-group approach will be a novel tool to obtain important insights into what proteins with activity intrinsically break the symmetry types, resulting in
Conclusions

In summary, a Lie group study of the micro-Raman tissue spectra of the Gurken gradients of *Drosophila* oogenesis was carried out. (2×2) matrix representations extracted from the polarized Raman scattering were employed to assess the roles of Dlp in follicle cells. It was found that the expansion of the Gurken distribution caused by Dlp reveals an $X_1$ Lie point symmetry, while that of the wild-type egg shows an $X_{23}$ Lie point symmetry. The correlation between the corresponding continuous symmetry operations and the observed Gurken localization corroborates the significance of the Lie group analysis by means of the reaction-diffusion equation in a prolate spheroidal coordinate system. The view of fluctuating asymmetry in morphogen gradients presented here is rather different from accounts to be found in other modern developmental biology studies. It is believed that the group-theoretical approach can be applied to characterize the developmental stability in a wide variety of organisms.

Acknowledgement

We thank Tze-bin Chou for providing the fly stocks. Many thanks also go to the Microscope Facility at Chang Gung University for their excellent assistance with the
confocal microscopy. We also thank the staff of GALOIS (Group of Abel and Lie Operations In Sciences) and the QUEST Laboratory (Quantum Electro-optical Science and Technology Laboratory), Chang Gung University, for their technical support. This work was supported by the National Science Council of the Republic of China under Contract No. NSC 97-2112-M-182-002-MY3.
The reaction-diffusion equation is solved in a prolate spheroidal coordinate system [20]. The relation between the prolate spheroidal \((\xi, \eta, \theta)\) and Cartesian \((x, y, z)\) coordinates is given by \(x = a \sinh \xi \sin \eta \cos \theta\), \(y = a \sinh \xi \sin \eta \sin \theta\), and \(z = a \cosh \xi \cos \eta\), where \(\xi\) is a nonnegative real number and \(\eta \in [0, \pi]\). The azimuthal angle \(\theta\) belongs to the interval [0,2\(\pi\)). The Lie point symmetries can be spanned as

\[
X_1 = \frac{1}{a \sqrt{\sinh^2 \xi + \sin^2 \eta}} \frac{\partial}{\partial \xi},
\]

\[
X_2 = \frac{1}{a \sqrt{\sinh^2 \xi + \sin^2 \eta}} \frac{\partial}{\partial \eta},
\]

\[
X_3 = \frac{1}{a \sinh \xi \sin \eta} \frac{\partial}{\partial \theta},
\]

\[
X_{12} = -\frac{\sinh \xi \sin \eta}{\sqrt{\sinh^2 \xi + \sin^2 \eta}} \left[ \sin \theta \frac{\partial}{\partial \xi} - \cos \theta \frac{\partial}{\partial \eta} \right],
\]

\[
X_{23} = -\frac{\cosh \xi \cdot \cos \eta}{\sqrt{\cosh^2 \xi - \cos^2 \eta}} \frac{\partial}{\partial \theta} - \sin \theta \frac{\partial}{\partial \phi},
\]

\[
X_{31} = \cos \theta \frac{\partial}{\partial \phi} - \frac{\cosh \xi \cdot \cos \eta}{\sqrt{\cosh^2 \xi - \cos^2 \eta}} \frac{\partial}{\partial \xi},
\]

\[
Y_1 = a \frac{\sinh^2 \xi \sin^2 \eta}{\sqrt{\sinh^2 \xi + \sin^2 \eta}} \left( \cos 2\theta \frac{\partial}{\partial \xi} + \sin 2\theta \frac{\partial}{\partial \eta} \right) - a \frac{\cosh^2 \xi \cos^2 \eta}{\sqrt{\cosh^2 \xi - \cos^2 \eta}} \frac{\partial}{\partial \xi},
\]

\[
+ 2a \cosh \xi \cos \eta \cos \theta \frac{\partial}{\partial \theta} - a \sinh \xi \sin \eta \cos \theta \left( \frac{\partial}{\partial u} + \frac{\partial}{\partial \eta} \right),
\]
\[ Y_2 = \frac{a \sinh^2 \xi \sin^2 \eta}{\sqrt{\sinh^2 \xi + \sin^2 \eta}} \left( \sin 2\theta \frac{\partial}{\partial \xi} - \cos 2\theta \frac{\partial}{\partial \eta} \right) - a \frac{\cosh^2 \xi \cos^2 \eta}{\sqrt{\cosh^2 \xi + \cos^2 \eta}} \frac{\partial}{\partial \eta}, \]
+ 2a \cosh \xi \cos \eta \sin \theta \frac{\partial}{\partial \theta} - a \sinh \xi \sin \eta \sin \theta u \frac{\partial}{\partial u} \]

\[ Y_3 = a \cosh \xi \cos \eta \left[ 2 \frac{\sinh \xi \sin \eta}{\sqrt{\sinh^2 \xi + \sin^2 \eta}} \left( \sin \theta \frac{\partial}{\partial \eta} + \cos \theta \frac{\partial}{\partial \xi} \right) + \coth \xi \cdot \cot \eta \frac{\partial}{\partial \theta} - u \frac{\partial}{\partial u} \right] \]

\[ - a \sinh \xi \sin \eta \cos 2\theta \frac{\partial}{\partial \theta}, \]

\[ Z_1 = \frac{\sinh \xi \sin \eta}{\sqrt{\sinh^2 \xi + \sin^2 \eta}} \left( \cos \theta \frac{\partial}{\partial \xi} + \sin \theta \frac{\partial}{\partial \eta} \right) + \coth \xi \cdot \cot \eta \frac{\partial}{\partial \theta}, \text{ and} \]

\[ Z_2 = u \frac{\partial}{\partial u}. \]

The commutator table of the eleven-dimensional Lie symmetry algebra is given in Table 1.
References


Table 1 The commutator table of the eleven-dimensional Lie symmetry algebra.
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Table 1
Figure Captions

Figure 1 (a) The partial distribution of the Gurken gradient for stage 10A wild-type egg chambers. (b) The partial distribution of the Gurken gradient obtained by overexpressing Dlp for stage 10A 1st filial generation egg chambers. The scale bars both are 12 μm in Fig. 1 (a) and (b), respectively.

Figure 2 Raman spectra of the global distribution of the Gurken gradient for (a) wild-type and (b) over-expressing Dlp after linear background subtraction. The experimental data were contingent on linear polarization by vertical and horizontal polarizers, respectively.

Figure 3 The asymmetric distribution of the Gurken gradient possessed of (a) $X_{23}$ type and (b) $X_1$ type symmetric operators for stage 10A wild-type egg chambers and Dlp, respectively. The insets show schematically the global distribution of Gurken gradient for stage 10A egg.
Figure 1
Figure 2
Figure 3