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Figure 5d), revealing that this data analysis scheme is highly sensitive to receptor interaction. The $V(\overline{R_r^2})$ value of the correlated Qdot585-EGF-EGFRs is considerably lower in A431 cells, attributable to highly effective receptor-lipid and receptor-receptor interactions in A431 cells Türkcan et al. (2013). To inspect the nature of interactions and the relevance to receptor-induced lipid ordering, we again took advantages of the drug effects with nystatin and M β CD. Figure 6b and c display the MSD histograms of the correlated Qdot585-EGF-EGFRs. Pretreatment of HeLa cells with M β CD shifts the MSD profile of liganded EGFRs to the side of higher diffusion constant. M β CD treatment also broadens the MSD profile of liganded EGFRs in A431 cells. The $V(\overline{R_r^2}) - \overline{R_r^2}$ plots for the three cell lines pretreated with nystatin are presented in Figure 6(e). Correlated Qdot585-EGF-EGFRs appear to experience a weaker interaction in the nystatin-treated A431 cells, as evidenced by an increased $V(\overline{R_r^2})$ value. This observation may be explained with less stable lipid domain due to lower amount of cholesterol, resulting in larger variance of diffusing step size of the correlated receptors. By contrast, the effective interaction becomes stronger in nystatin-treated MCF-12A cells, suggesting the effect of cholesterol-mediated interaction is opposite to that of receptor-lipid interaction. The $V(\overline{R_r^2})$ of correlated Qdot585-EGF-EGFR in A431 increases by two orders of magnitude from 10^{-2} of native cells to 1 of M β CD treated cells. Noteworthy, the $V(\overline{R_r^2})$ value can be increased to higher than 10 in M β CD treated HeLa and MCF-12A cells, revealing that a deterministic dimerization interaction will dominate after membrane cholesterol is depleted. These observation results exhibit the vital role of membrane cholesterol in mediating the interaction between liganded receptors in the three cell lines under study.

4 Discussion

A receptor protein can induce order in the surrounding lipids through the receptor-lipid interaction Gómez-Llobregat et al. (2013). The degree of induced lipid order is determined by the effects of receptor-lipid interaction and the amount of cholesterol in the plasma membrane. Recent molecular dynamics (MD) simulations of human receptor tyrosine kinases in various lipid bilayers revealed that the predominant drivers of the receptor-induced lipid ordering domains may originate from electrostatic interactions between the anionic lipids and clustering basic residues in the juxtamembrane starting region of receptors "Hedger et al. (2015). Lipid domains had been predicted to exist in multicomponent membranes and experimentally observed on artificial membranes. For example, thermal fluctuations on a multicomponent membrane can produce inhomogeneities of lipid phases because the order parameters of lipid systems depend not only on the lipid composition but also on the compositional difference of two lipid leaves Shlomovitz et al. (2014). Coupling between inner and outer leaves of an asymmetric lipid bilayer could also produce

2.2 Single-molecule optical measurement

The setup from a 562 nm laser line was used to excite quantum dots in the cells. The detection system was collected with a high numerical aperture (NA) oil immersion objective lens mounted on a inverted optical microscope (IX-70, Olympus Optical Co., Tokyo, Japan) and fitted with a 60x objective lens. We have detected the fluorescence signals with an electron multiplying charge-coupled device (EMCCD) camera (E-990, Photometrics Inc., Tucson, AZ, USA).

2.3 Data analysis

Single-molecule optical trajectories of protein under study were recorded for a long time with a frame period of ≈ 20 ns. Position coordinates of single-molecule protein were extracted from a set of images. A typical MSD (step of 100 nm) in a long cell is presented in Figure 2. The mean position in consecutive frames was connected to form a single-molecule trajectory by using single-step tracking algorithm (Segal, 2008). Events of correlated diffusion were extracted from a single-molecule trajectory by using the correlation function approach (Mittelman et al., 2008). The mean squared displacement (MSD) $\langle R_r^2(t) \rangle = \langle [x(t) - x(0)]^2 + [y(t) - y(0)]^2 \rangle$ was calculated from single-molecule trajectories. The localization accuracy of our apparatus was approximately 40 nm, implying an accuracy of 0.002 μm^2 for $\overline{R_r^2}$ determination. We presented a histogram of MSD and statistical values $V(\overline{R_r^2}) = \overline{R_r^2}^2 / \overline{R_r^2}^2$ as a comparison plot for $\overline{R_r^2}$ and $V(\overline{R_r^2})$ to identify the nature of receptor-induced diffusion in environment, and $V(\overline{R_r^2})$ can reveal the nature of interaction or mechanism of interaction between receptor protein and its environment (Lee et al., 2014). An increase of $V(\overline{R_r^2})$ value when a molecule repeatedly visits a restricted domain, the characteristic of $\overline{R_r^2}$ and $V(\overline{R_r^2})$ of the lipid domain is compared to the trajectory, resulting in the formation of a peak of the corresponding protein in the plot.

The mathematical foundation of the method has been detailed in Gómez-Llobregat et al. (2013). Here we summarize some key findings to facilitate further discussion. For molecules under free diffusion, $V(\overline{R_r^2})$ has a constant value of 1. As a receptor protein diffuses under a strong confinement of its environment, $V(\overline{R_r^2})$ can be a large positive value (Türkcan et al., 2013). In contrast, $V(\overline{R_r^2})$ of a receptor is reduced to value 2 when it is confined in a lipid domain. This can be understood as follows. As a receptor protein is confined in a lipid domain, the diffusion process for it is 2D (Gómez-Llobregat et al., 2013; Ash & Orr, 2008). As a receptor protein diffuses over an area A , the self-avoidance factor may not be the diffusion process for a short receptor, which causes a large variance in the diffusion step size. Furthermore, the lower the protein diffusion, the larger the variance is. In the case of free diffusion, $V(\overline{R_r^2})$ can reach a constant level.

Figure 2. Single-molecule trajectory of a protein under study. The plot shows the position coordinates (x, y) in nanometers over time (t) in seconds. The trajectory starts at the origin (0,0) and moves in a generally random direction, with some periods of slower movement and some periods of faster movement. The x-axis ranges from 0 to 1000 nm, and the y-axis ranges from 0 to 1000 nm. The time axis ranges from 0 to 1000 s.

Figure 2

Figure 3. Histogram of the mean squared displacement (MSD) and the variance of the MSD. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²). The MSD values are concentrated between 0 and 500 nm², and the variance values are concentrated between 0 and 500 nm². The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 3

Figure 4. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 5. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 6. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 7. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 8. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 9. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 10. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 11. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 12. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 13. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 14. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 15. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 16. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 17. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 18. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

Figure 19. Histogram of the mean squared displacement (MSD) and the variance of the MSD for different receptor-lipid and receptor-receptor interactions. The plot shows the distribution of MSD values (x-axis, 0 to 1000 nm²) and the corresponding variance values (y-axis, 0 to 1000 nm²) for different receptor-lipid and receptor-receptor interactions. The x-axis is labeled 'MSD (nm²)' and the y-axis is labeled 'Variance (nm²)'.

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