Probing Membrane Lipids: a Perspective from Solid-State NMR Study

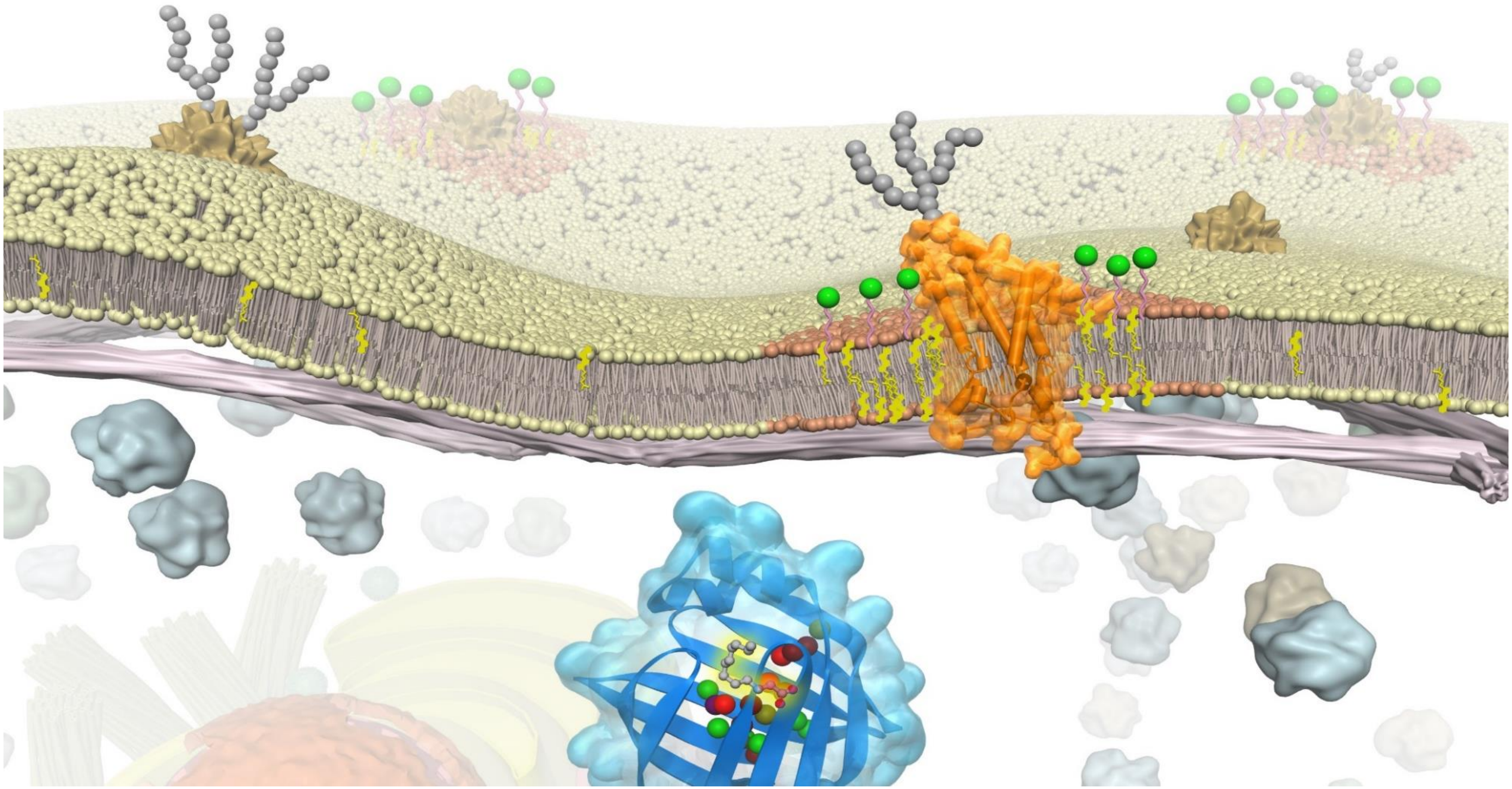
Michio Murata

村田道雄

大阪大学大学院理学研究科

JST ERATO脂質活性構造プロジェクト

Biomembrane comprise diverse lipids and proteins and form complex structures without proteins



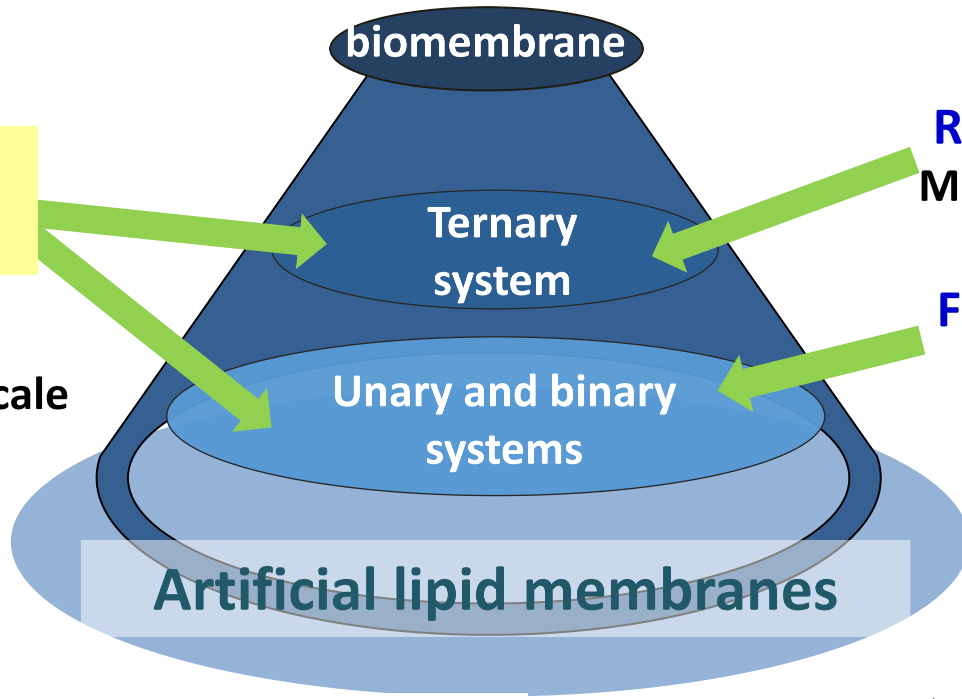
Contents

Approaches towards membrane lipids with variable time and spacious scales

Our objective: **Elucidation of the molecular basis of lipid raft formation**

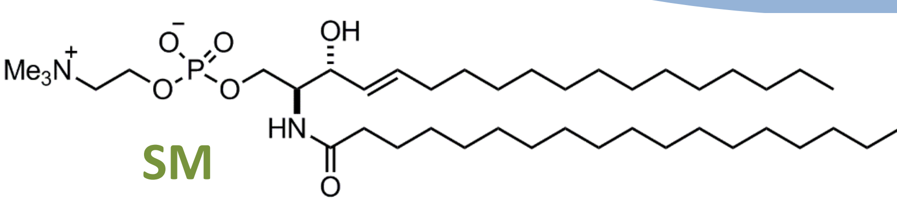
Solid state NMR
(^{2}H NMR, REDOR)

Molecular level
10 μs – 10 ms time scale

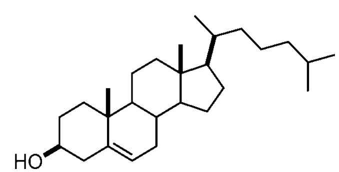


Raman Imaging
Macroscopic membrane

Fluorescent lifetime
Molecular level
several ns time scale



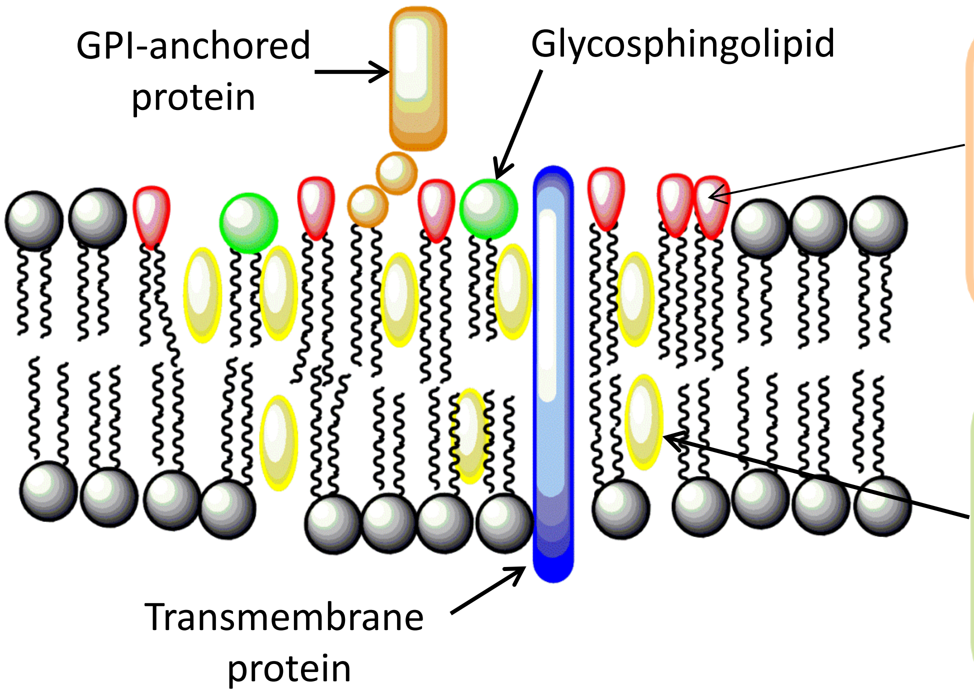
SM



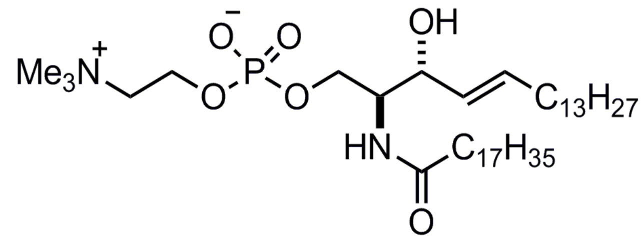
Cho

Lipid behavior in various membranes
(mobility and intermolecular interaction)

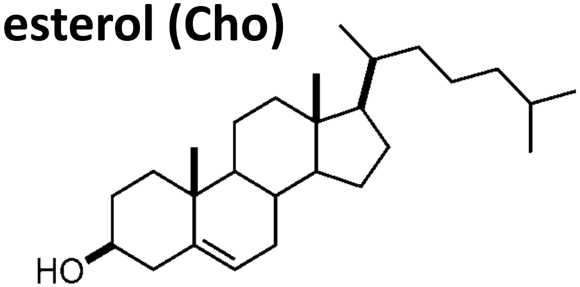
Lipid rafts



Sphingomyelin (SM, SSM)



Cholesterol (Cho)



- Resistance to solubilization with Triton X-100 (DRM)
- Ordered lipids (Lo phase) undergoes domain formation
- Implication in many cellular processes (signal transduction etc.)

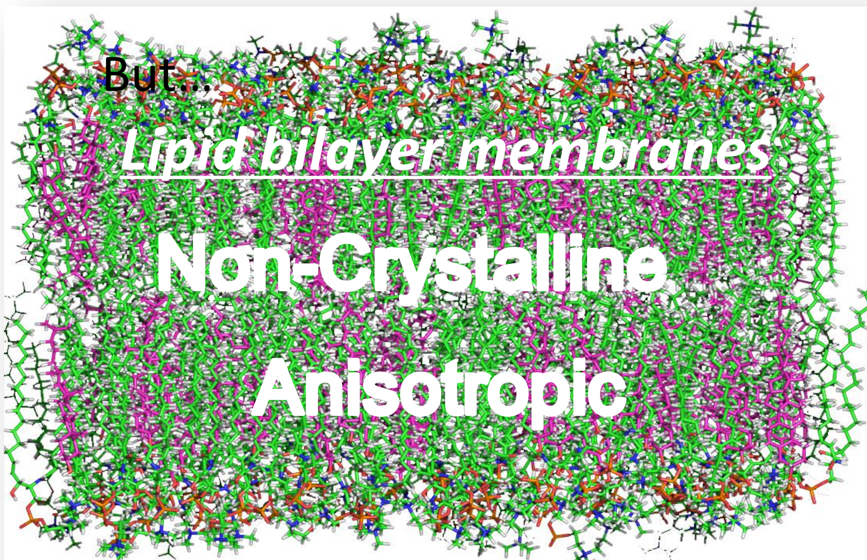
Molecular basis of lipid raft formation ?

1) Simons,K.; Ikonen,E. *Nature*, **1997**, *387*, 569-572. 2) Pike, L. J. *J. Lipid Res.* **2006**, *47*, 1597-1598.

How can we elucidate the conformatoin and interactions of lipids in membrane?

- Lipid-lipid & lipid-protein interaction in membrane
- Drug-membrane interaction

→ **Elucidation of 3D structures and interactions of lipids in membrane is essential**



→ Difficulties in structure elucidation

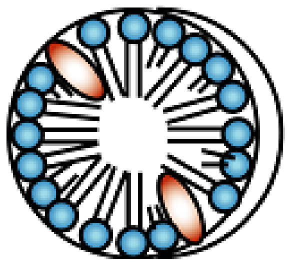
× X-ray Crystallography

△ Solution NMR

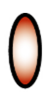
→ **Solid state NMR works in such weird systems ?**

Micelles vs Bicelles for membrane mimic

Micelles

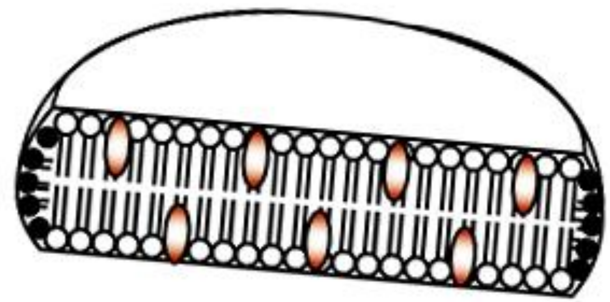


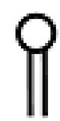
Detergent



Ster

Bicelles





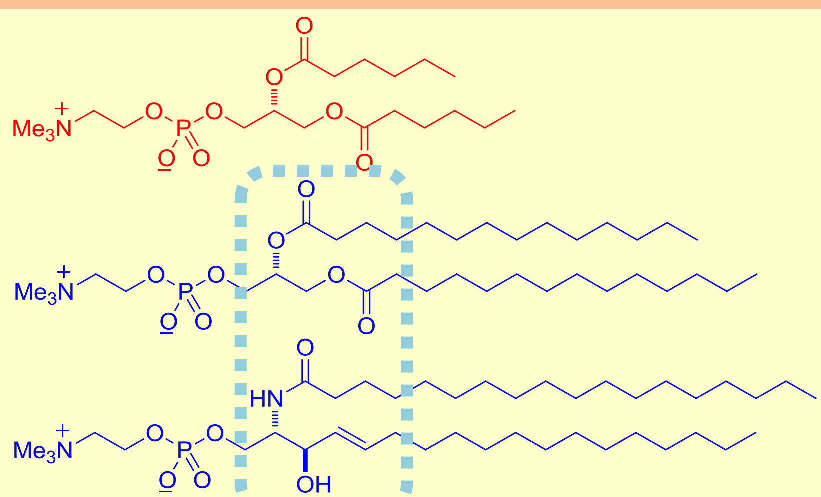
Phospholipid

nt

DHPC

DMPC

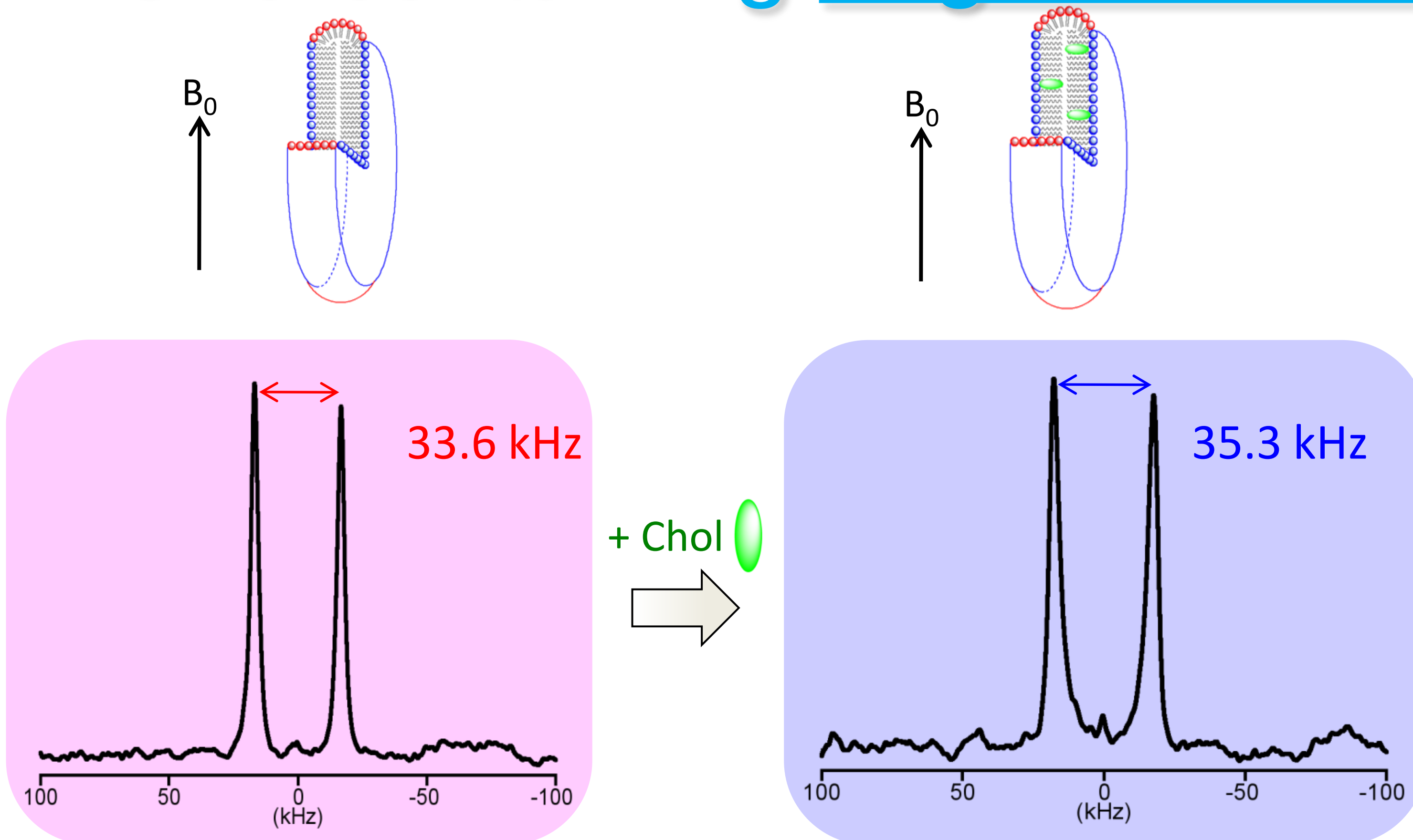
SM



- Many exam
- High curvat

structure
litions;
nc.

Ordering of SM-d_2 bound in Cho-containing large bicelles

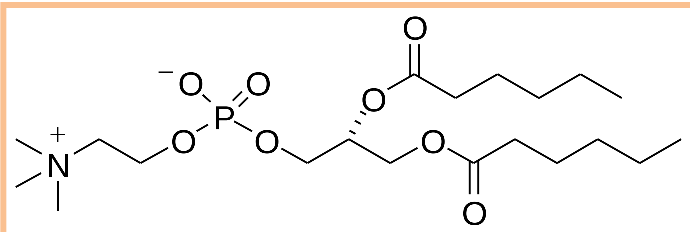


10'-d_2-SM/DHPC(4/1)

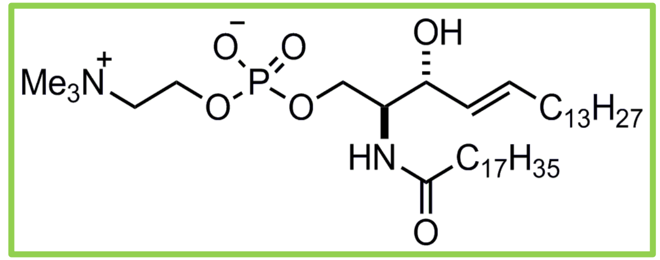
10'-d_2-SM/DHPC/Chol (4/1/0.4)

10% Cho siginificantly ehnaces the ordering of SM bicelle membranes

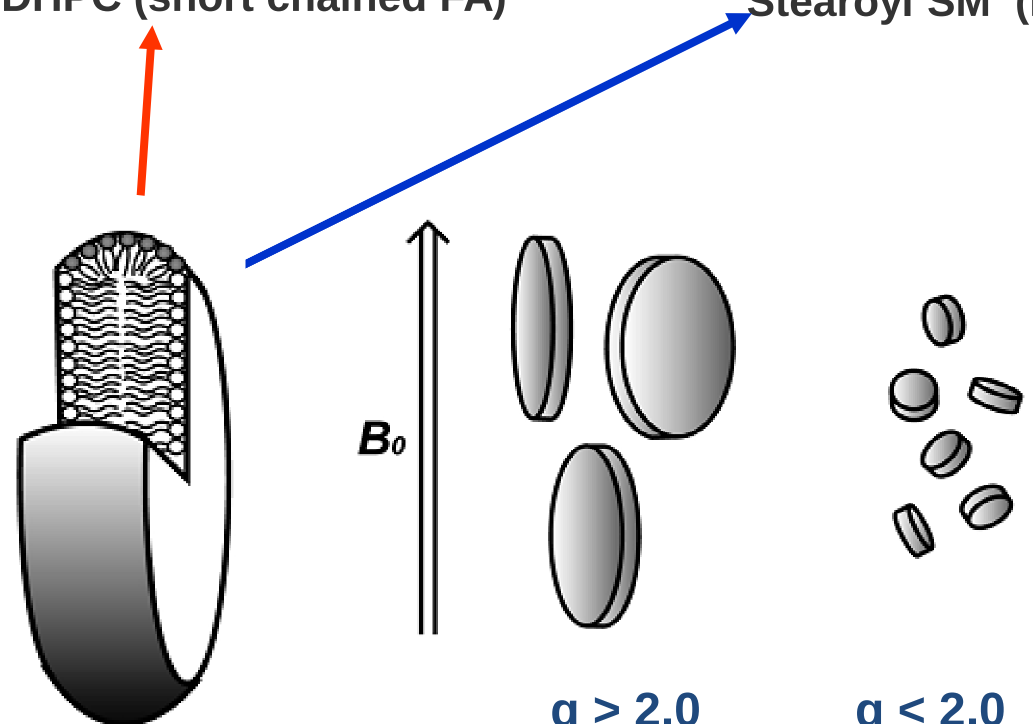
Size-dependent orientation of bicelles along magnetic field



DHPC (short chained FA)



Stearoyl SM (major constituent)



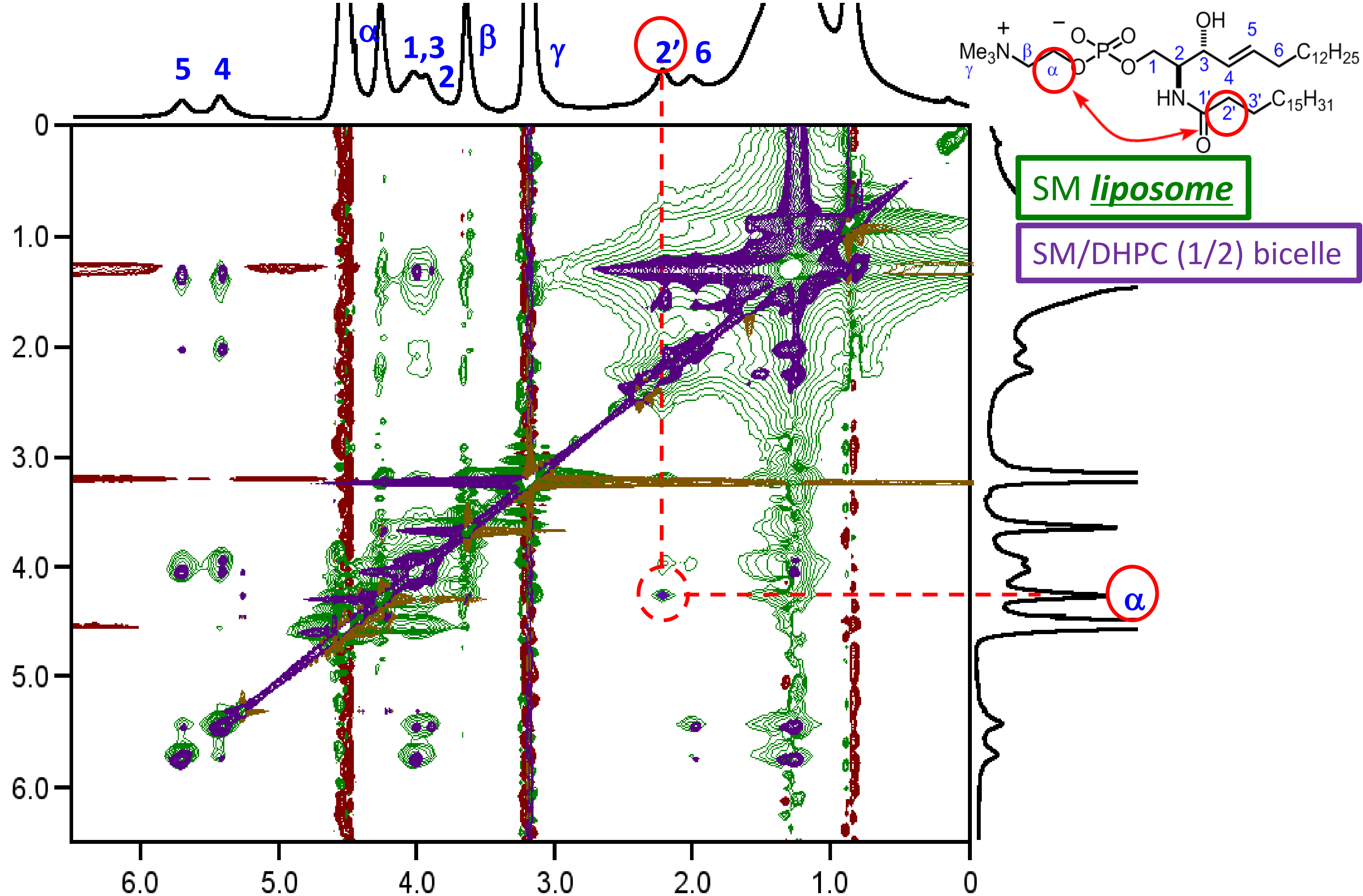
q = [SSM] / [DHPC]

Small Bicelles

- **Planar bilayer structure**
- **Non-orientation along B_0**

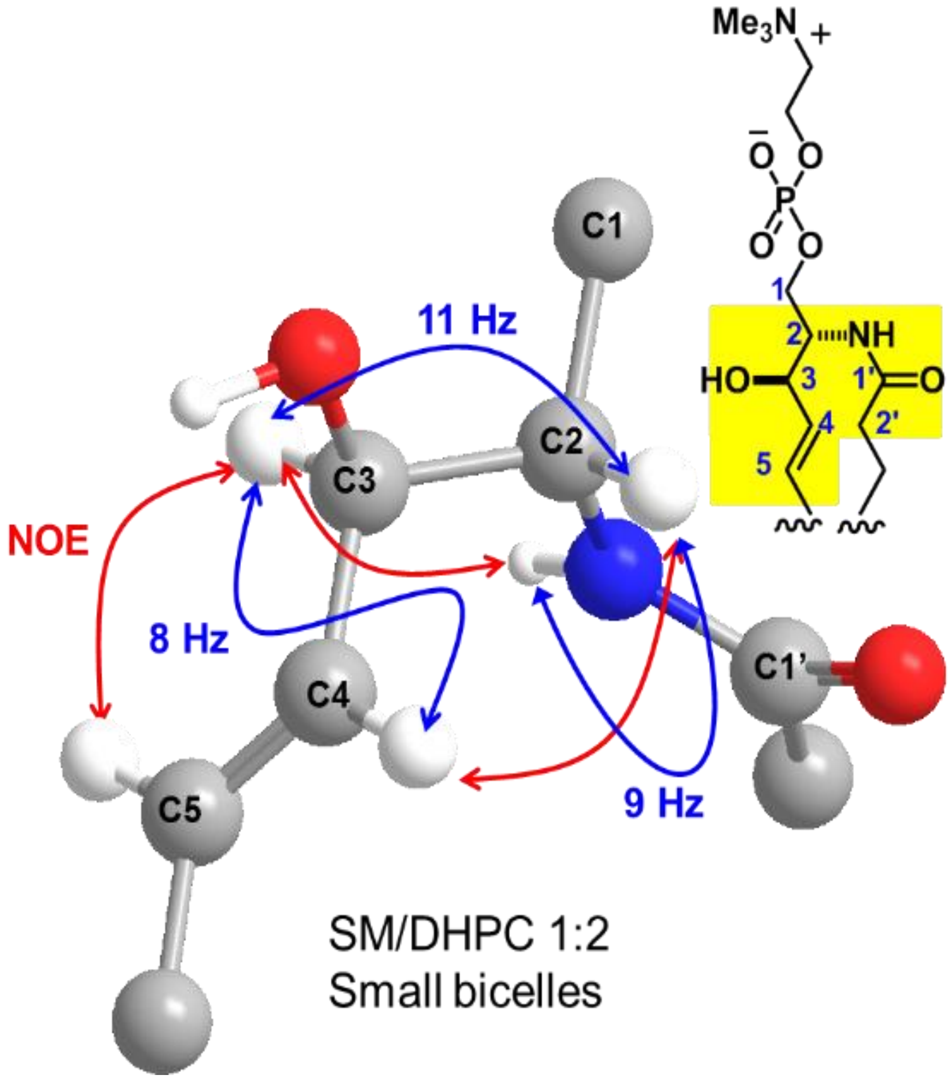
High mobility of small bicelles enables high resolution NMR spectra even for ^{1}H nucleus.

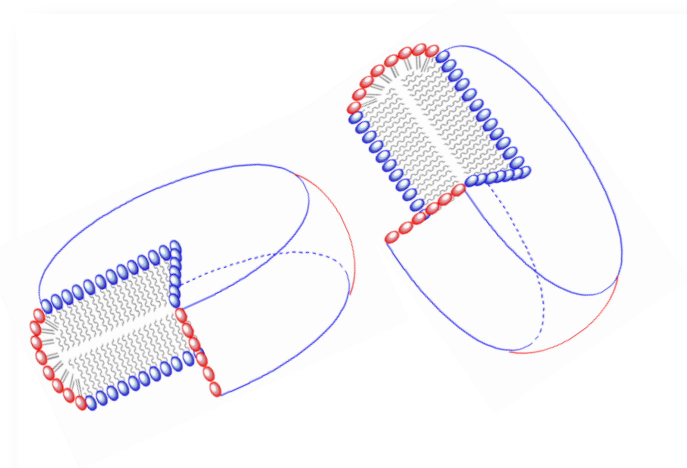
^{1}H NMR NOESY of bicelles under MAS



MAS: 5 kHz, Mixing time: 30 ms, Temp.:37 ^oC

Conformation of SM head group deduced from NOEs and *J* coupling in small bicelles



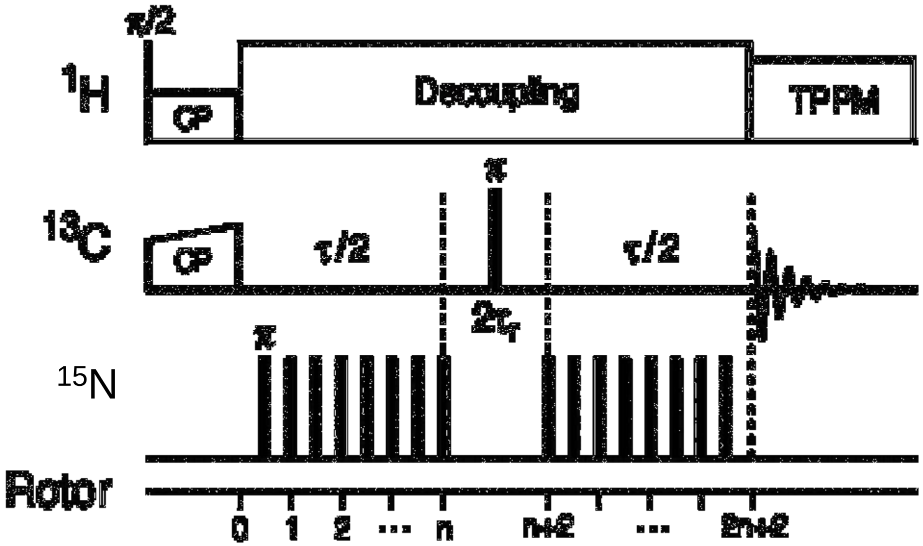


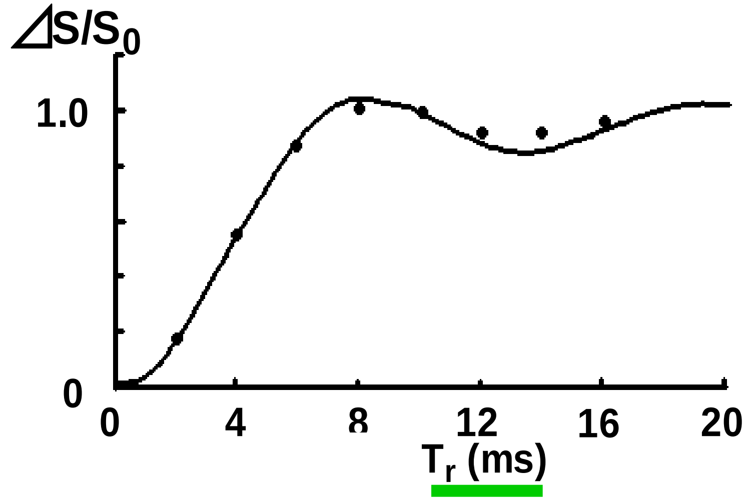
NOEs are similar between the Cho-containing and Cho-free bicelles

Conformation of SM is similar between pure SM and SM-Cho

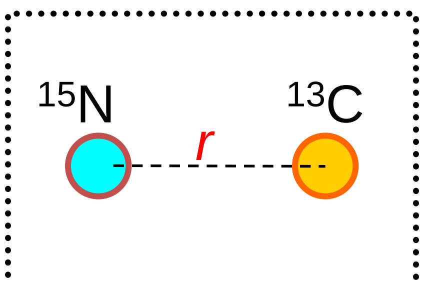
Yamaguchi, T. Suzuki, T., Yasuda, T. Oishi,T., Matsumori, N., Murata, M. *Bioorg. Med. Chem.* **20,** 270-278 (2012).

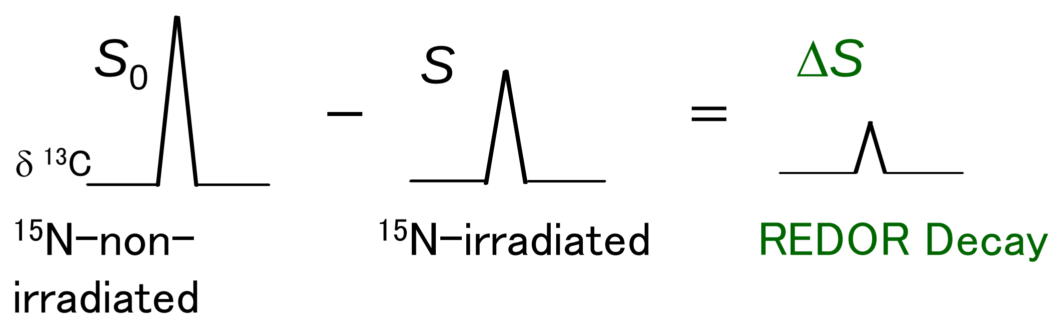
How REDOR works I





Synchronous irradiation
to magic angle spinning





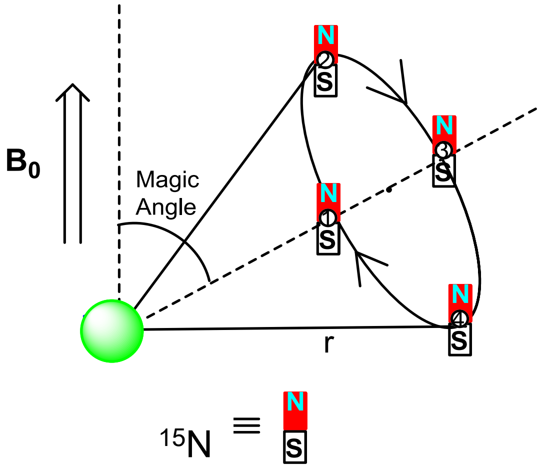
Accuracy is <0.1 Angstrom !

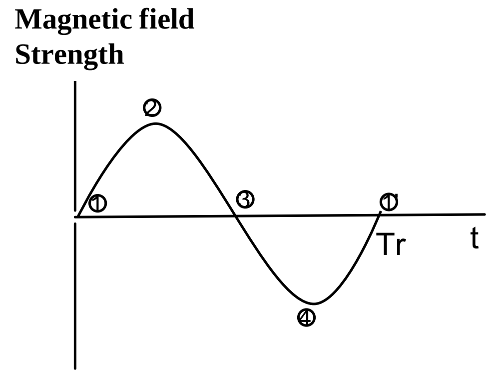
T. Gullion, J. Schaefer, *J. Magn. Reson.*, 1989, 13, 57

*REDOR data; A. Naito, et al., *J. Phys. Chem.* 1996, *100,* 14995

How REDOR works II

MAS (Magic Angle Spinning): S_0



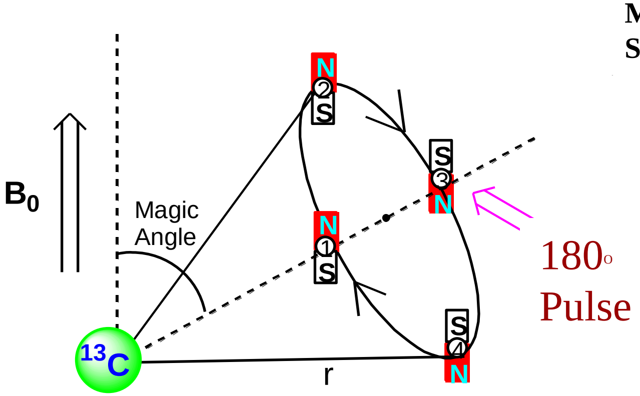


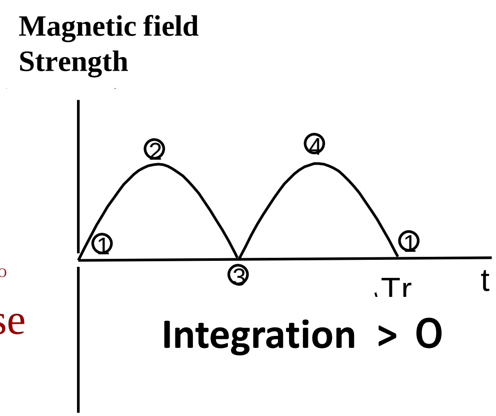
Dipole Coupling

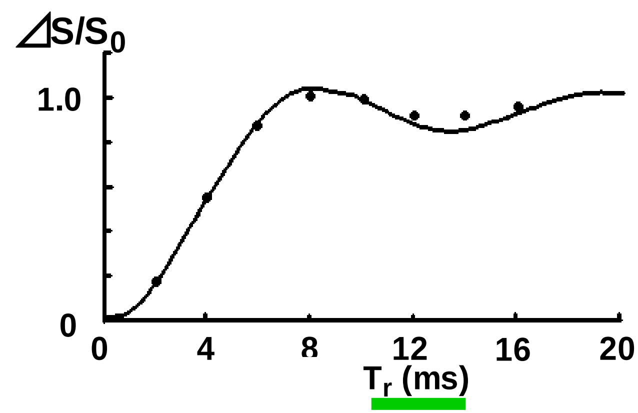
$$D = \frac{\gamma_I \gamma_S h \mu_0}{16 \pi^3 r^3}$$

$$\frac{\Delta S}{S_0} = 1 - [J_0(\sqrt{2} n \tau_r D)]^2 + 2\sum_{k=1}^{\infty} \frac{1}{16k^2 - 1}[J_k(\sqrt{2} n \tau_r D)]^2$$

REDOR: S





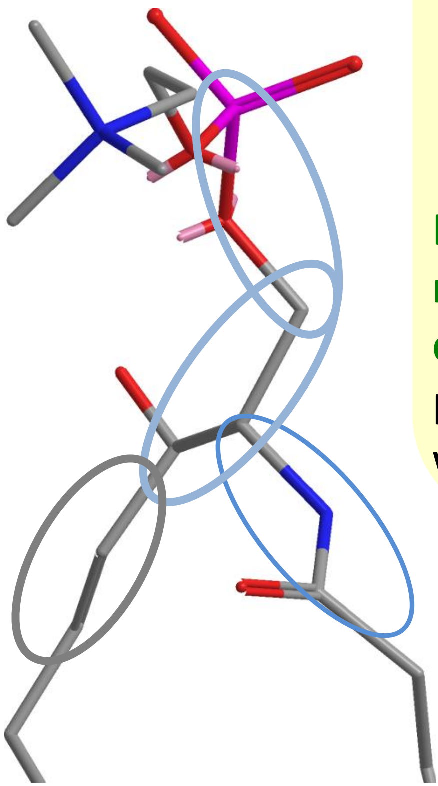


J_n: Vessel Function, $n\tau_r$: REDOR dephasing time γ_I: Gyromagnetic Ratio of I nucleus. γ_S: That of S nucleus
h: Plank const., μ_0: Permeability of Vacuum

Gullion, T. *et al*. *Adv. Magn. Reson.* 13, 57 (1989); Gullion, T. *et al*. *J. Magn. Reson.* 89, 479 (1990).

$^{13}C\{^{15}N\}$REDOR used for evaluation of mobility and orientation

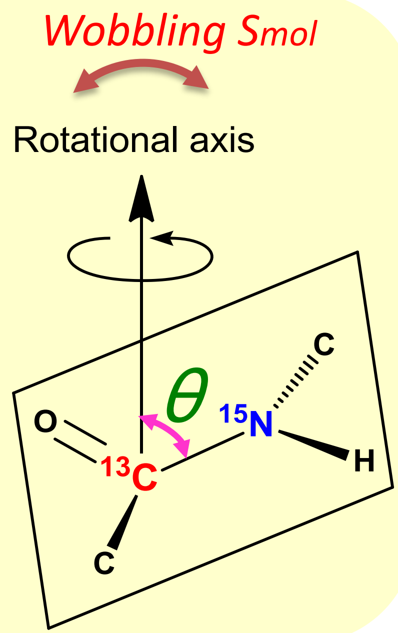
$$D_{C-N} = D_0 \bullet S_{mol} \bullet \frac{3\cos^2\theta - 1}{2}$$

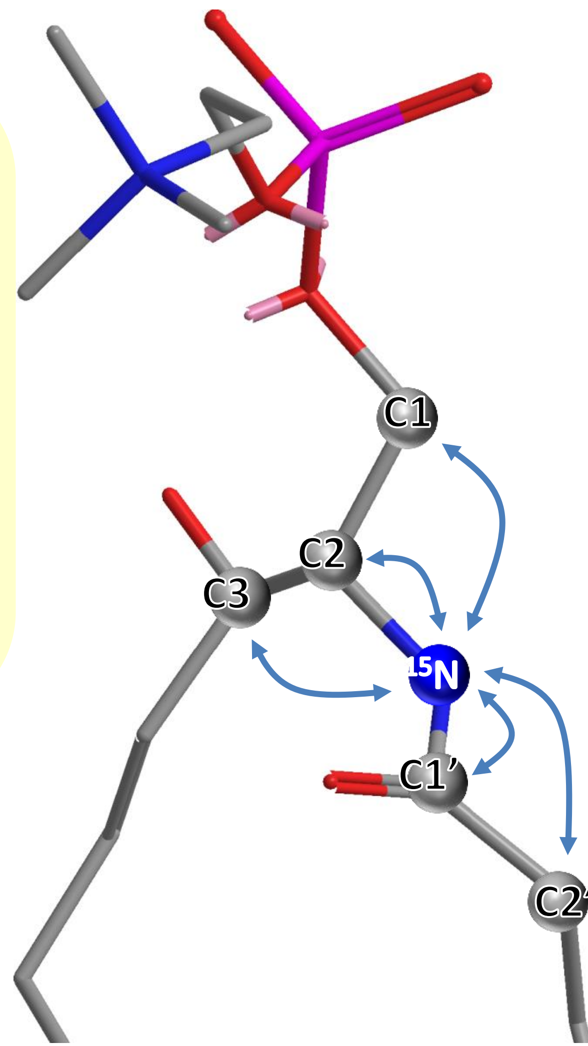


Dipole coupling of rapidly moving mol. depends on

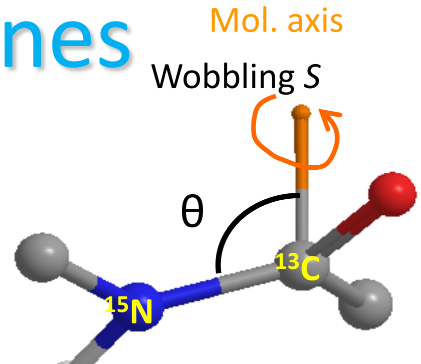
Mol. axis angle θ

Wobbling S_{mol}



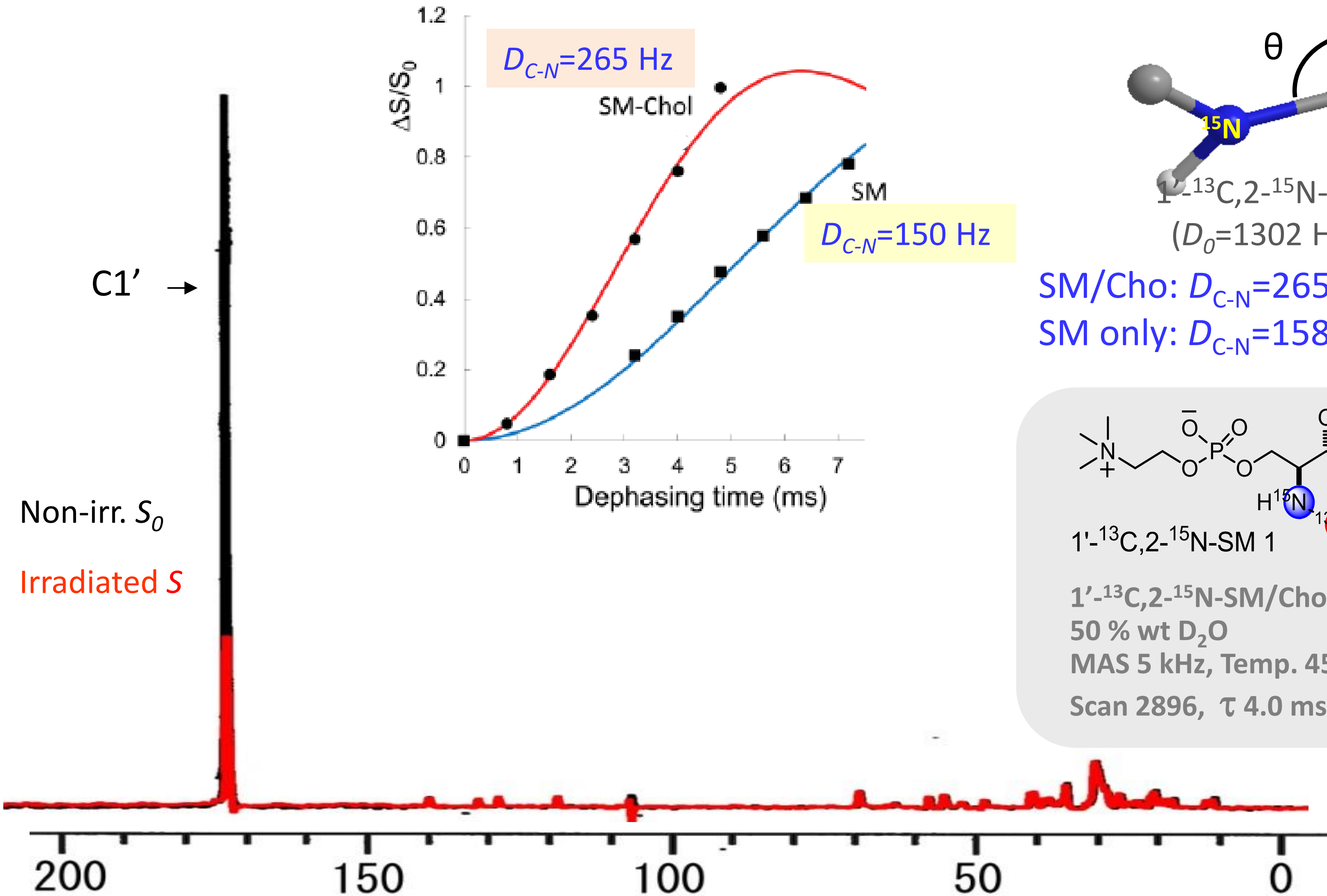


REDOR data for ^{13}C-^{15}N-labeled SM in SM/Chol and SM only membranes



1'-^{13}C,2-^{15}N-SM
(D_0=1302 Hz)

SM/Cho: $D_{C\text{-}N}$=265 Hz
SM only: $D_{C\text{-}N}$=158 Hz

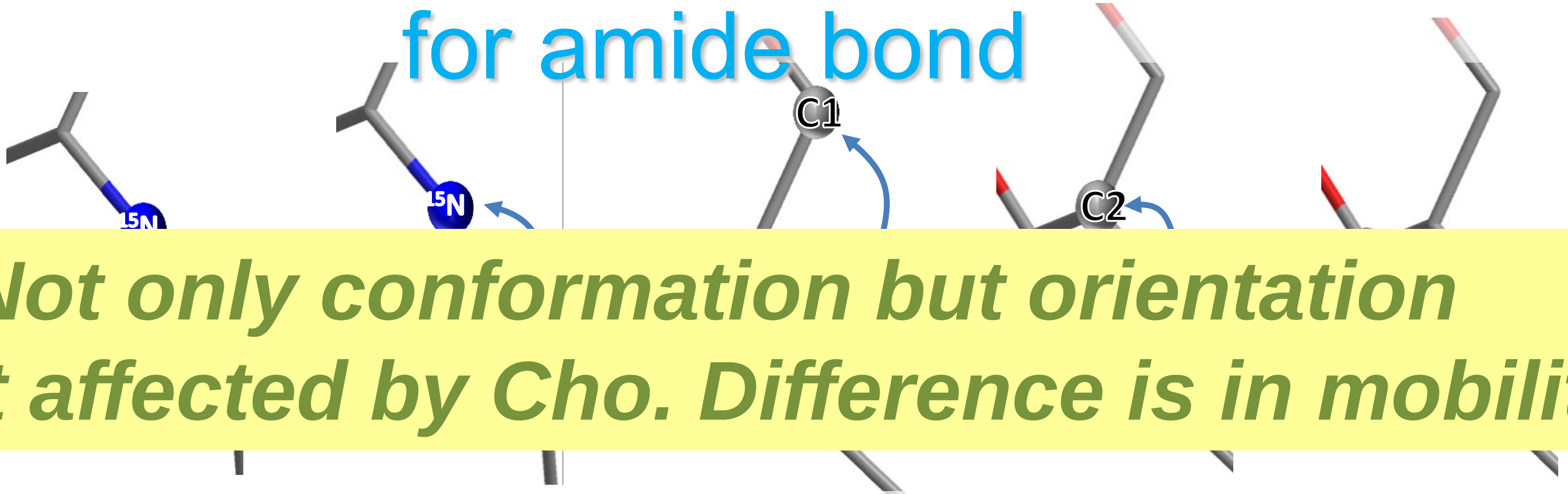


1'-^{13}C,2-^{15}N-SM 1

1'-^{13}C,2-^{15}N-SM/Chol (1/1)
50 % wt D_2O
MAS 5 kHz, Temp. 45˚C,
Scan 2896, τ 4.0 ms

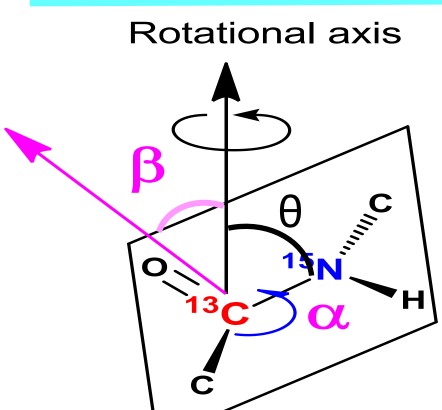
1) Gullion, T *et al. Adv. Magn. Reson.* 1989, *13*, 57-83.

REDOR reveals S_{mol} and orientation for amide bond



Not only conformation but orientation is not affected by Cho. Difference is in mobility

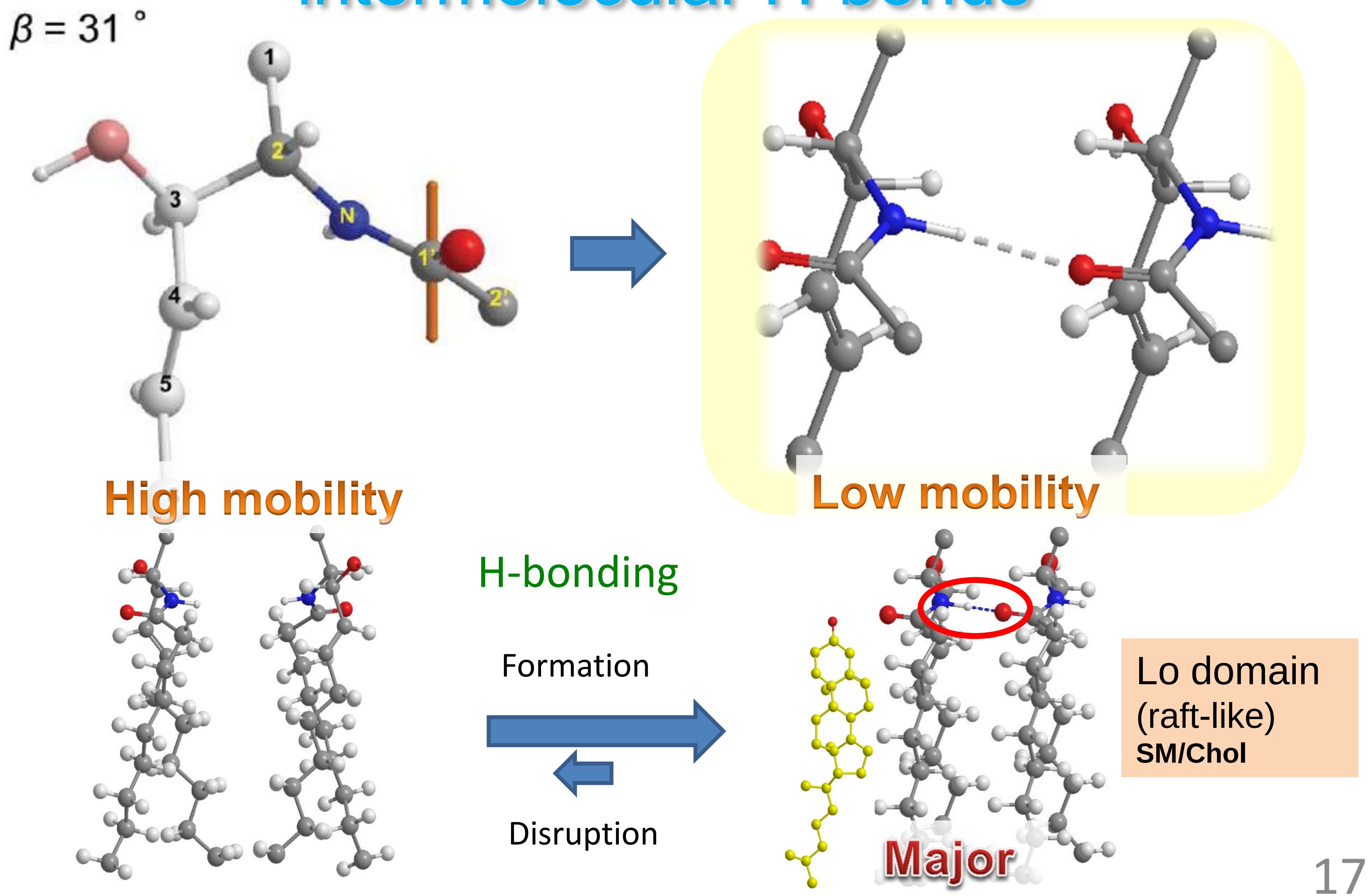
	C1′ / ^{15}N	C2′ / ^{15}N	C1 / ^{15}N	C2 / ^{15}N	C3 / ^{15}N
D_0 (Hz)	1302	232	233	1073	229
$D_{C\text{-}N}$ SM/Chol	265	12	63	82	33
$D_{C\text{-}N}$ SM only	158	2	69	55	48



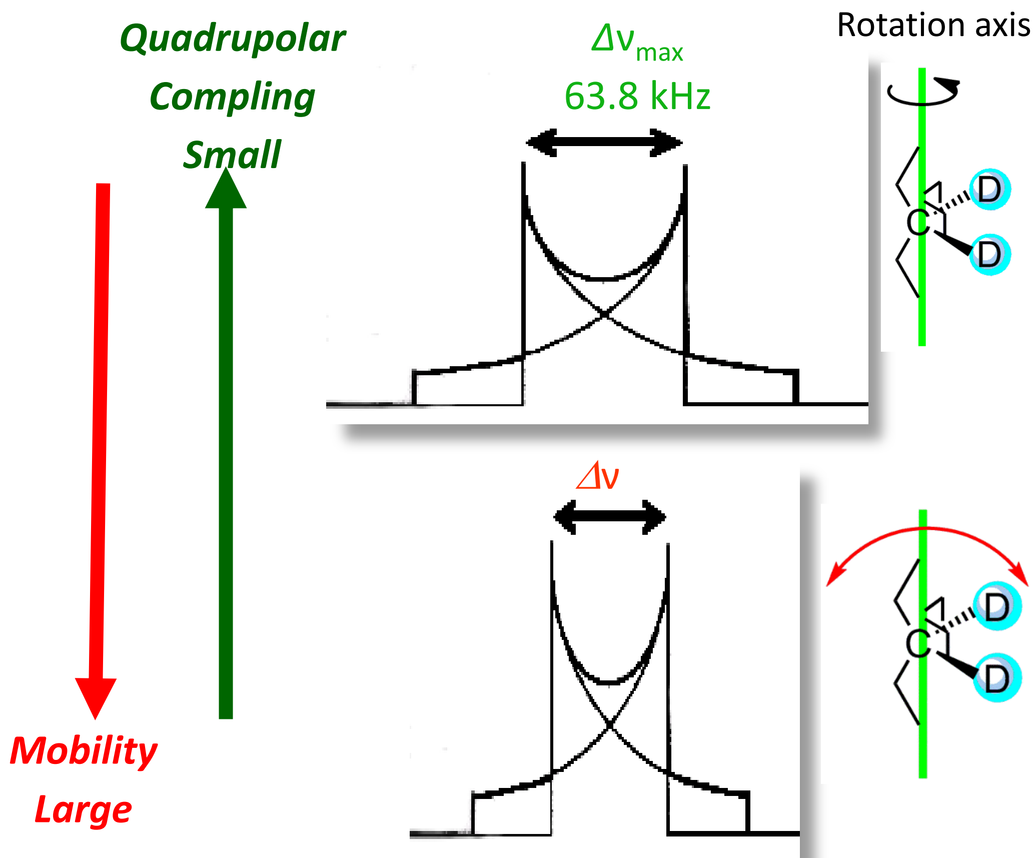
$$D_{C-N} = D_0 \bullet S_{mol} \bullet \frac{3\cos^2\theta - 1}{2}$$

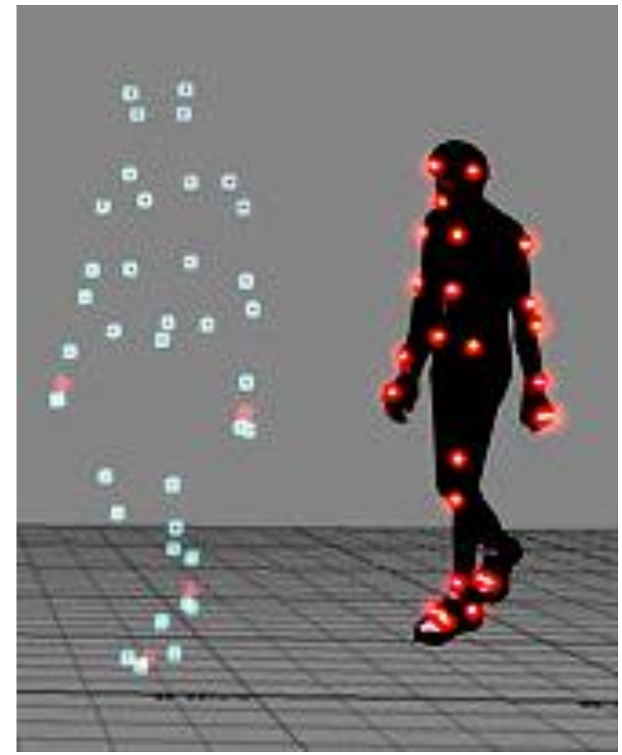
Major conformer in SM-Chol: S_{mol}: 0.94, (α, β) = 166°, 32°
Major conformer in SM only : S_{mol}: 0.70, (α, β) = 158°, 35°

Cho ordering effect and orientation lead to intermolecular H-bonds

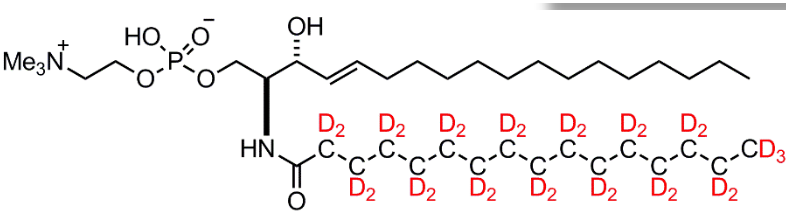


Motion capture of alkyl chains of membrane lipid by ^{2}H NMR



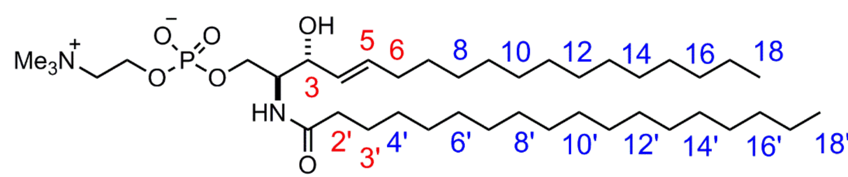


Molecular motion capture



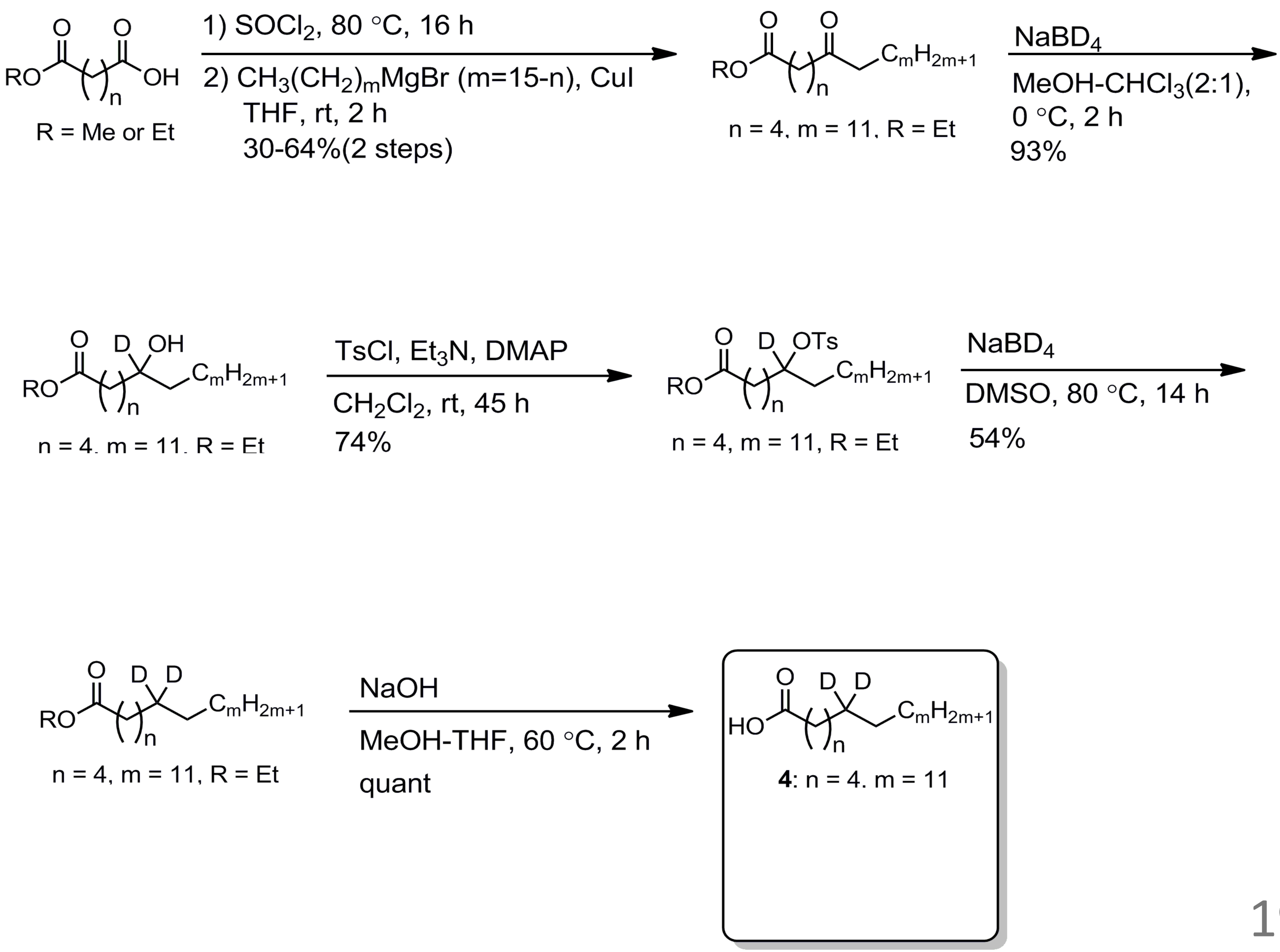
Perdeutero-acyl chain

Palmitoyl-sphingomyelin (PSM)

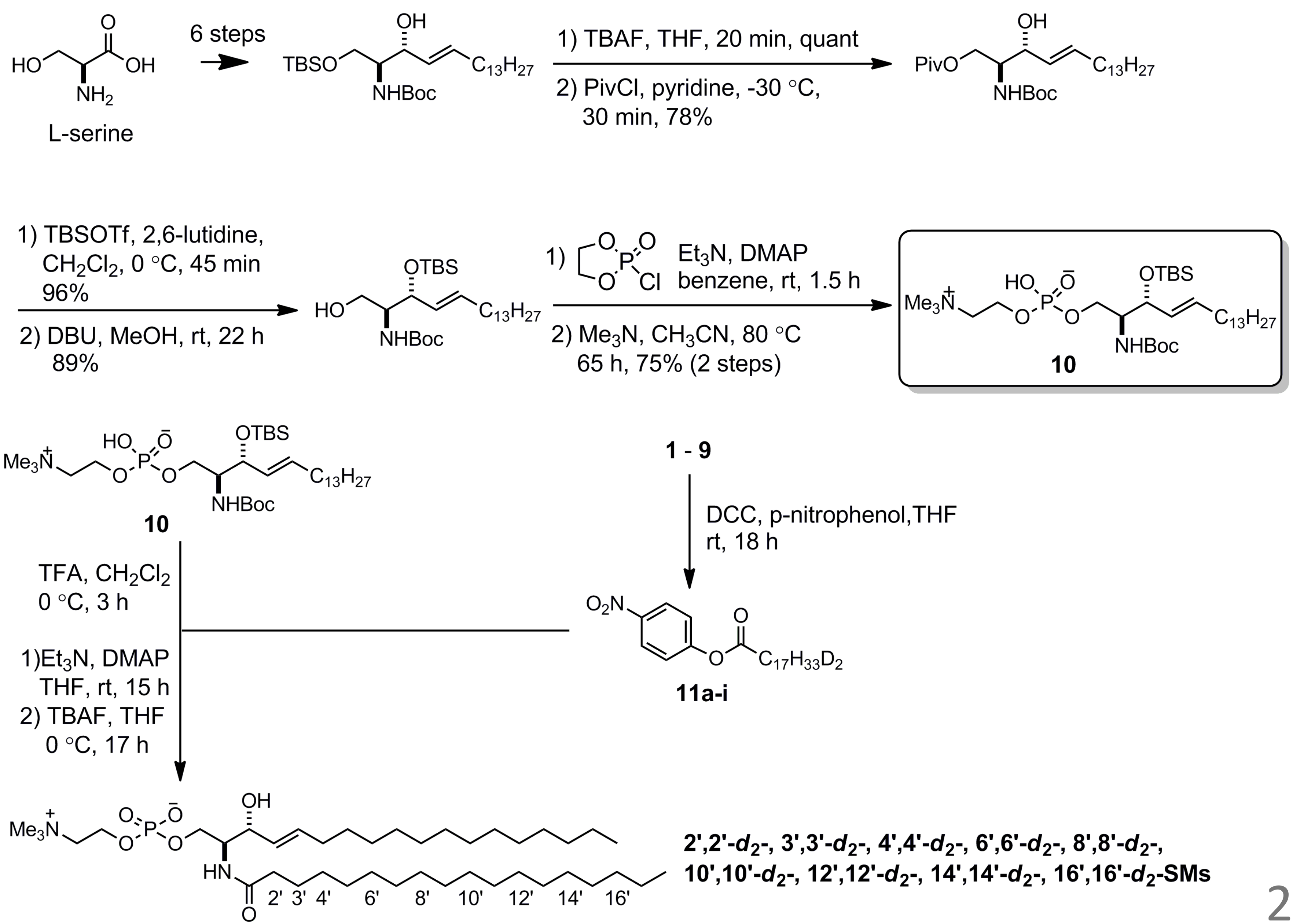


Library of site-specifically ^{2}H-labeled SM

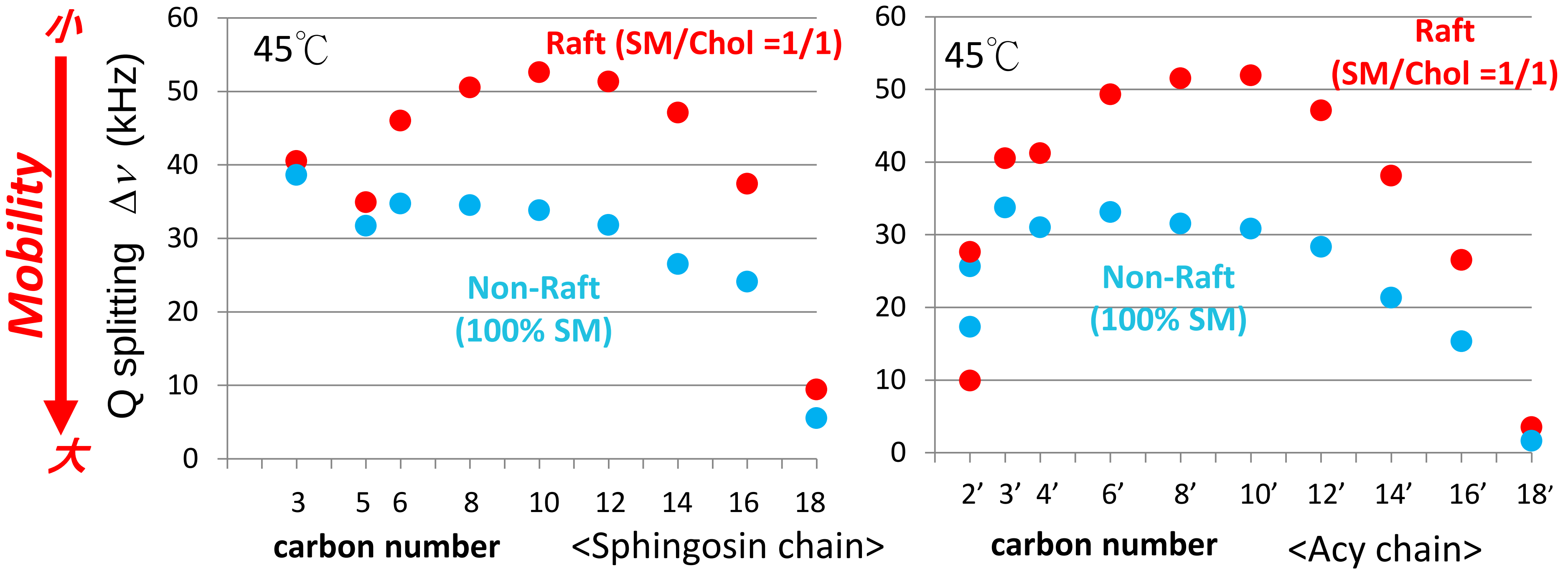
Synthesis of ^{2}H-labeled fatty acids

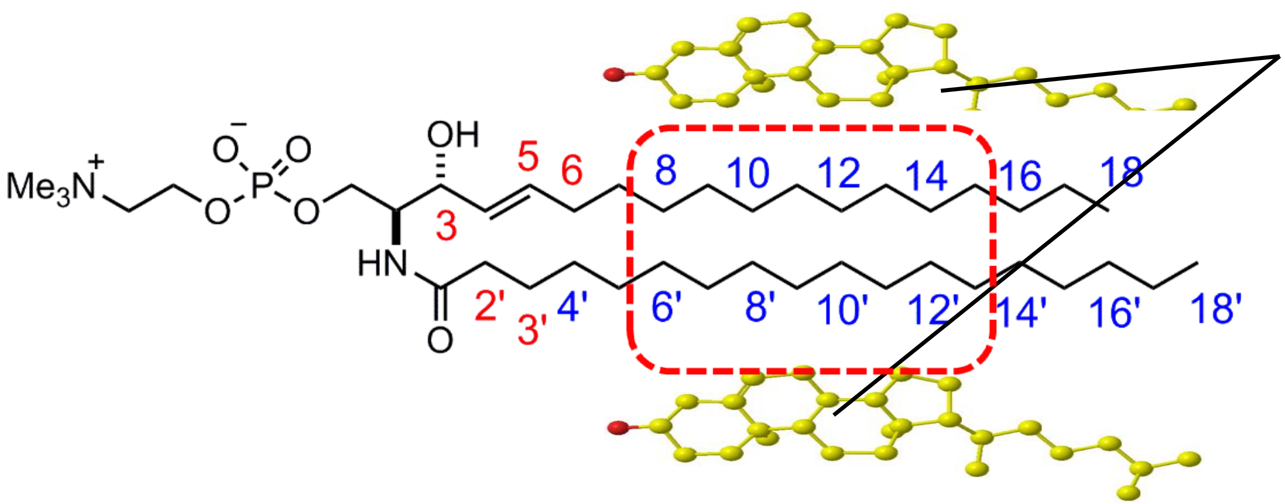


Synthesis of ^{2}H-labeled SM



Depth-dependent order of SM by ^{2}H NMR





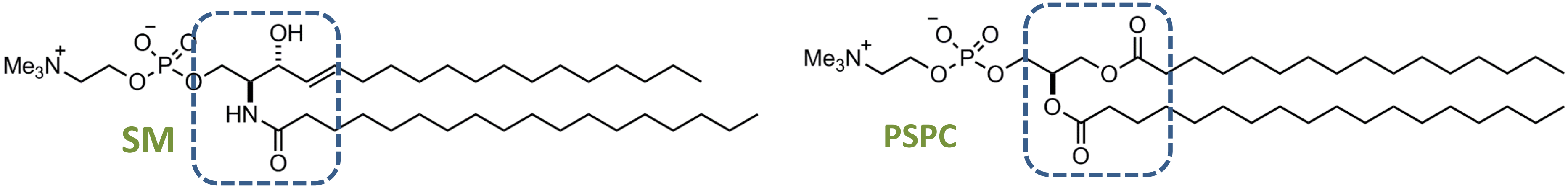
Both alkyl chains interact with Cho similarly.

Matsumori, N.; Yasuda, T. *et al. Biochemistry* **2012**, *51*, 8363-8370.

Contents

Comparison between SM and PC

Both SM and saturaed PC are known to form Lo domains



What is the difference between SM and PC in formation of Lo domains.

Systematic comparison between SM and saturated PC

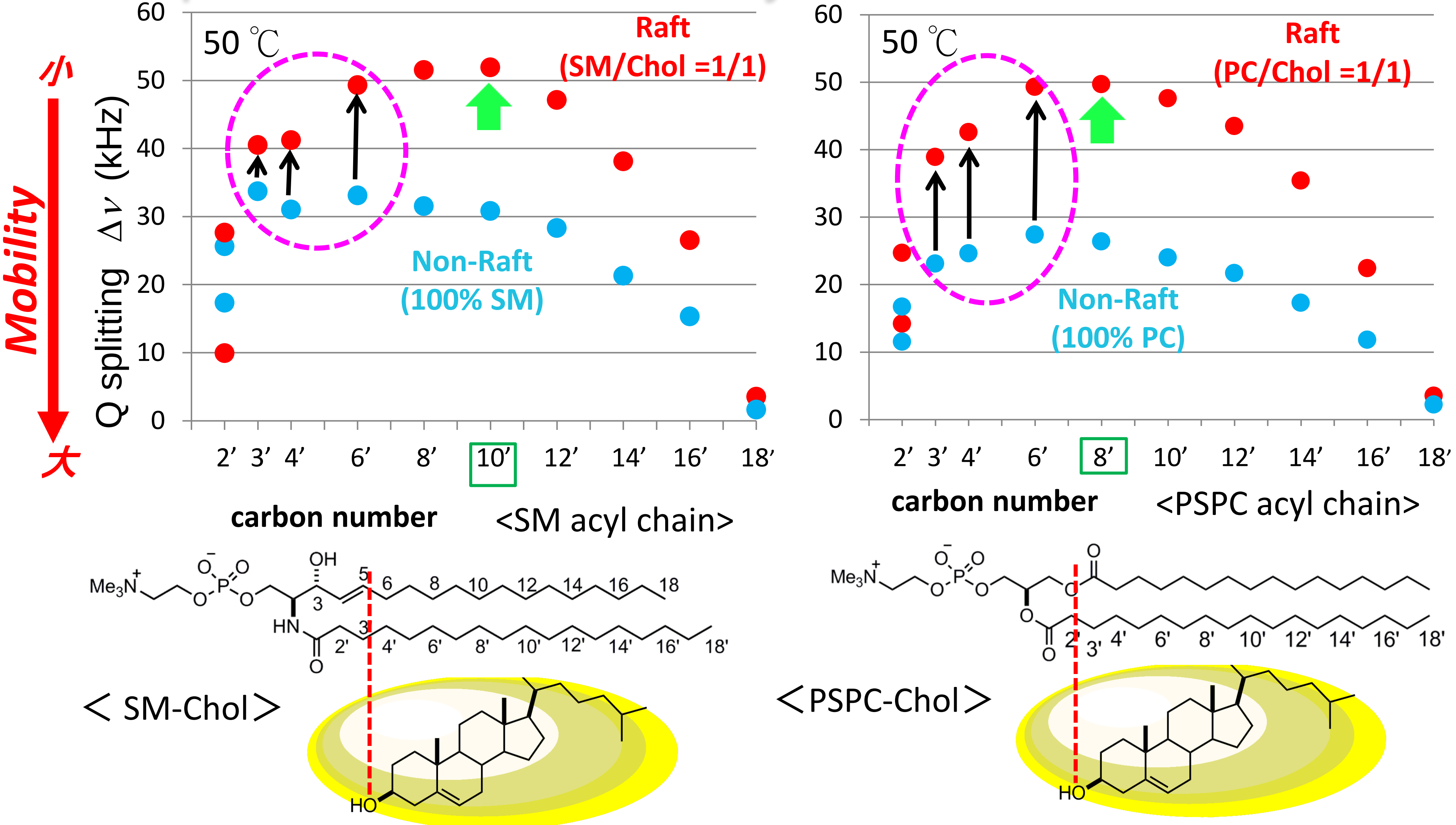
Space : Atomic ～ Molecular ～Entire membrane

Time : nanosecond ～ millisecond

Lipid constituents : Unary system ～ Ternary system

The structure properties make SM preferentially form lipid rafts

Comparison of chain mobility between SM and PSPC

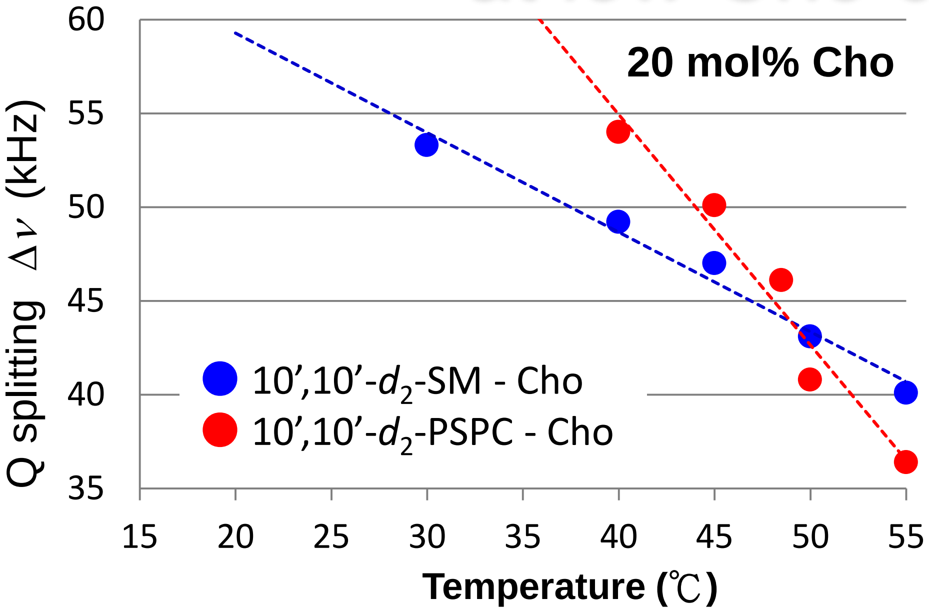


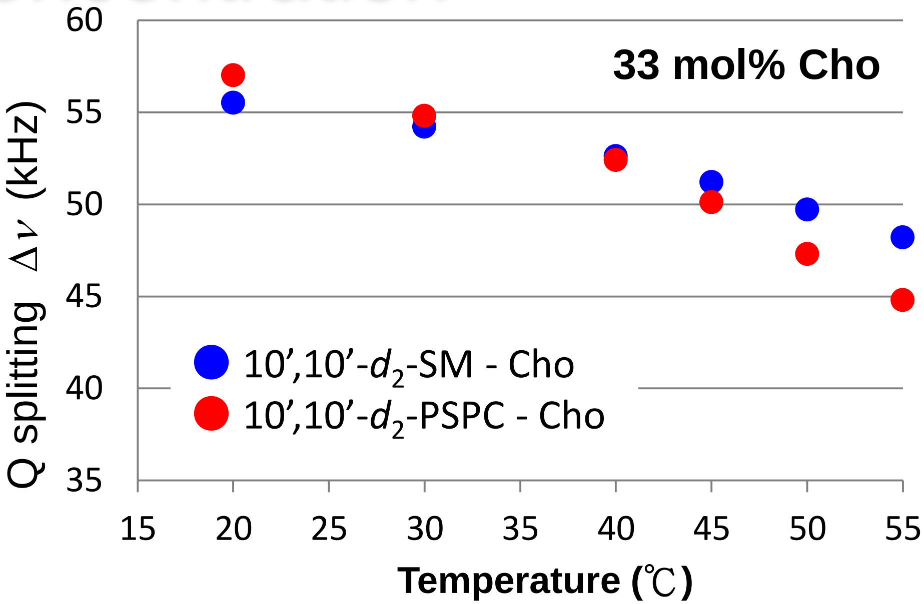
The rigid tetracycle of Cho is located more deeply in SM membrane

Probably due to hydrogen bond network by amide groups of SMs

1) Matsumori, N.; Yasuda, T. *et al*. *Biochemistry* **2012**, *51*, 8363-8370. 2) Yasuda, T. *et al*. *Biophys. J.* **2014**, *106*, 631-638.

Temperature dependent ordering of SM and PC at low Cho concentration

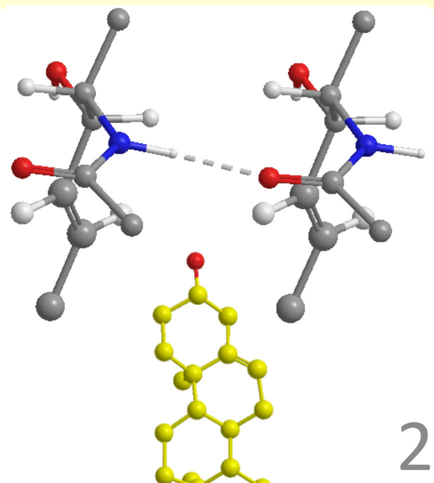




SM-Cho membrane is more tolerant to temperature change than PC-Cho membrane.
(Lesser temperature dependence)

Higher thermal stability

SM intermolecular H-bond (membrane surface)
+
Cho ordering effect (membrane interior)



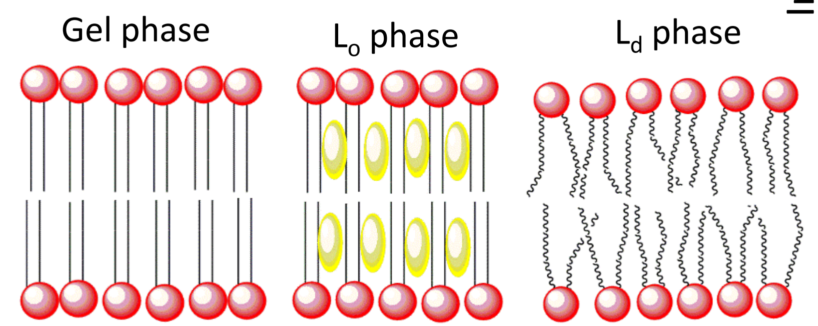
Yasuda, T. *et al*. *Biophys. J.* **2014**, *106*, 631-638.

Evaluation of membrane fluidity in nanosecond time domain -Fluorescent lifetime experiment

Fluorescent lifetime τ

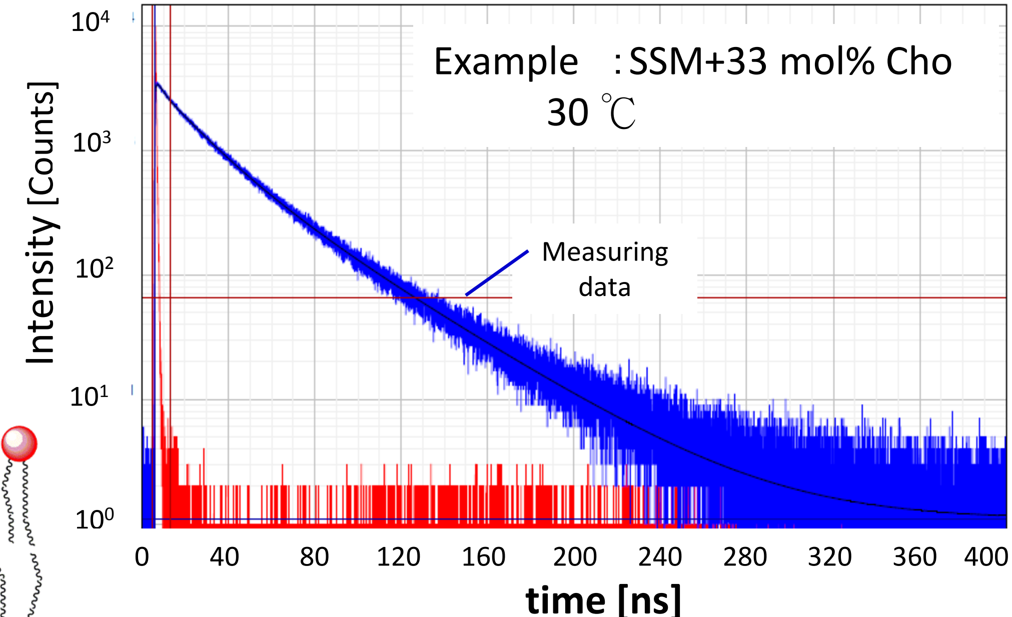
The average time that fluorophore remains in the excited state (ns)

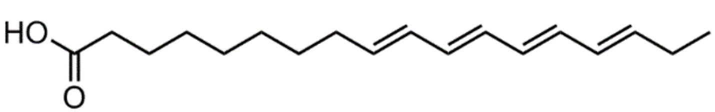
Dependence on lipid phase state



Fluidity Low → High

Lifetime Long ← Short





trans parinaric acid (tPA)

λ_{ex} = 295 nm, λ_{em} = 405 nm

2 mol% of total lipids

※ Deconvolution by two lifetime components

$$I(t) = \sum_{i=1}^{n} \alpha_i \exp(-t/\tau_i)$$

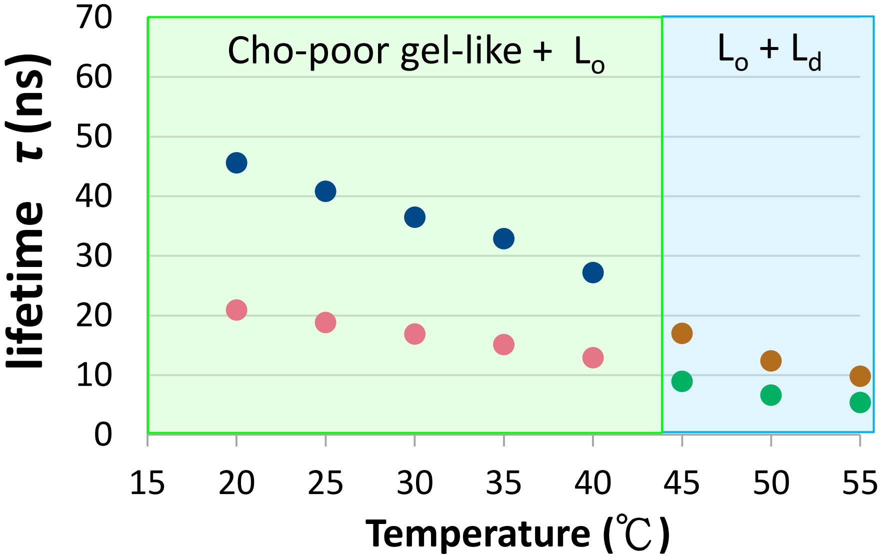
$$= \alpha_1 \exp(-t/\tau_1) + \alpha_2 \exp(-t/\tau_2)$$

τ_1 , τ_2 … lifetime of each component

α_1 , α_2 … fractional amplitudes of each component

Membrane fluidity on nanosecond time scale

SM/33 mol% Cho



τ_1 ● ● Longer lifetime
→ Lower fluid domain

τ_2 ● ● Shorter lifetime
→ Higher fluid domain

Membrane heterogeneity

NMR cannot detect the coexistence of domains.

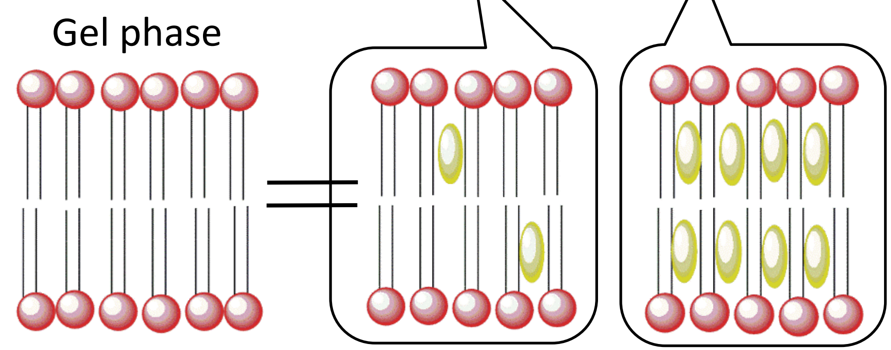
Lipid cluster with short lifetime

The fluidity of phase state : Gel < L_o < L_d

No gel phase exists above T_m.

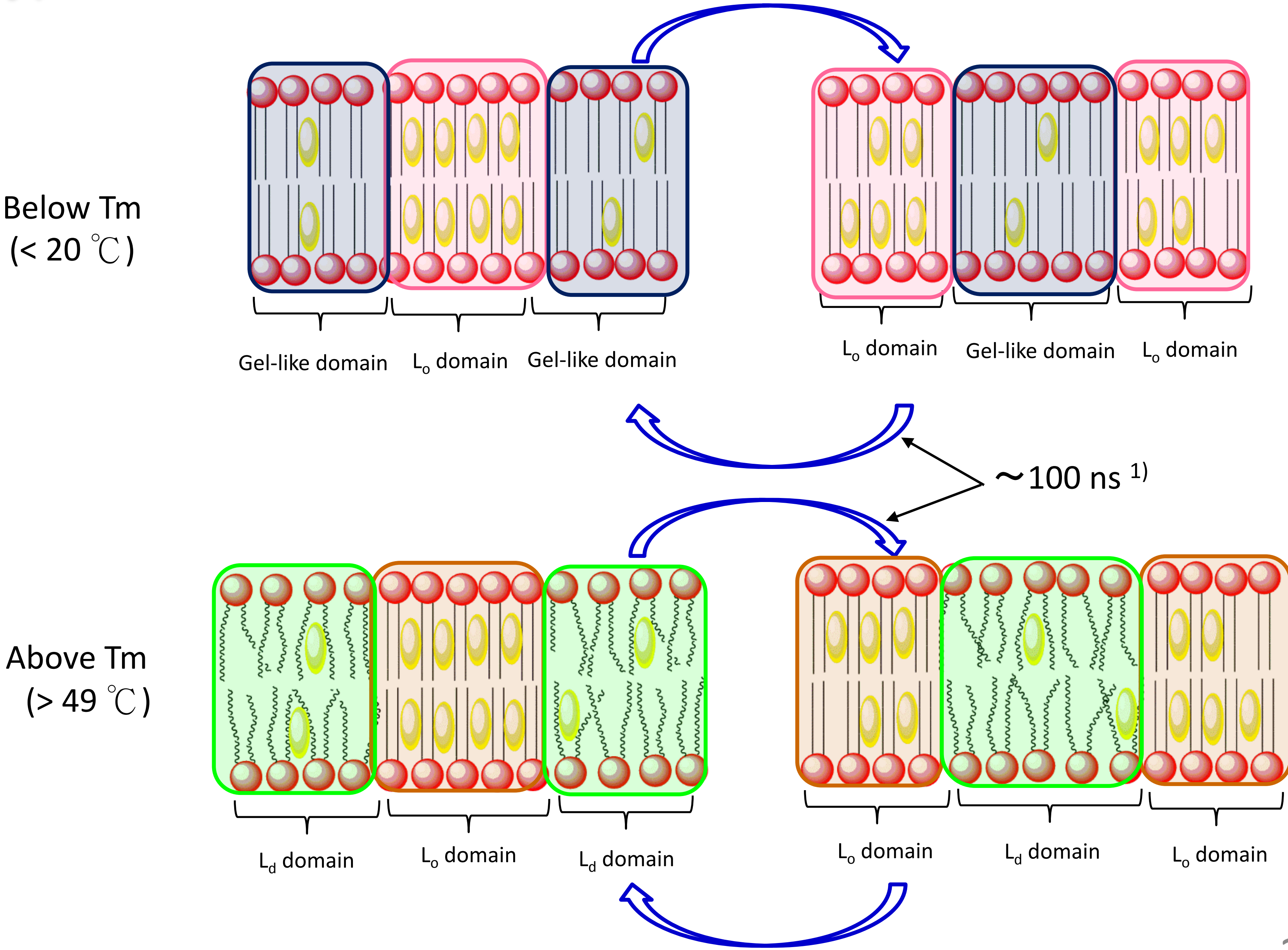
Over T_m (> 45 ℃): L_o domain | L_d domain

Under T_m (< 45 ℃): Cho-poor gel-like domain | L_o domain



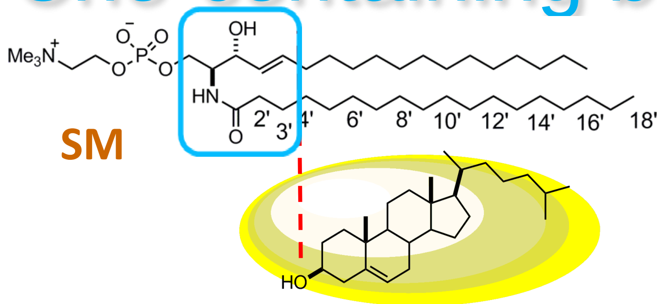
Low concentration of Cho →
Similar behavior with gel phase

Hypothetical model for interconversion of nano-domains

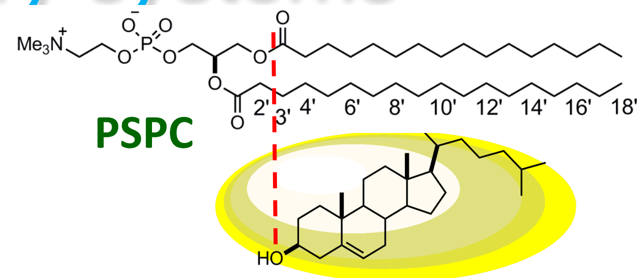


1) Chachaty, C. *et al. Biophys. J.* **2005**, *88*, 4032-4044.

Difference in dynamic behavior between SM and PC in Cho-containing binary systems



SM



PSPC

^{2}H NMR
Lipid mobility
at atomic level

Present	Hydrogen bond network	Absent
Deeper	Location of Cho	Shallower

Smaller	Temperature dependence of lipid ordering	Larger
		...wer
	...time	

Fluorescent lifetime

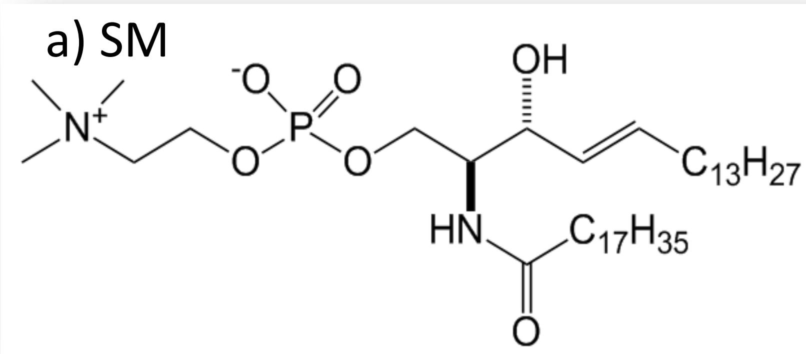
Membrane flu...
nanosecond tim...

These data suggest that SM-SM H-bonding plays major roles rather than SM-Cho interaction.

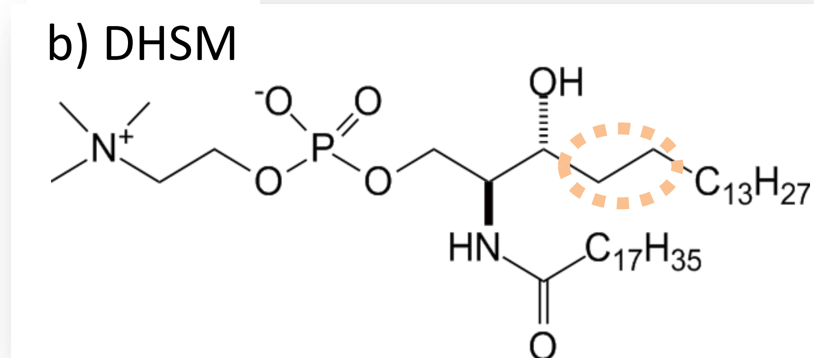
Can SM form macroscopic domains without Cho？

SM: Sphingomyelin (C18)

DHSM: Dihydrosphingomyelin (C18)



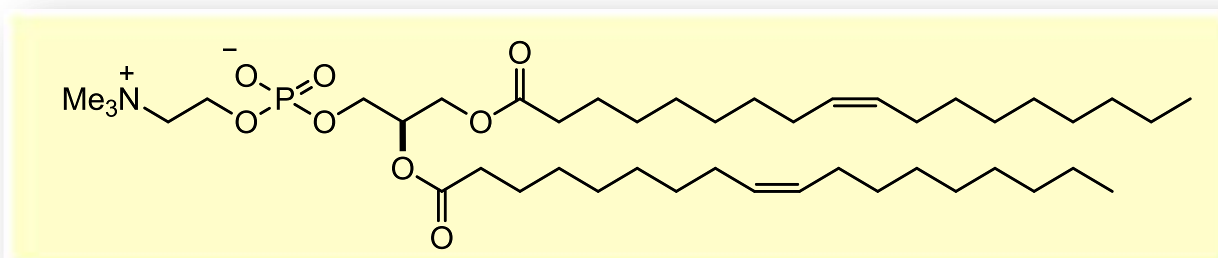
vs



- Major SM in human
- Raft model lipid

＋

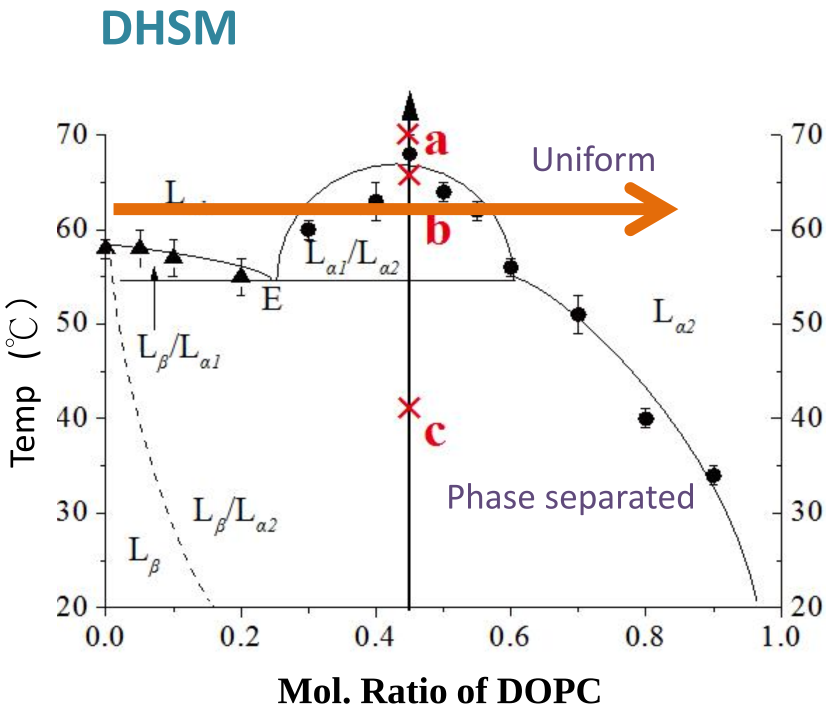
- Relatively abundant SM homologues
- Form more stable Lo domains than SM

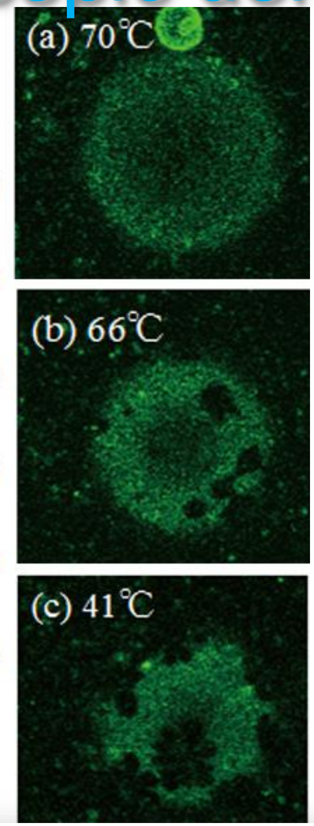


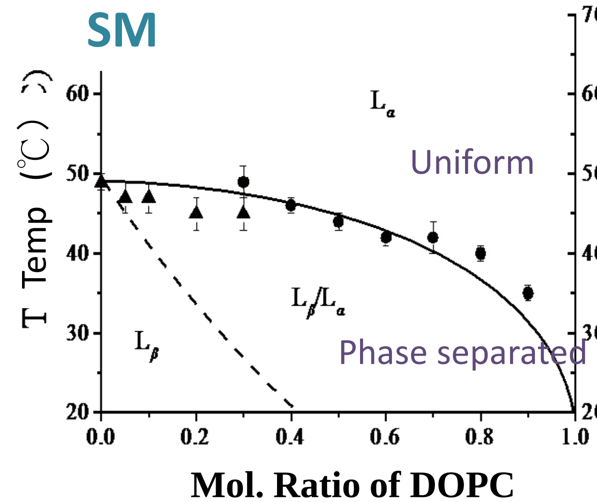
DOPC： Unsaturated PC, a typical L**d** lipid in the presence of SM and Cho

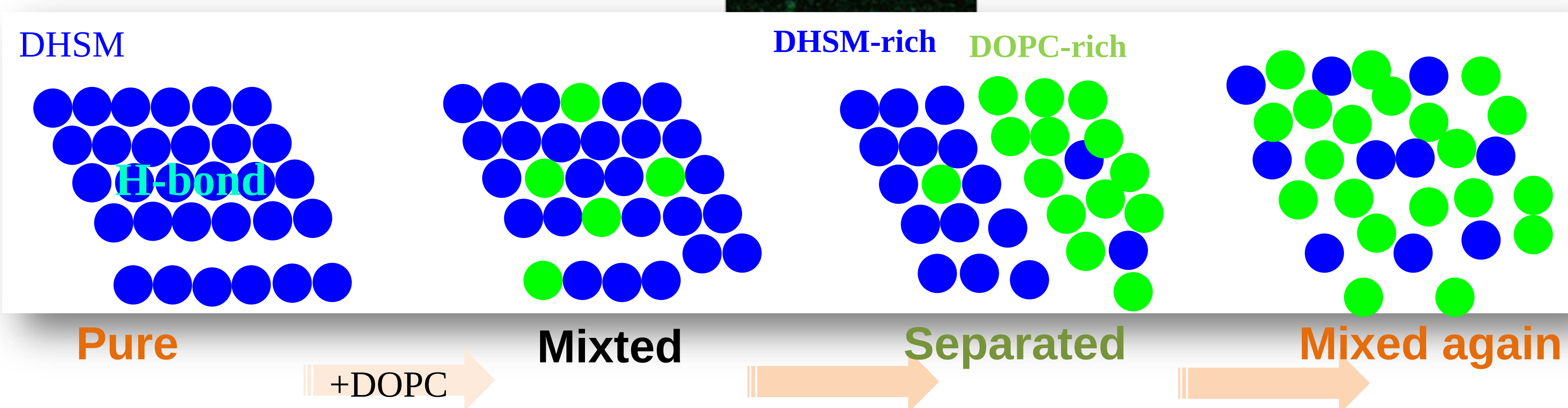
Kinoshita, M., Goretta, S., Tsuchikawa, H., Matsumori, N., Murata, M., *Biophysics* 9, 37-49 (2013).

DHSM forms macroscopic domains without Cho



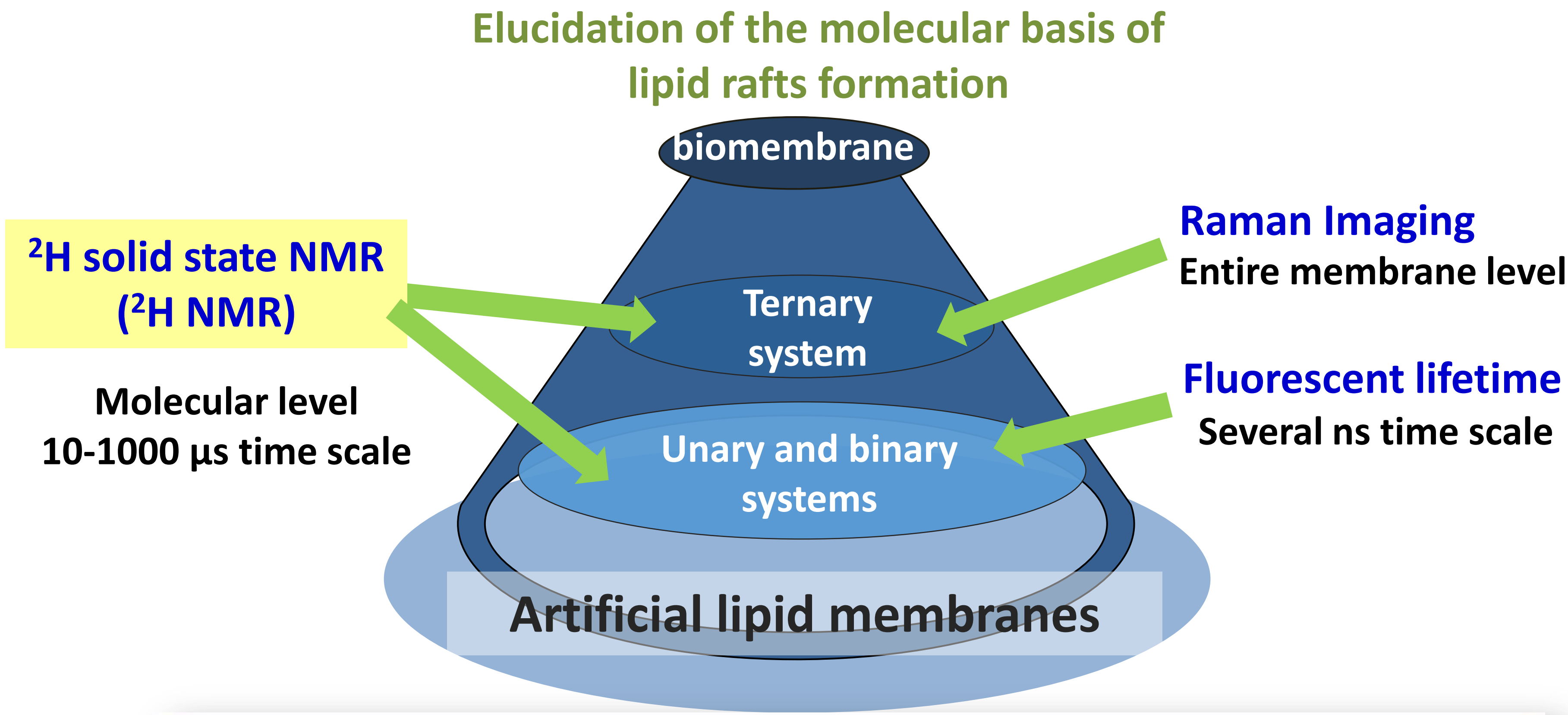


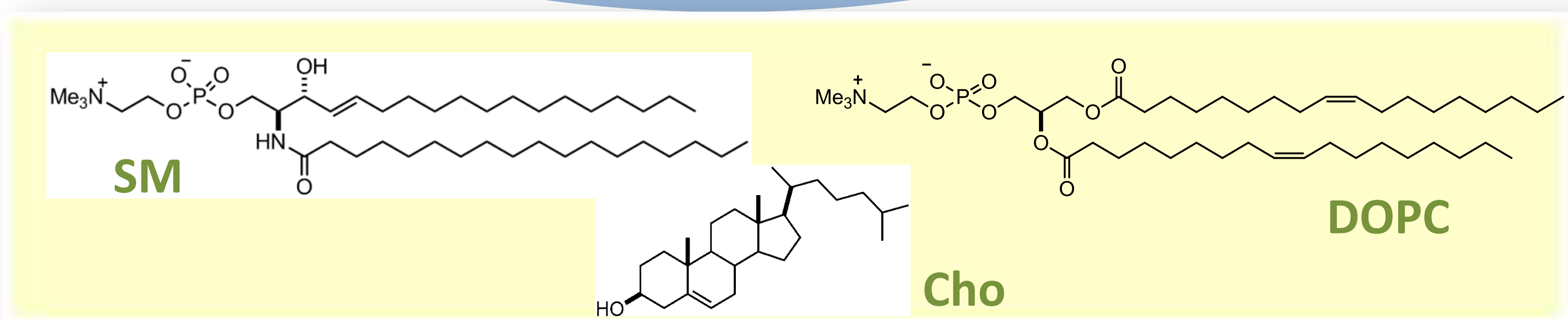




Kinoshita, M., Matsumori, N., Murata, M. *Biochim. Biophys. Acta* 1838, 1372-1381 (2014).

Approaches towards Membrane Lipids with Variable Time and Spacious Scales



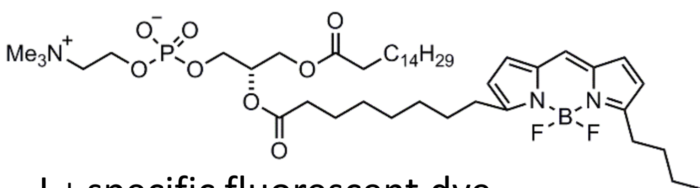


Domain separation of ternary SM/Cho/DOPC as observed by microscope and ^{2}H NMR

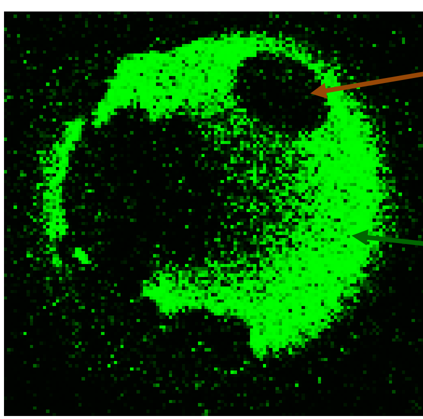
Fluorescence microscope

GUV Sample : SM/Cho/DOPC (1/1/1)
+ 0.2 mol% Bodipy- PC (λ_{ex} = 488 nm)

T : 30 ℃



Ld-specific fluorescent dye

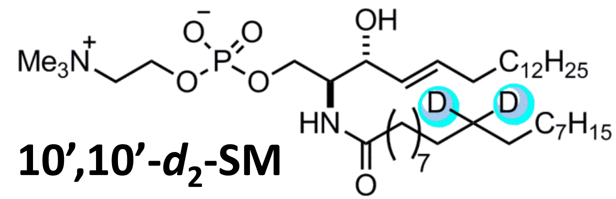


GUV of SM/Cho/DOPC (1/1/1)

SM rich ラフト相
(L_o 相)

DOPC rich 液晶相
(L_d 相)

Solid state ^{2}H NMR

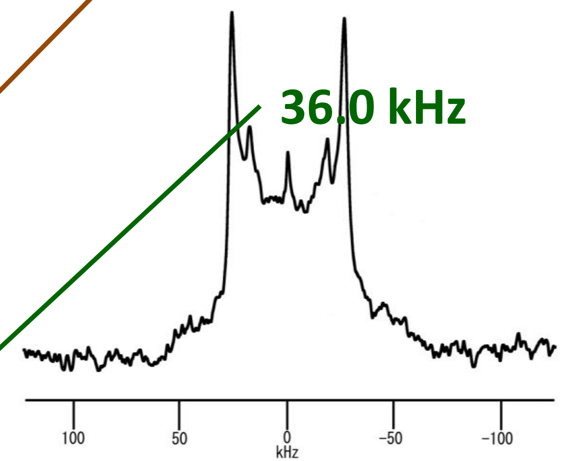


10',10'-d_2-SM

30 ℃

51.5 kHz

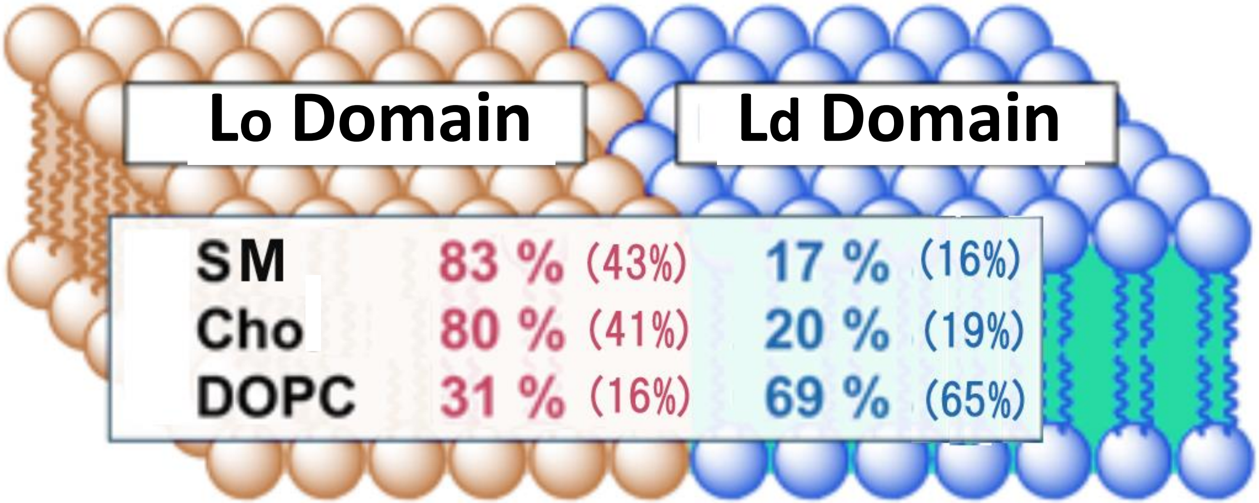
36.0 kHz



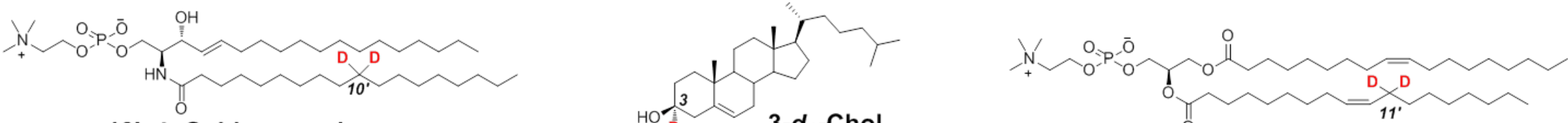
10',10'-d_2-SM/Cho/DOPC (1/1/1) の^{2}H NMRスペクトル

Two pairs of doublets

Fractional abundance of Ternary SM/Cho/DOPC system as revealed by ^{2}H NMR



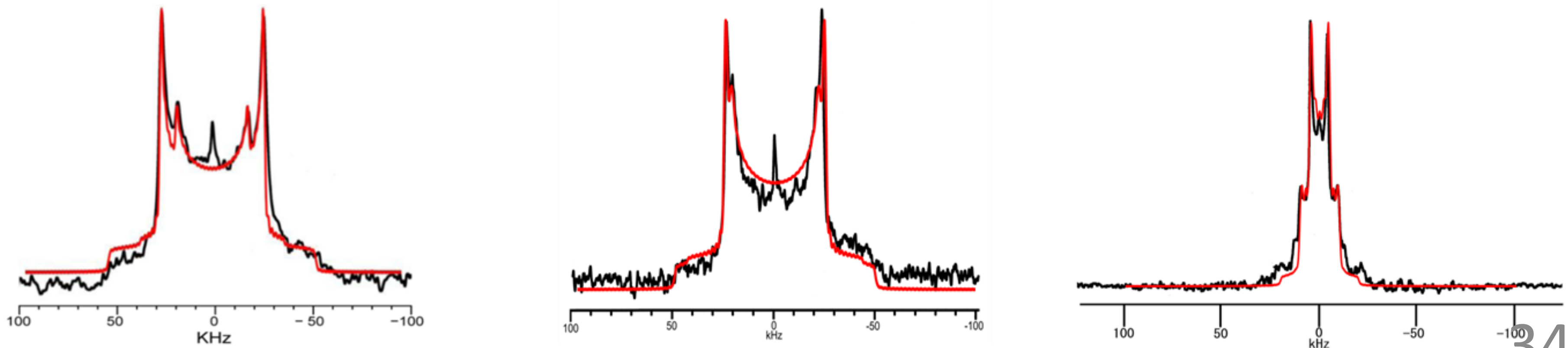
	Lo Domain	Ld Domain
SM	83 % (43%)	17 % (16%)
Cho	80 % (41%)	20 % (19%)
DOPC	31 % (16%)	69 % (65%)



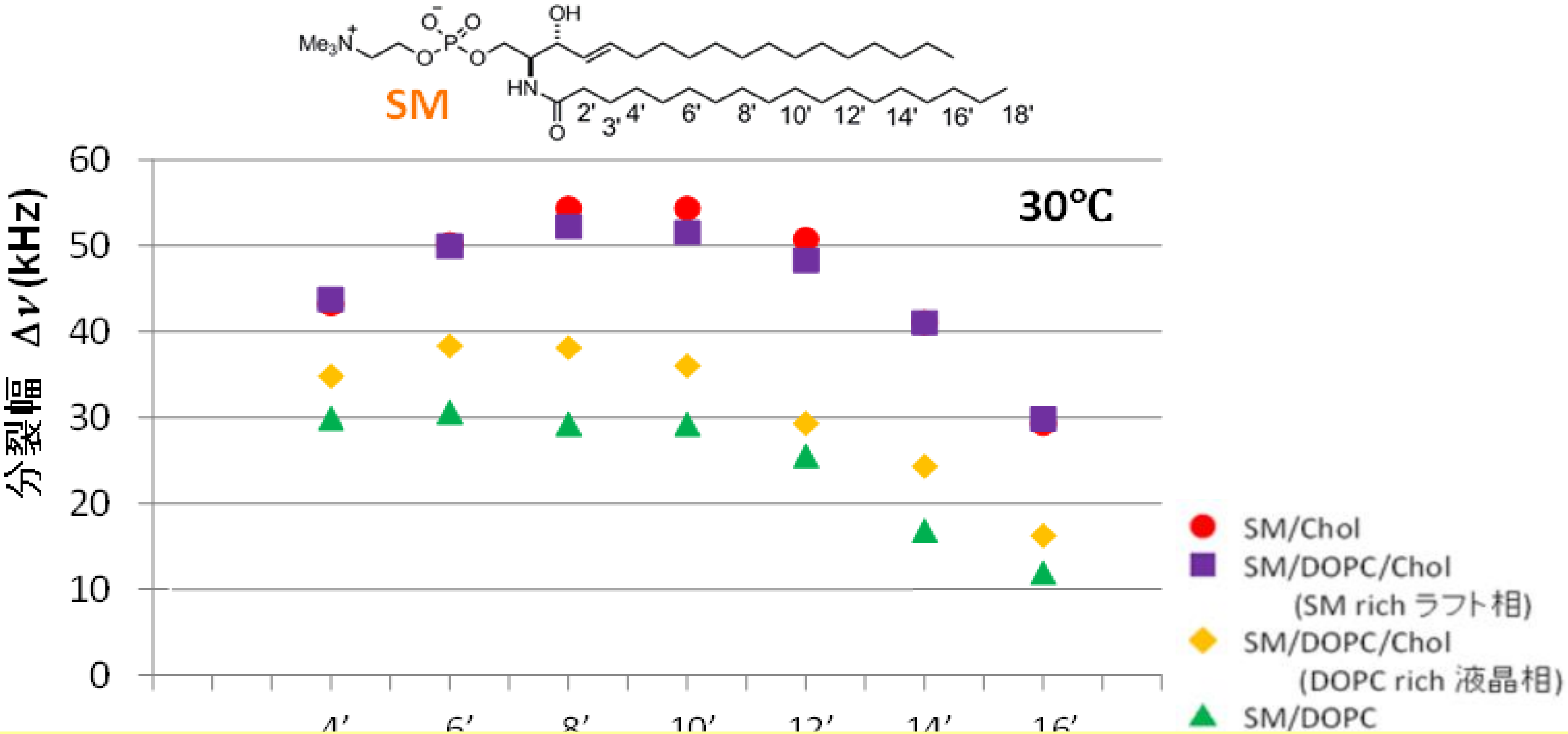
10'-d_2-Sphingomyein

3-d_1-Chol

11'-d_2-DOPC



Depth-dependent order of Lo and Ld domains in SM-Cho-DOPC system



Lo domains of ternary and binary systems showed similar ordering

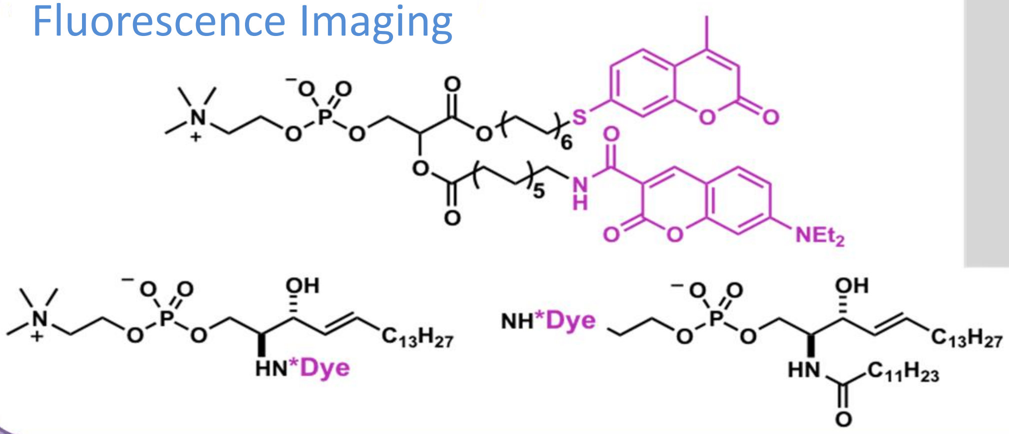
↓

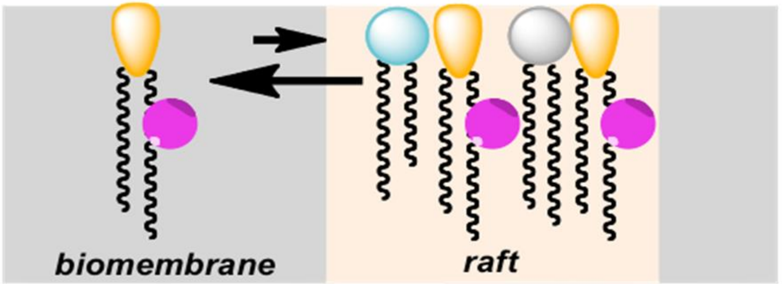
Occurrence of SM-only domains even in ternary systems

Contents

Labelled lipids for fluorescence spectroscopy do not reproduce original lipids due to balky substituents

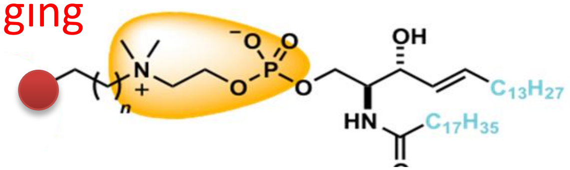
Fluorescence Imaging



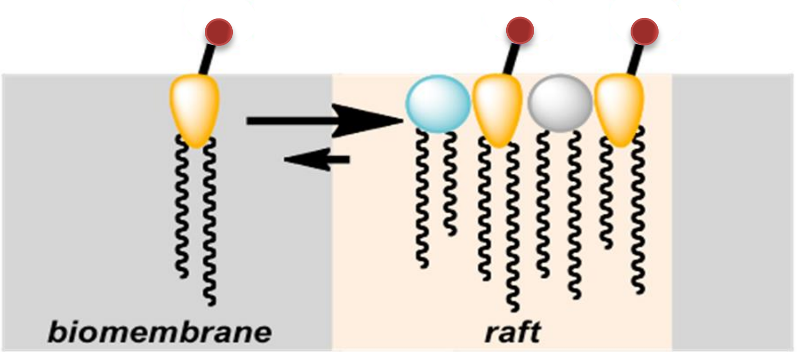


Drawback:
- alteration of lipid structure
- lower packing ability
- lesser accumulation in the raft

Raman Imaging

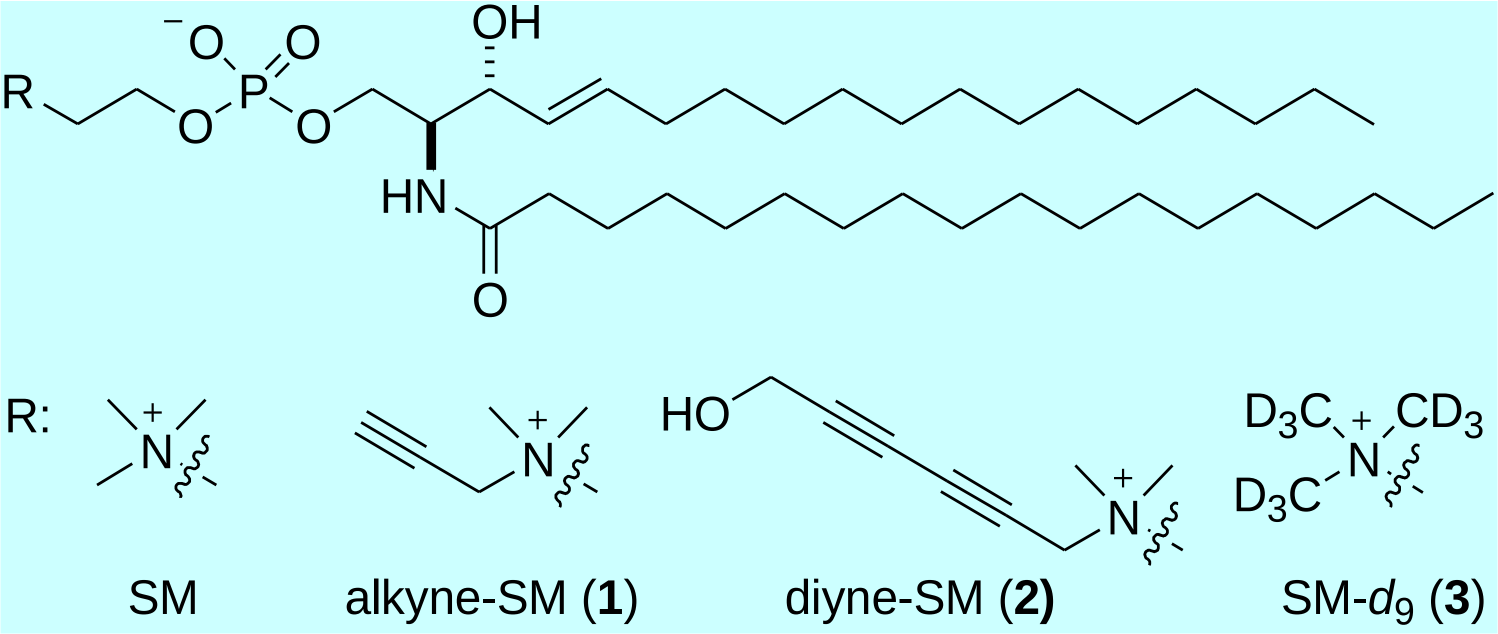


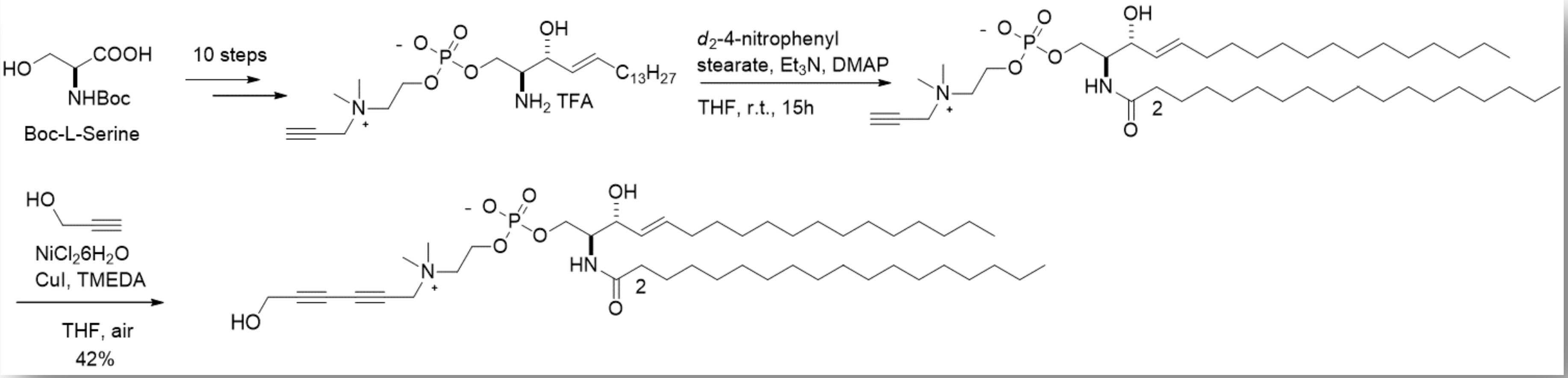
Small Raman tag



Advantages of such a model:
- structures of lipid and analogue are similar
- should retain most of lipid properties
- should closely mimic native lipid behaviour

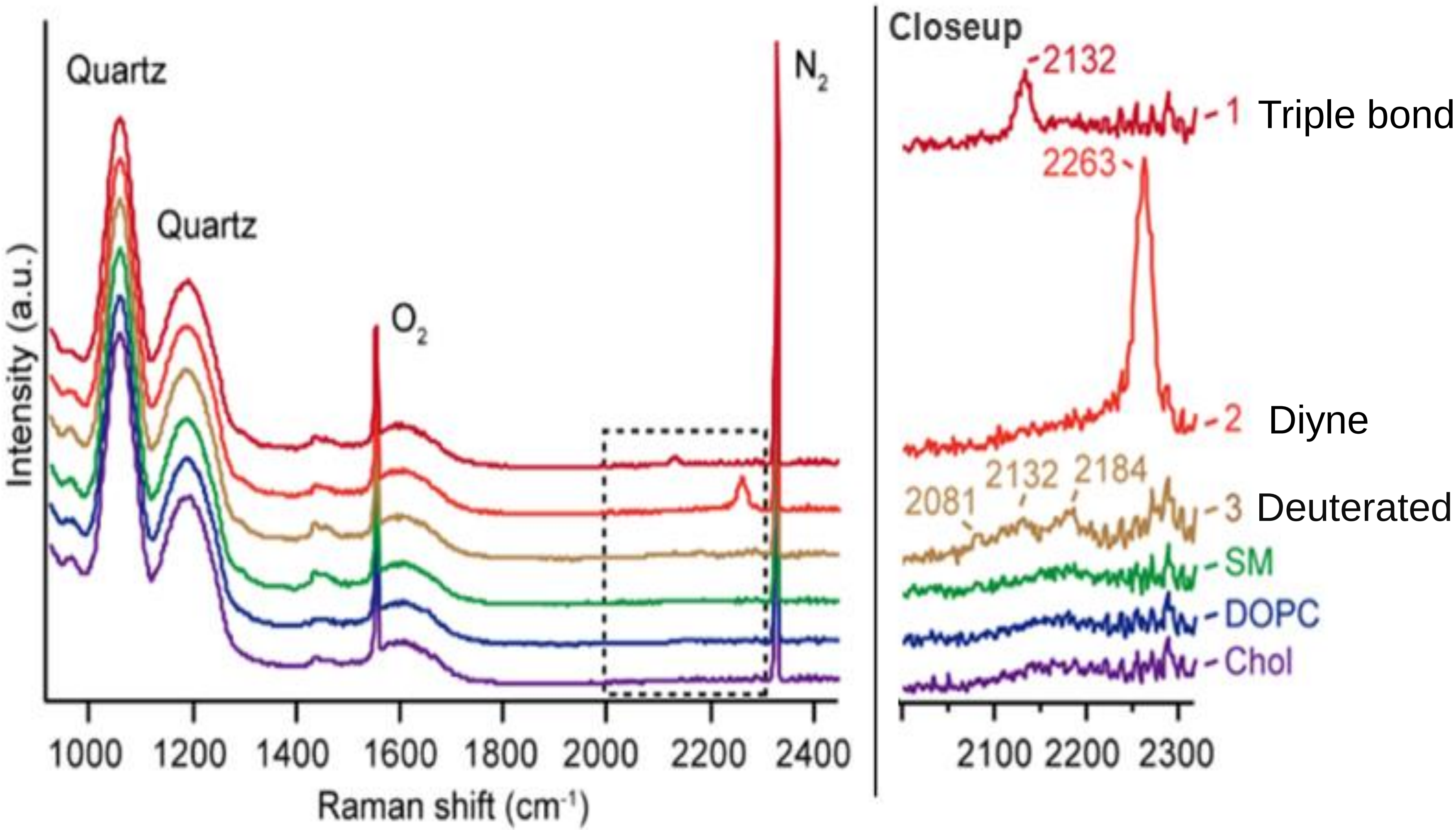
Small Raman tags of SM for imaging





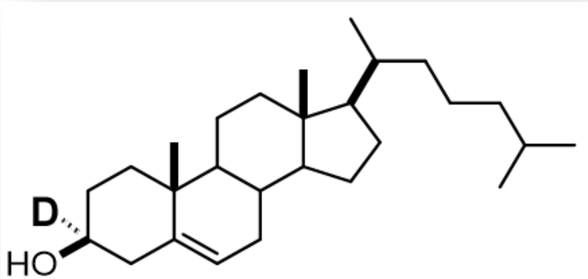
Goretta, S. A., Kinoshita, M., Mori, S., Tsuchikawa, H., Matsumori,N., Murata, M. *Bioorg. Med. Chem.* **2012,** *20,* 4012-4019.

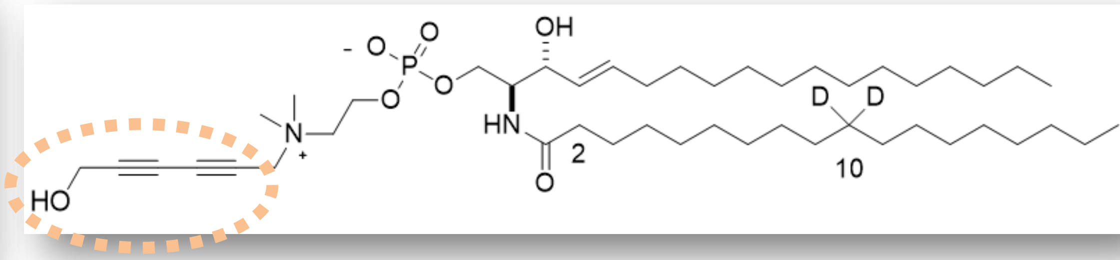
Diyne moiety shows strong intensity in background-free area



Cui, J., Lethu, S., Yasuda, T., Matsuoka, S., Matsumori, N., Sato, F., Murata, M. *Bioorg. Med. Chem. Lett.* **25,** 203-206 (2015).

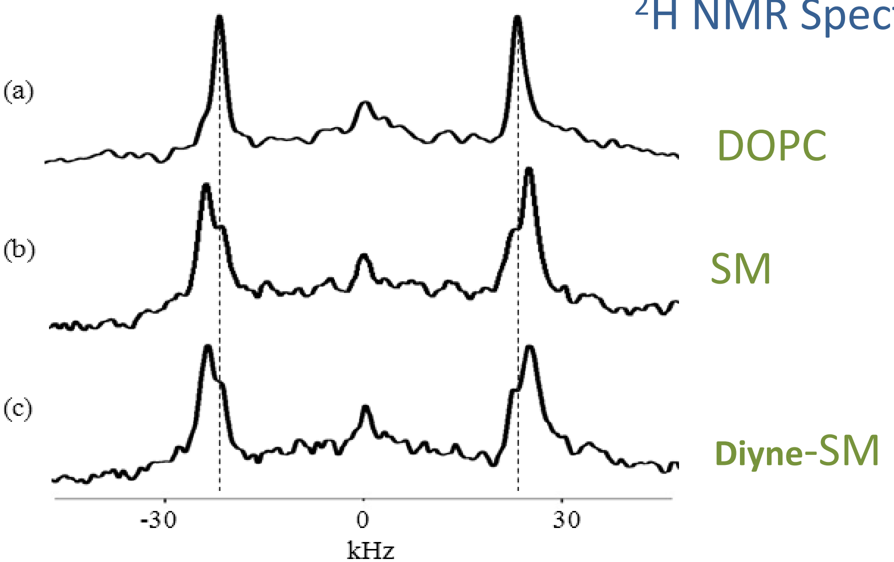
Diyne SM shows similar behavior to original lipid on ^{2}H NMR





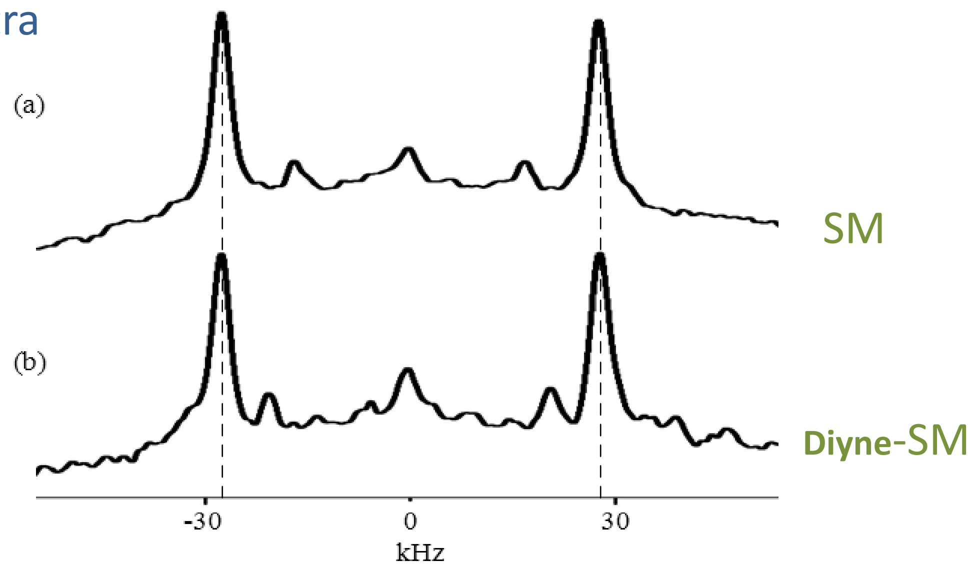
d-Cho

^{2}H NMR Spectra



(a)d-Cho/DOPC (1/1 mol),
(b)SM/*d*-Cho/DOPC (1/1/1 mol), and
(c)diyne SM/*d*-Cho/DOPC (1/1/1 mol) at 25 °C.

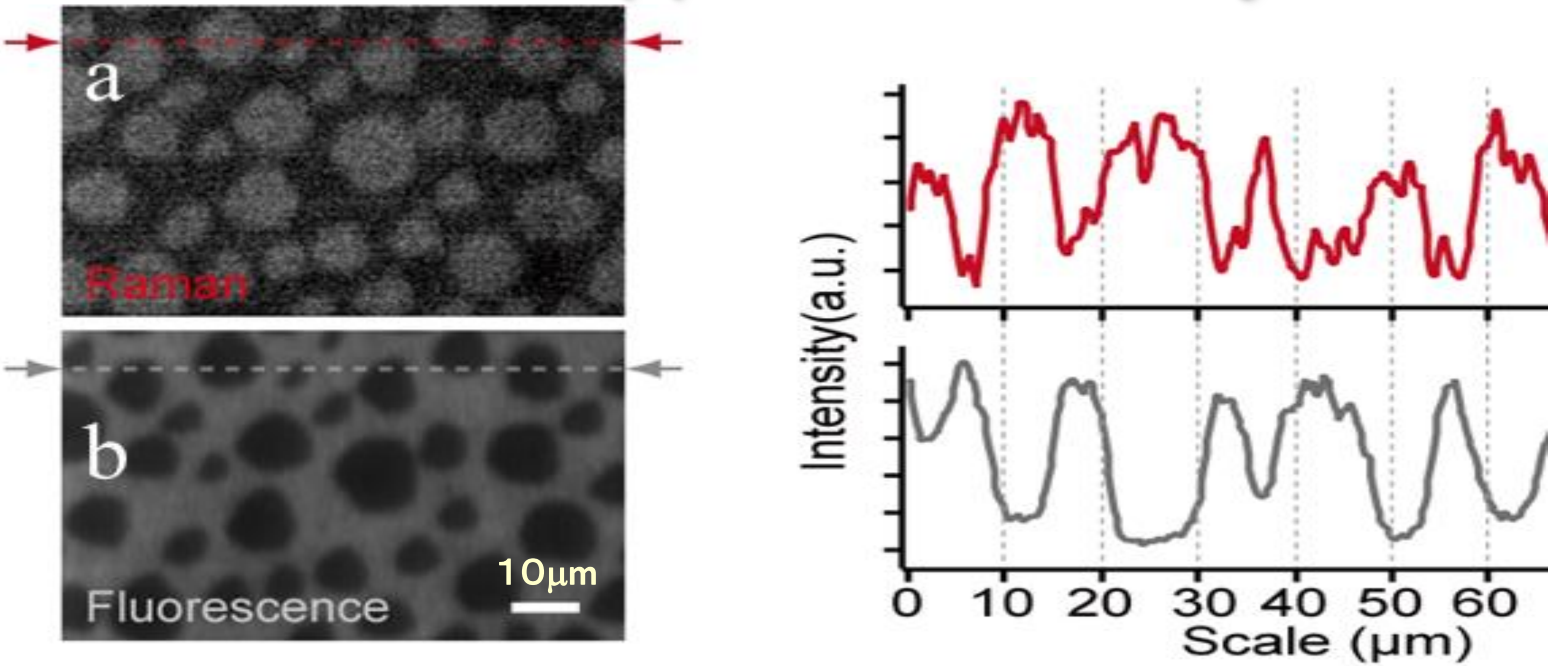
d₂-SM vs Diyne-d₂-SM

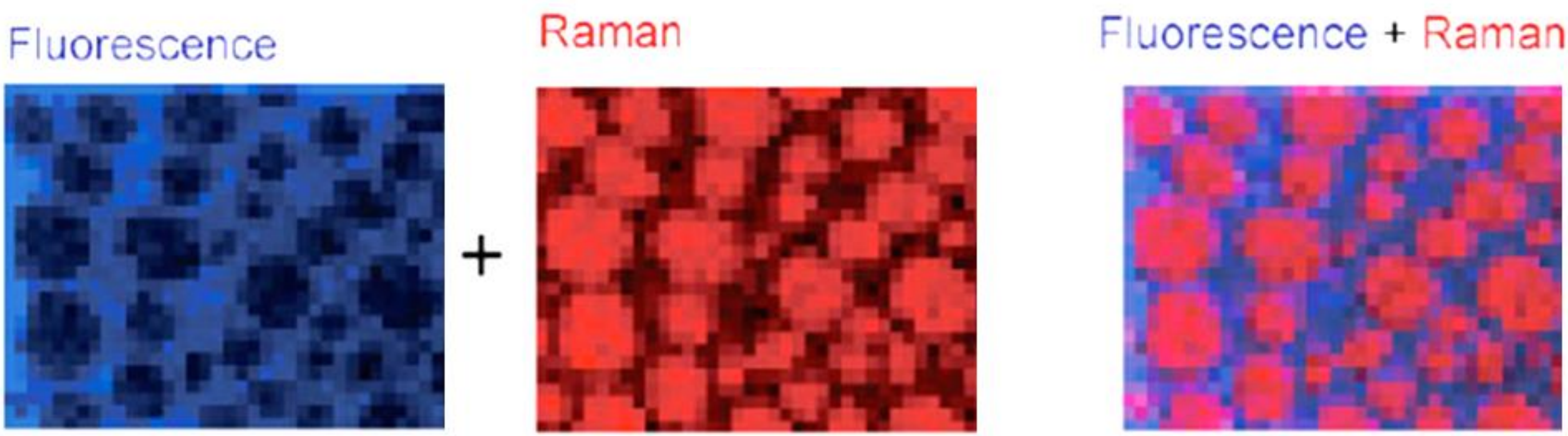


(a)d$_2$-SM/DOPC/Cho (1/1/1 mol), and
(b) *d$_2$*-diyne SM/DOPC/Cho (1/1/1 mol) at 25 °C.

Cui, J., Lethu, S., Yasuda, T., Matsuoka, S., Matsumori, N., Sato, F., Murata, M. *Bioorg. Med. Chem. Lett.* **25,** 203-206 (2015).

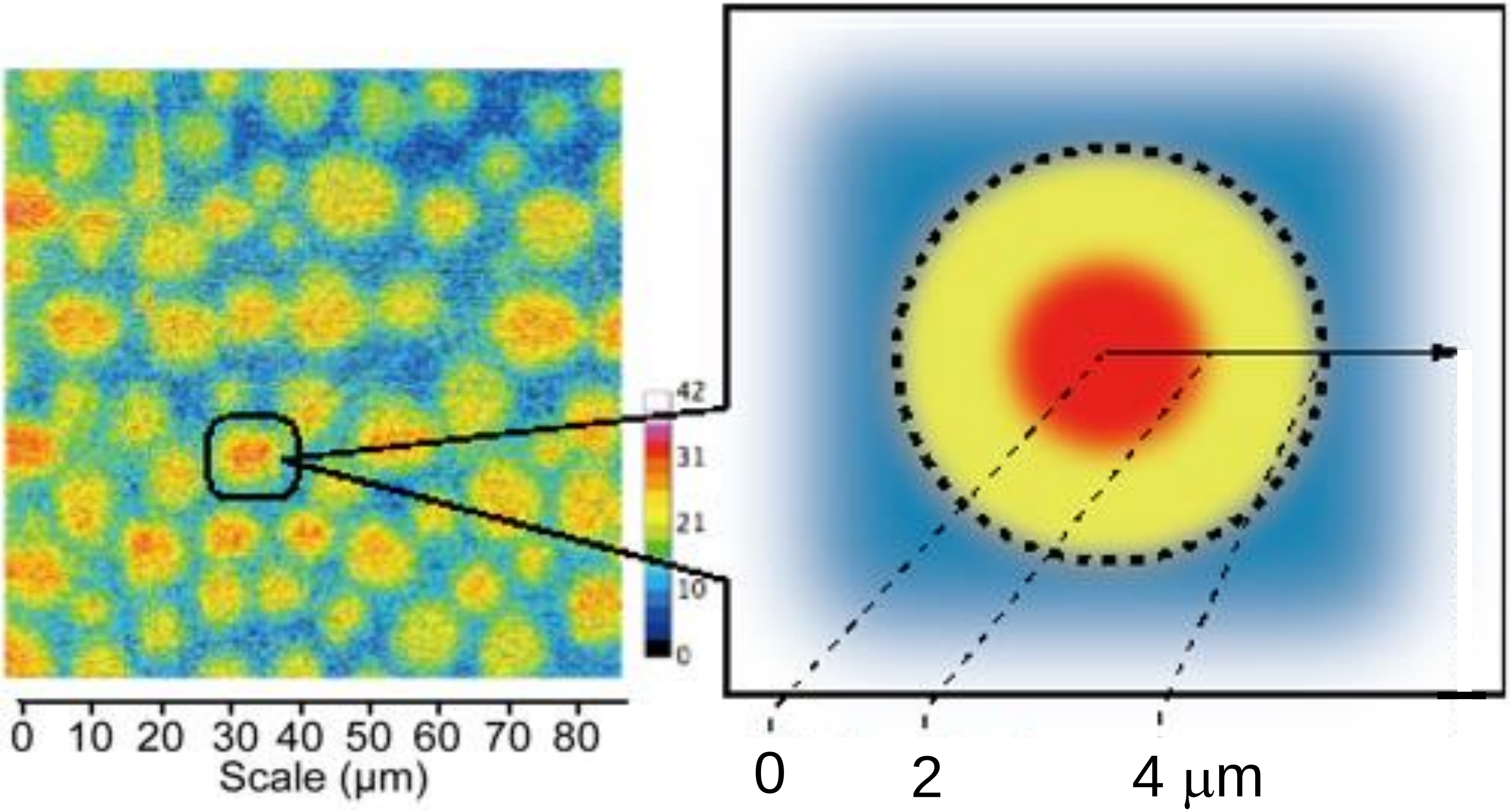
Diyne probe mimics SM in L_o domains on supported monolayer





Quartz-supported monolayer Diyne-SM/Cho/DOPC (1/1/1 mol)

Concentration graduation of SM revealed by Raman imaging



Monolayer of diyne-SM/DOPC/Cho (1:1:1)

Summary

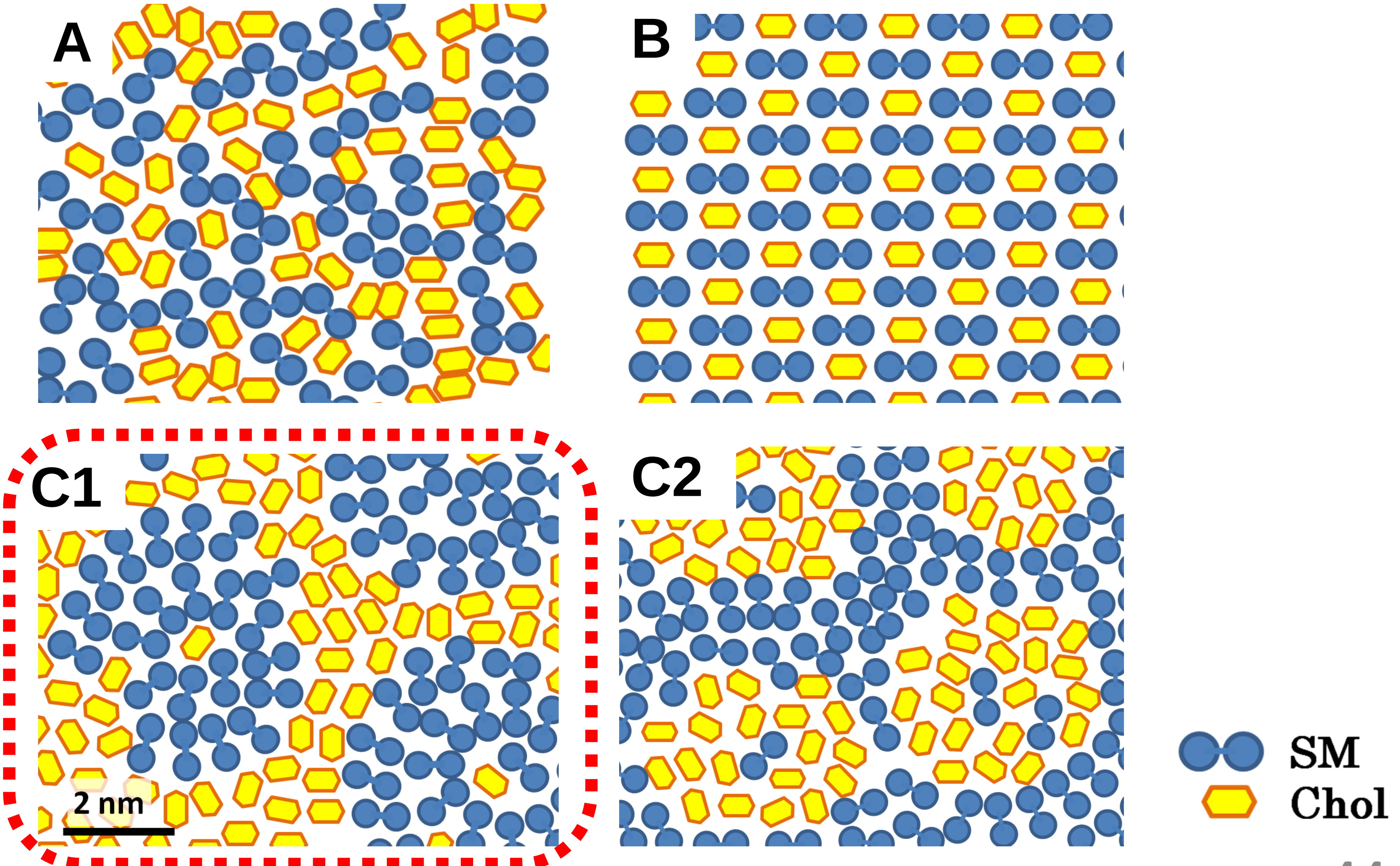
Site-selective ^{2}H labeling precisely discloses depth-dependent mobility of alkyl chains of SM and PC in L_o and L_d membranes

Intermolecular hydrogen-bonds play a key role in SM-SM interaction, which may lead to formation of raft-like L_o domains.

Nano-domains largely consisting of SM can be formed in the presence or absence of Cho.

Formation mechanism of SM/Cho-rich rafts in biological membranes

Hypothetical nano-sized cluster of SM



謝　　辞

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化学専攻

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(Dr. Sodeoka)
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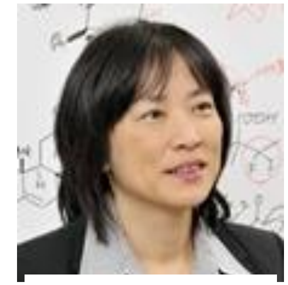
山越 博幸 博士
閬閬 孝介　博士
藤田　克昌准教授　(大阪大学)



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Mr. M. Lönnfors

Prof. Slotte

Dr. Yasuda

Dr. Jin Cui

Dr. Yamaguchi


Thank you for your attention

Our Campus

Osaka is the 2nd largest city in Japan.

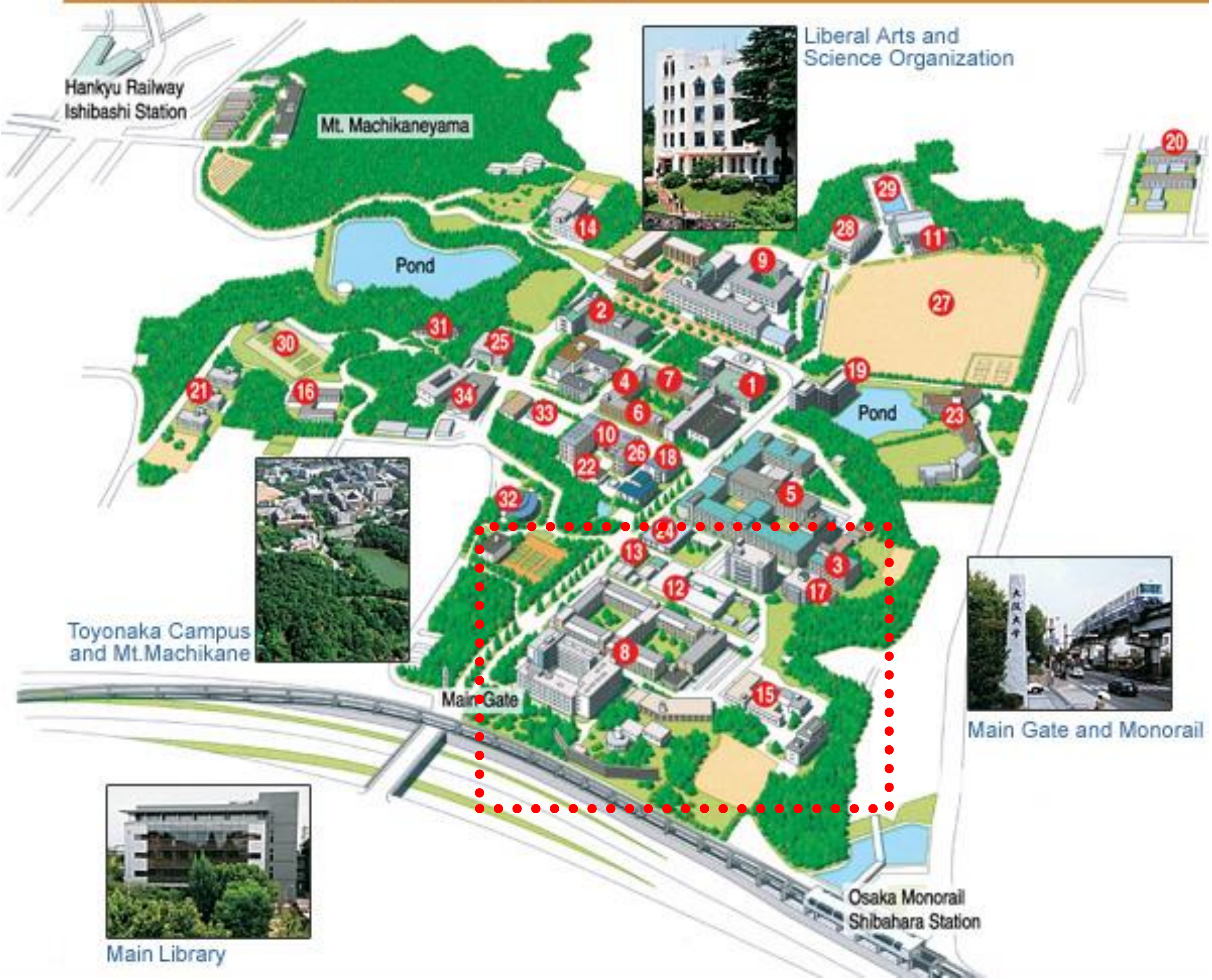
Stat. of Osaka University

Graduate schools: 20
Faculty members : 2600
Undergraduate students: 12000
Graduate students: 7800
(including 1000 foreign students)

The largest national university in Japan in terms of the number of undergraduate students.

OSAKA UNIVERSITY

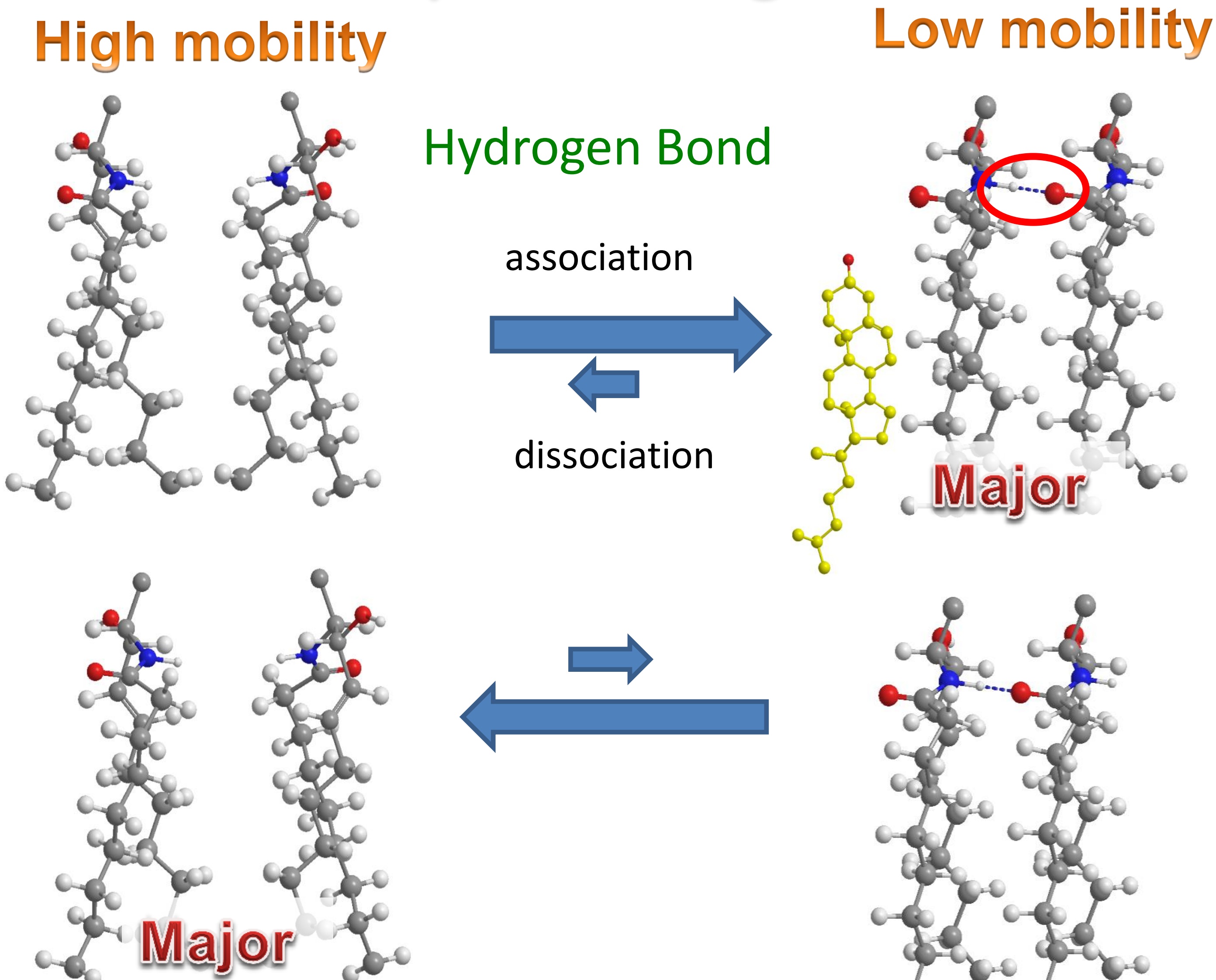
TOYONAKA CAMPUS OF OSAKA UNIV.



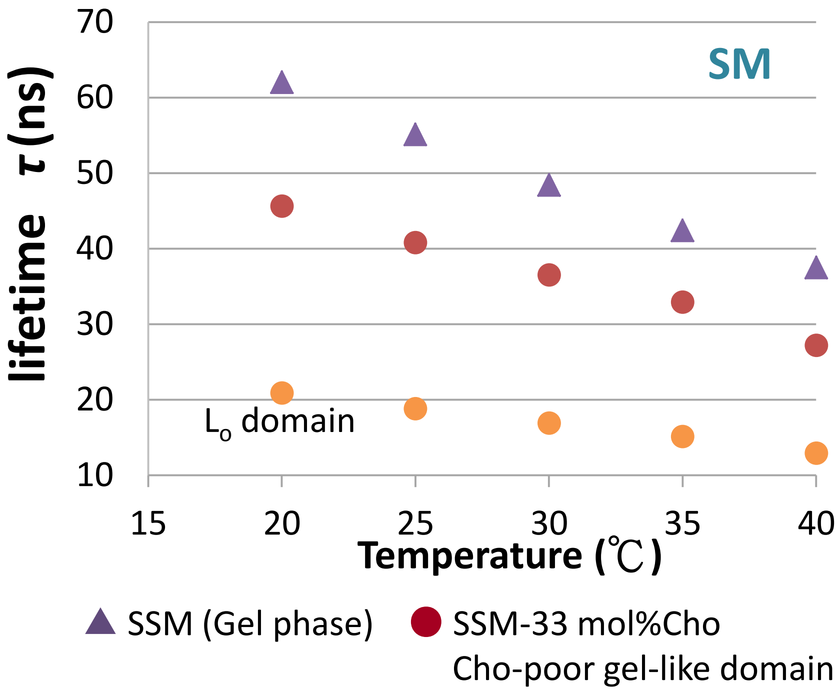
SM-Cho interaction results in stable SM-SM hydrogen bond formation while SM-Cho affinity is not high

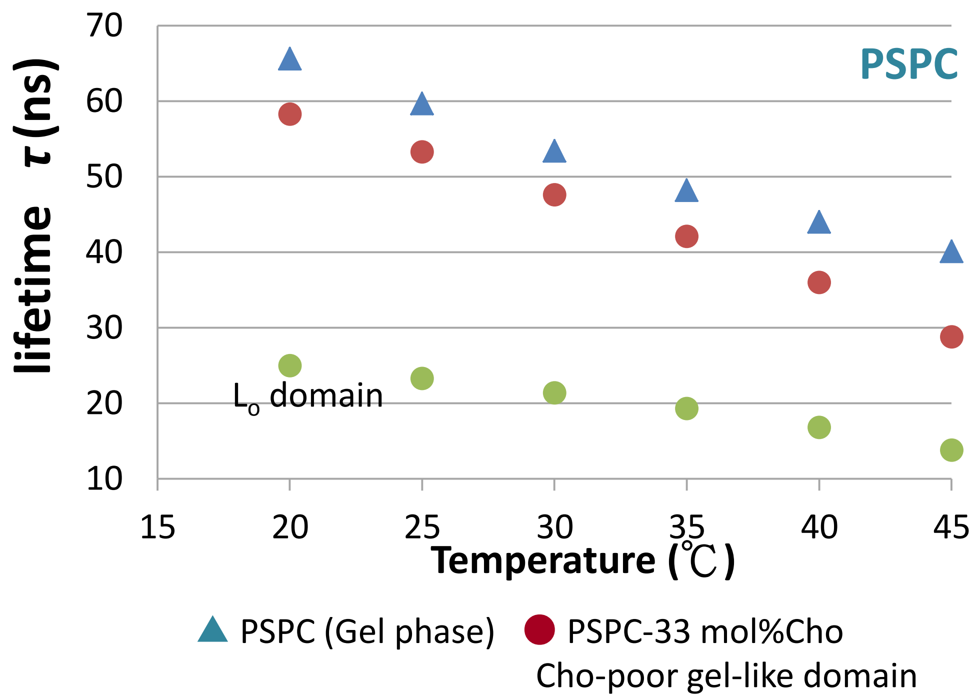
Lo phase
(raft model)
SM/Cho

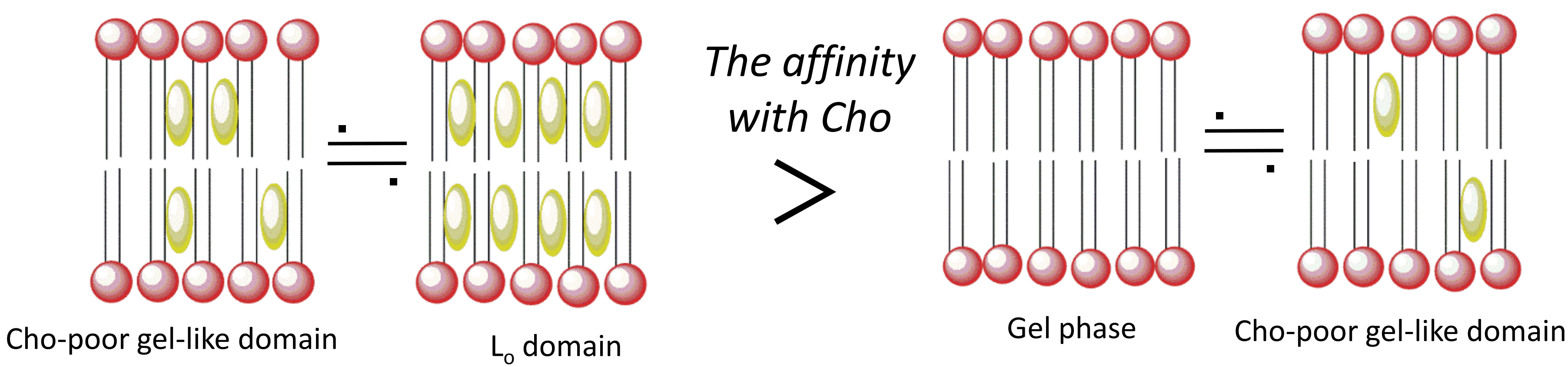
Ld phase
(non-raft)
SM 100%



Lo domain-forming ability in SM and PSPC memb.



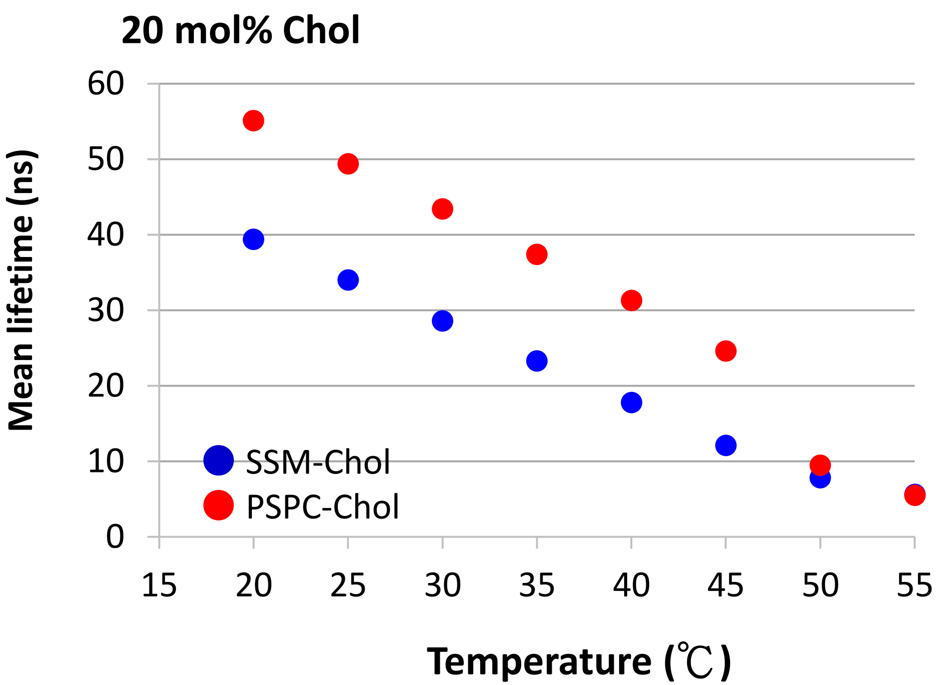


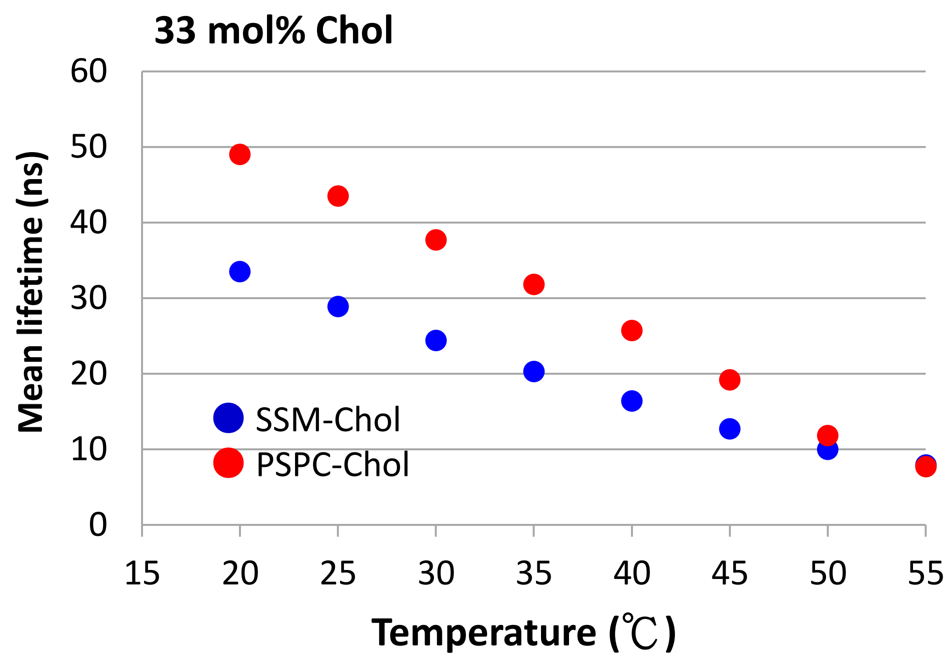


SM has a higher L_o domain-forming ability.

Temperature dependence of mean lifetime in SM and PSPC membrane containing Chol

Mean lifetime : the weighted average of fluidity in the bilayer on nanosecond time domain





Similar behavior to the data from ^{2}H NMR

The decreasing degree of lifetime in SM membrane is smaller with increasing temperature.

The local mobility of acyl chain in phospholipids is closely correlated to the entire membrane order.

ERATO脂質活性構造プロジェクト
本研究の3つの目標

膜タンパク質周辺脂質

3つグループで協力
固体NMR, 結晶X線回折,
合成化学, XAFS

脂質活性構造

タンパク質内部脂質

杉山Gと松岡Gが担当
結晶X線回折, 固体NMR,
カロリメータ, 計算機科学
Spring-8, SACLA,
表面プラズモン共鳴

マイクロドメイン

主に村田Gが担当
固体NMR, 化学合成,
物理化学計測,
共焦点顕微鏡,
ラマンイメージング

関連する戦略目標：生命システムの動作原理の解明と活用のための基盤技術の創出

生体膜中脂質分子Gの研究成果 ④

II　脂質ラフト形成の分子機構

III　SM膜の生物物理学的解析

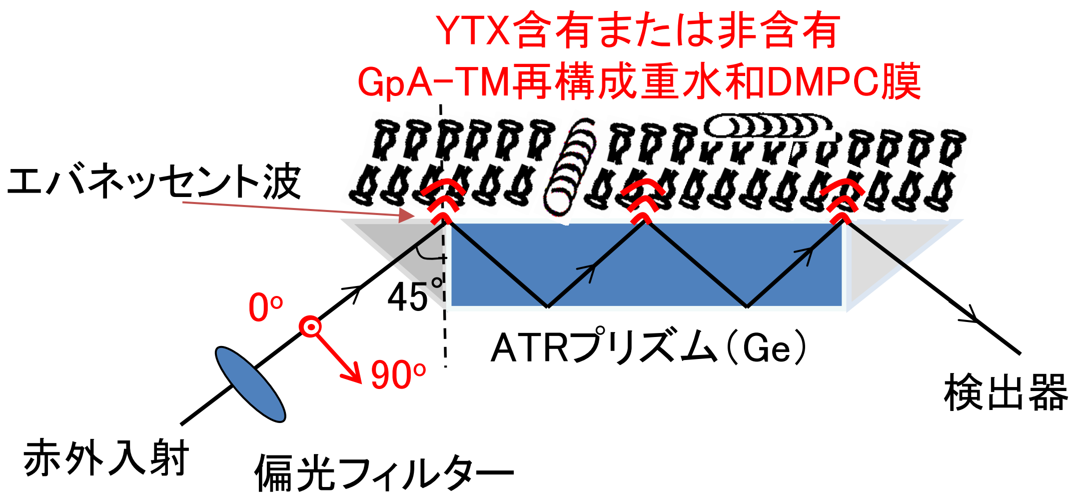
IV　ラマンイメージを用いた液体秩序相の観察

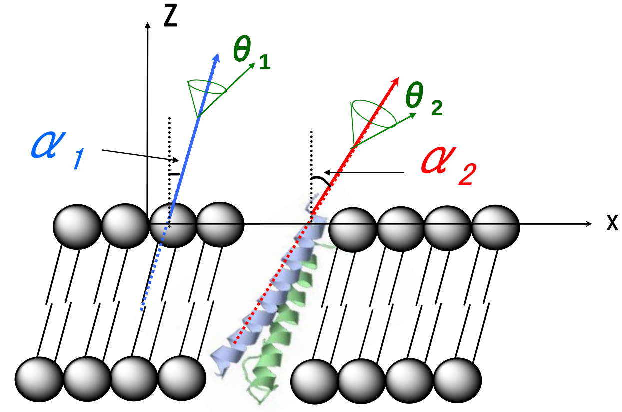
V　脂質二重膜における天然物との相互作用

1.梯子状ポリエーテル系天然物

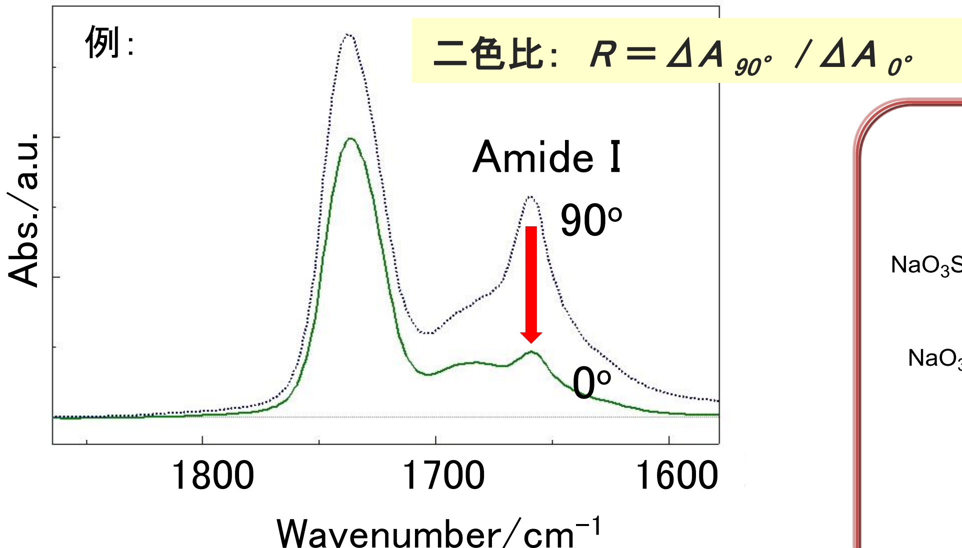
2.細胞膜内**Chol**と相互作用する天然物

偏光減衰全反射赤外分光法（pATR–FTIR）

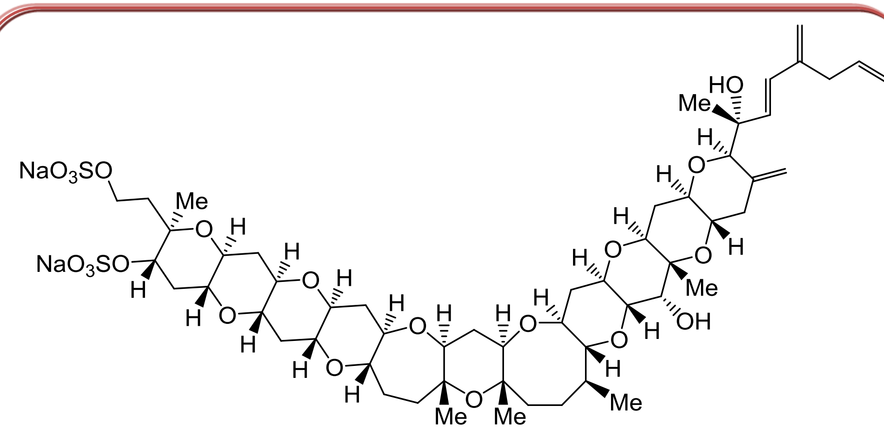




プリズム平面上におけるペプチド
含有脂質二重膜の簡略図



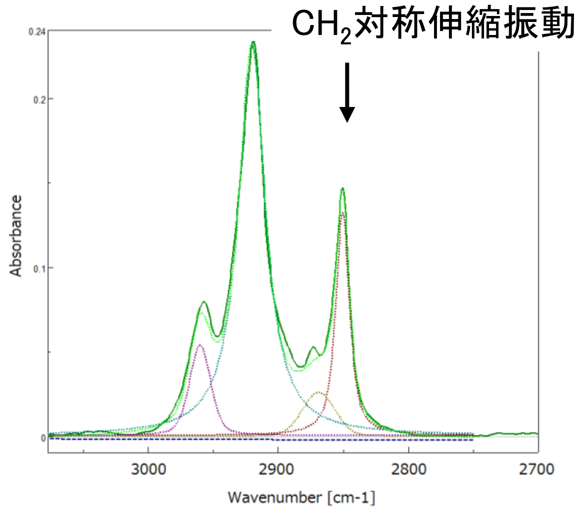
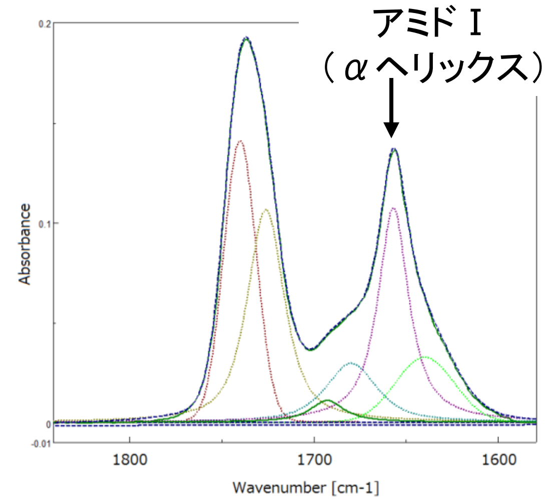
$$\cos^2\alpha = \frac{1}{3}\left(\frac{4}{3\cos^2\theta - 1}\,\frac{R-2.00}{R+1.45} + 1\right)$$



イエッソトキシン（YTX）[4]

有毒渦鞭毛藻によって生産される海洋生物毒

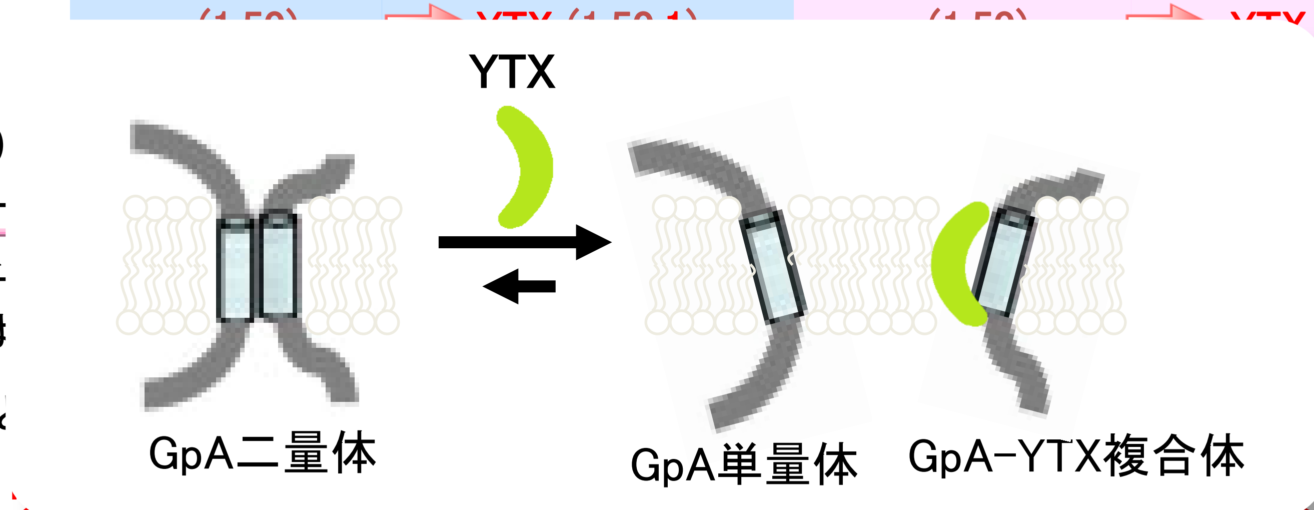
リン脂質膜中でYTXによるGpA−TMの配向変化の解析

配向	脂質分子DMPCのアシル鎖		GpA−TMのαヘリックス軸	
バンド				
試料名	重水和 GpATM−DMPC (1:50)	重水和 GpATM−DMPC−YTX (1:50:1)	重水和 GpATM−DMPC (1:50)	重水和 GpATM−DMPC−YTX (1:50:1)
α（°）				.23

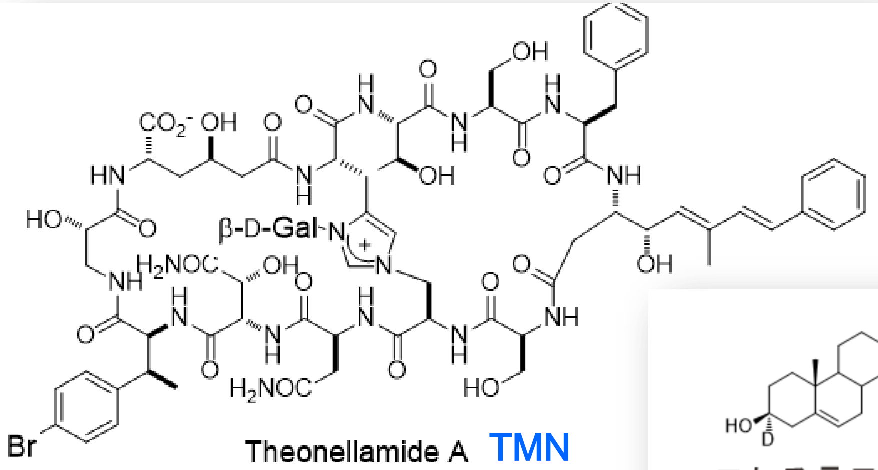
○ 脂質分子 … クス軸の配向はYTXによ …

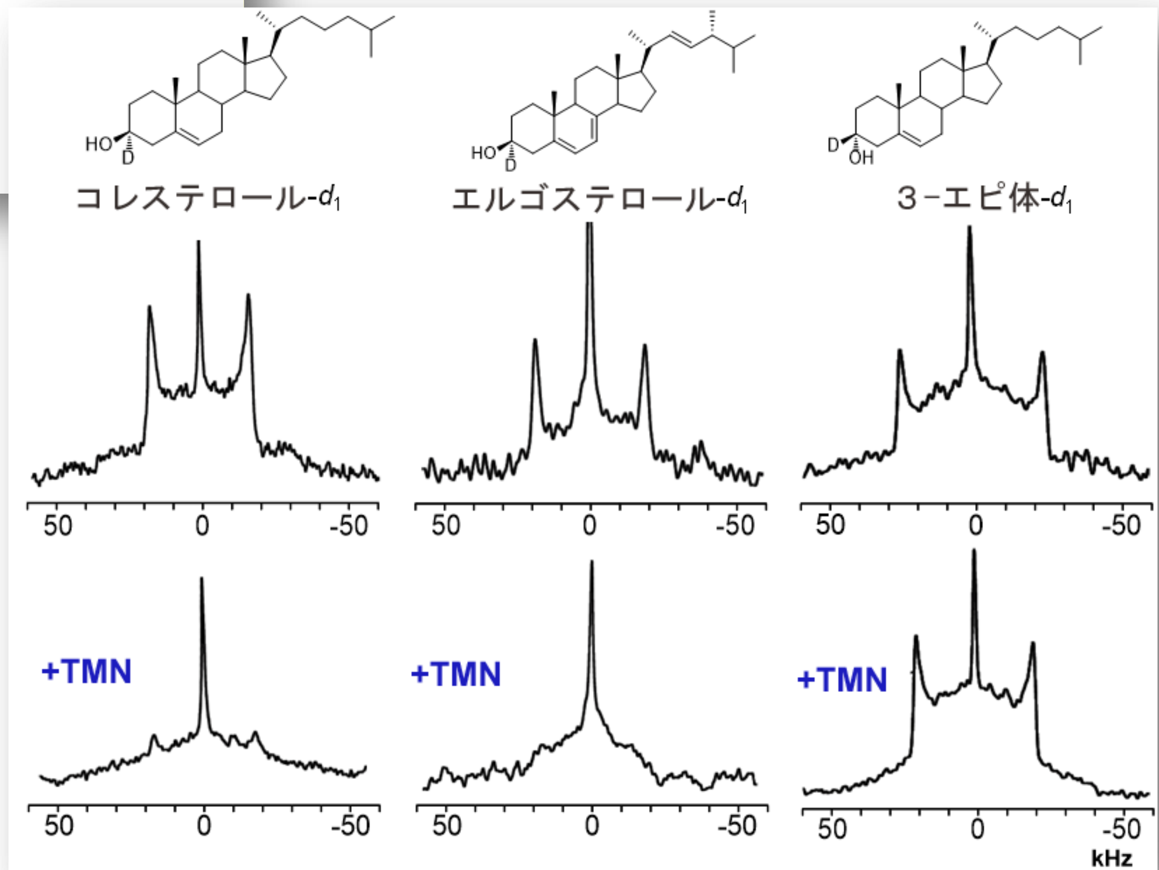
○ GpA−TM … 考えられる。

⇨ … された



細胞膜内ステロールと相互作用する天然物





ペプチド-膜脂質の持つ強い分子間相互作用と比較的小さな分子量に着目

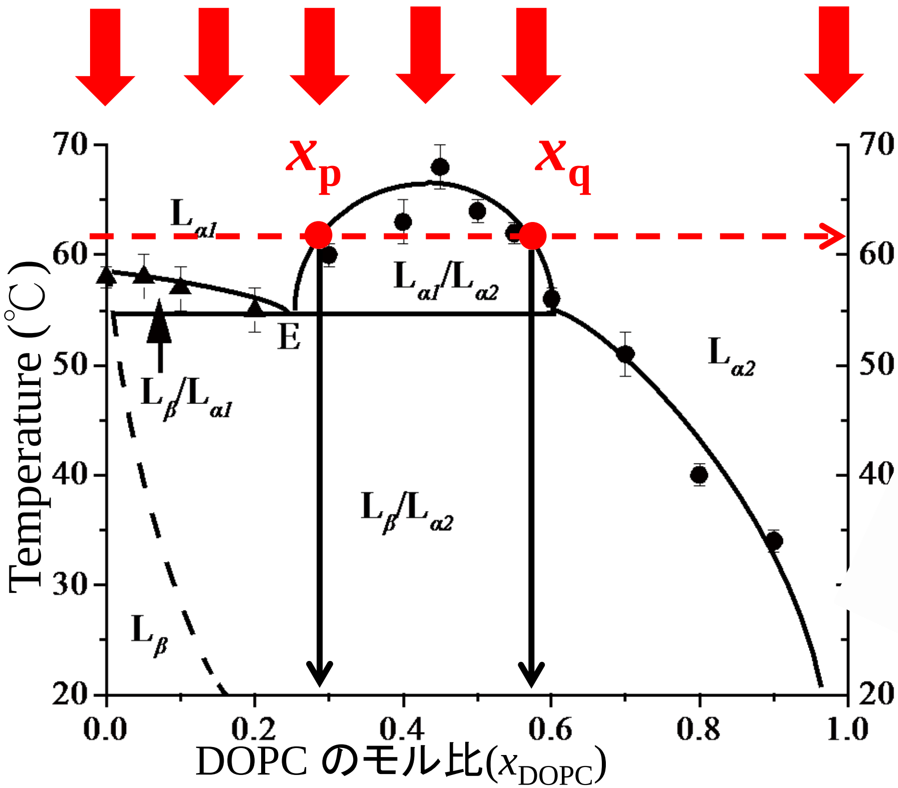
- 膜脂質検出用の低分子プローブの開発
- 固体ＮＭＲ実験の試行

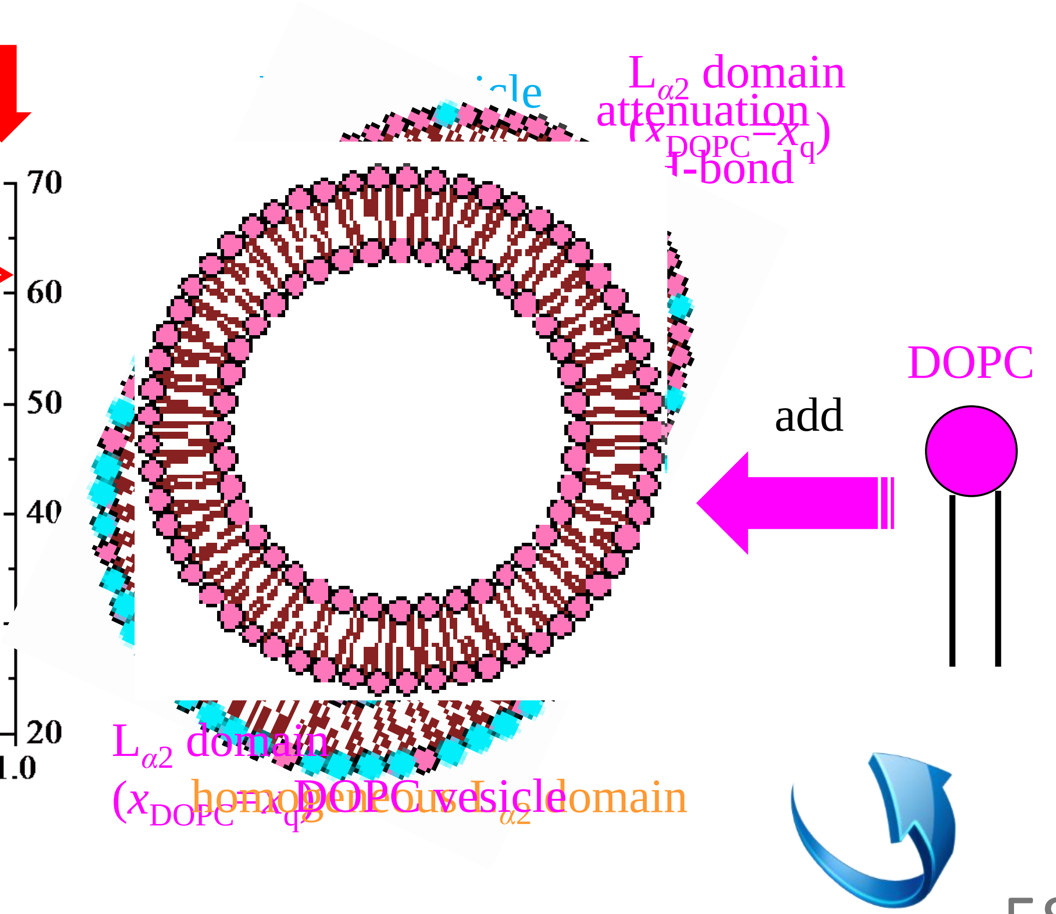
Espiritu, R. A., Matsumori, N., Murata, M., Nishimura, S., Kakeya, H., Matsunaga, S., Yoshida, M., *Biochemistry* **2013,** *52,* 2410.

DHMS相挙動のDOPC依存性

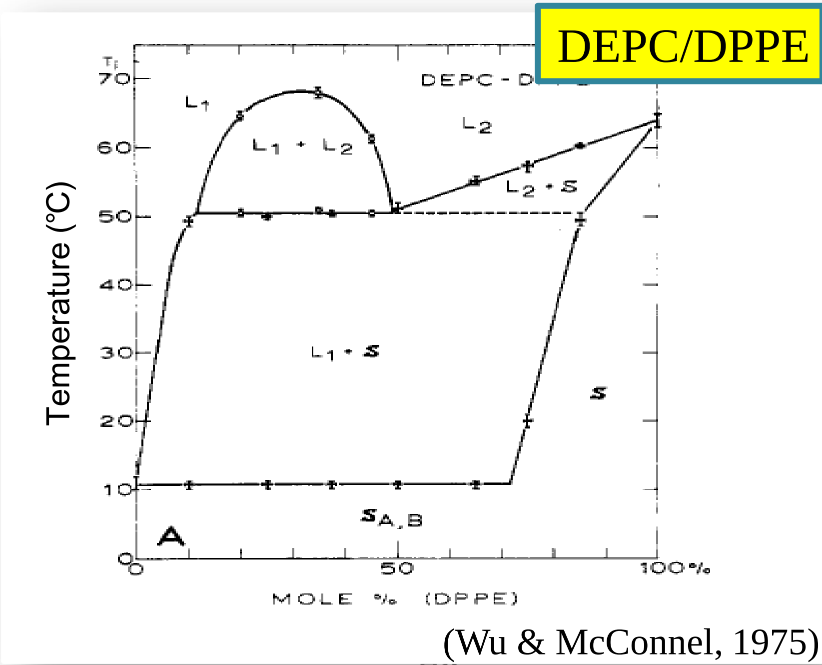
仮定

1. DHSMは強い分子間水素結合を形成する(H-bonds).
2. DHSM はDOPCより大きな曲率をもつ膜を形成する

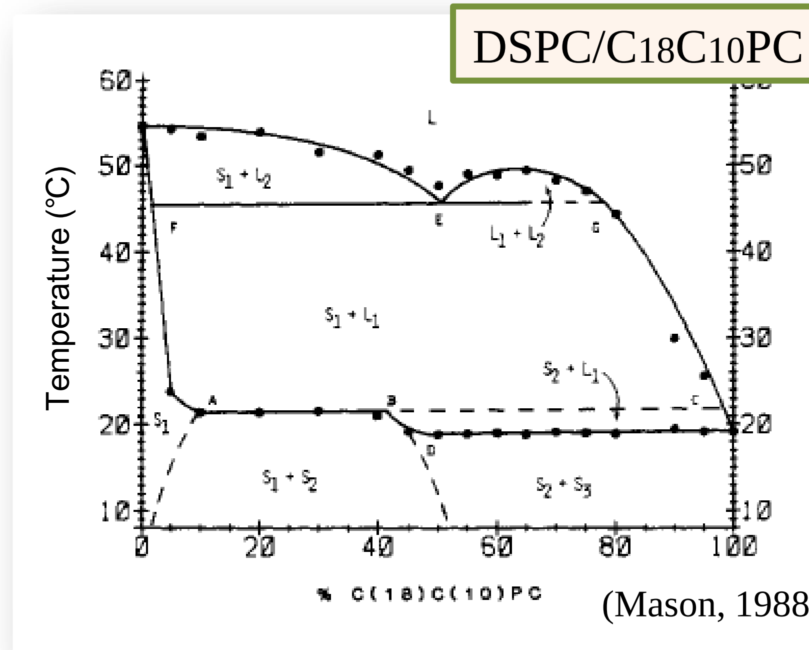




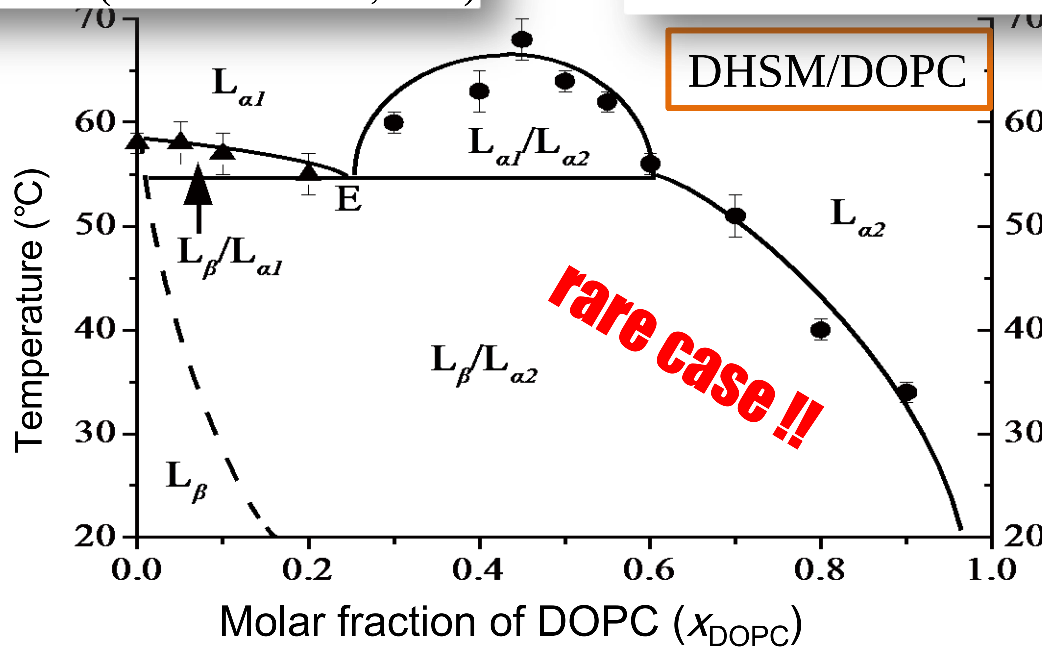
DHSM/DOPC系の相分離は珍しい例



(Wu & McConnel, 1975)



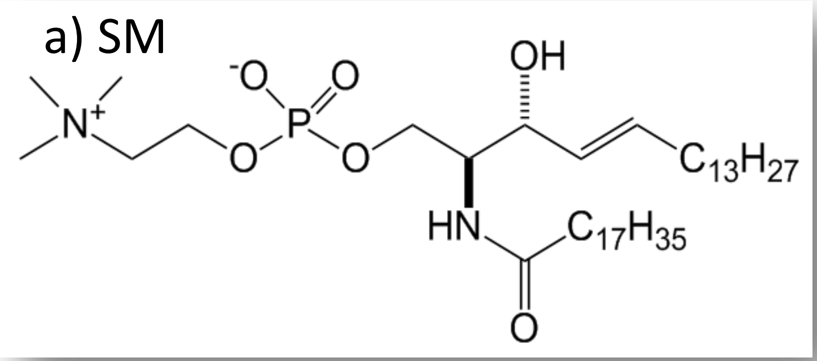
(Mason, 1988)



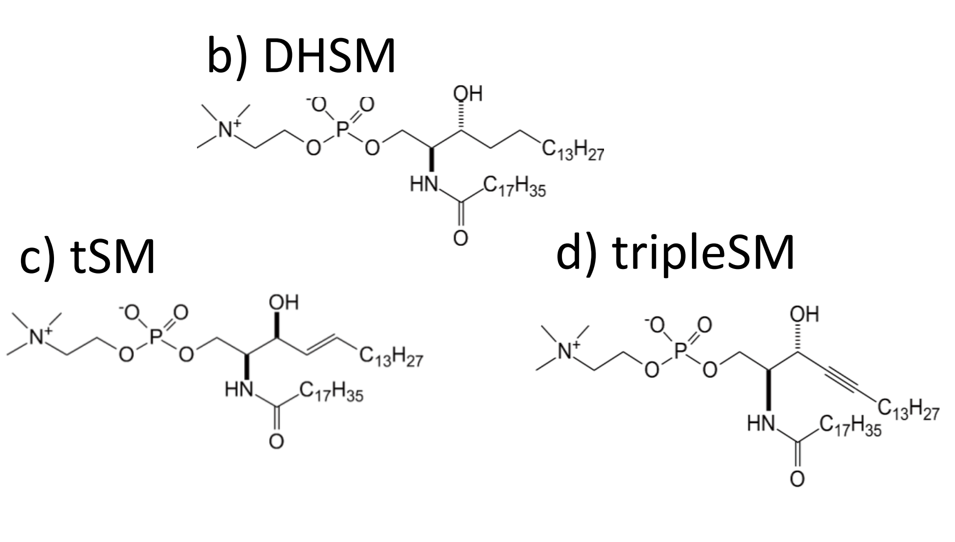
SM類縁体だけの相分離の観測
コレステロールがなくても強い相互作用を示すか？

SM: Sphingomyelin (C18)

DHSM: Dihydrosphingomyelin (C18)



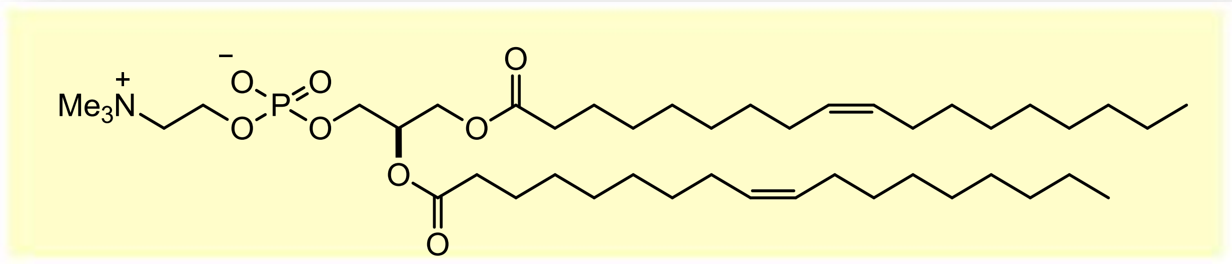
vs



- 代表的SM
- ラフトモデル膜に用いられる

＋

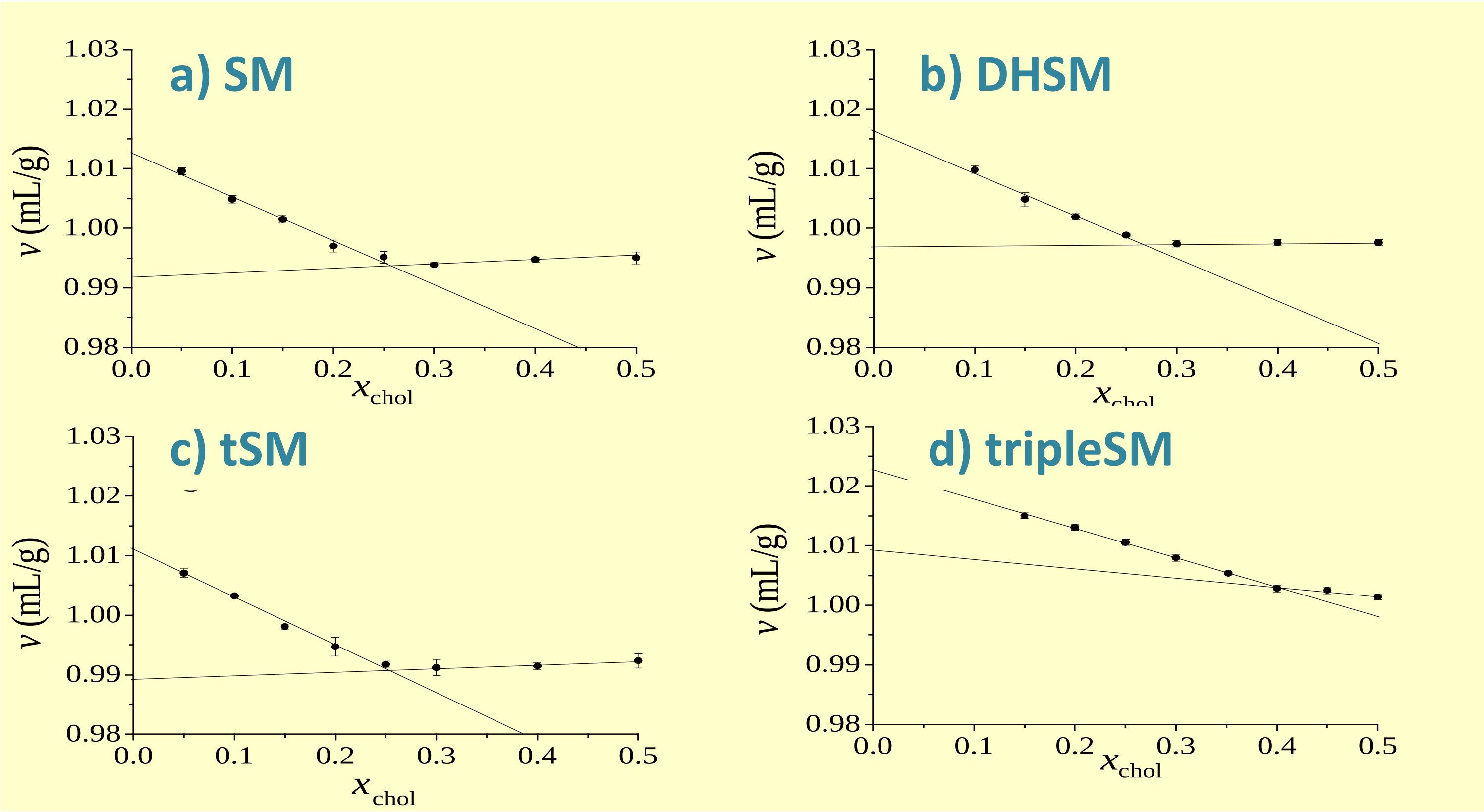
- 少量成分SM
- 通常のChol存在下SMより固い膜を形成

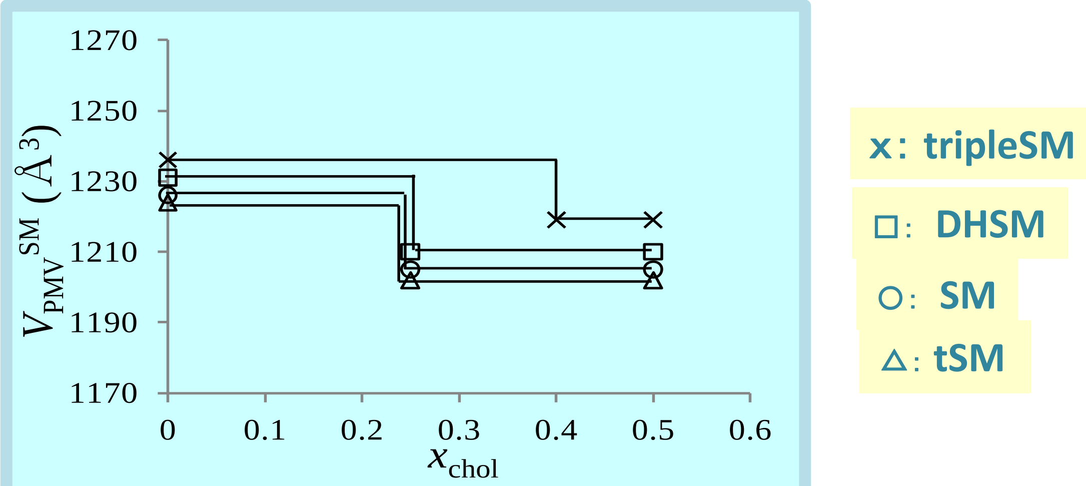


DOPC不飽和リン脂質：　相分離して軟らかい相を形成

Kinoshita, M., Goretta, S., Tsuchikawa, H., Matsumori, N., Murata, M., *Biophysics* 9, 37-49 (2013).

SM誘導体の物理学的膜物性の測定





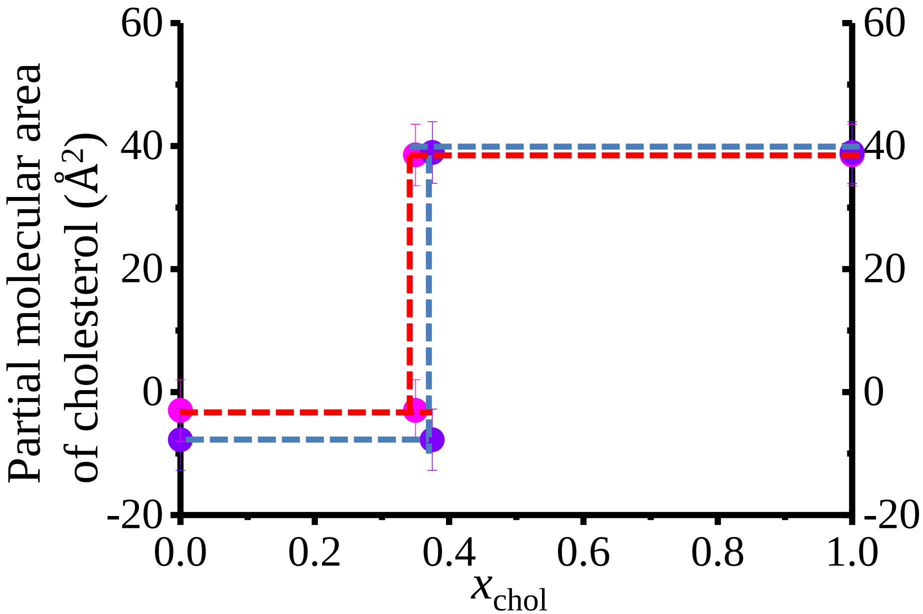
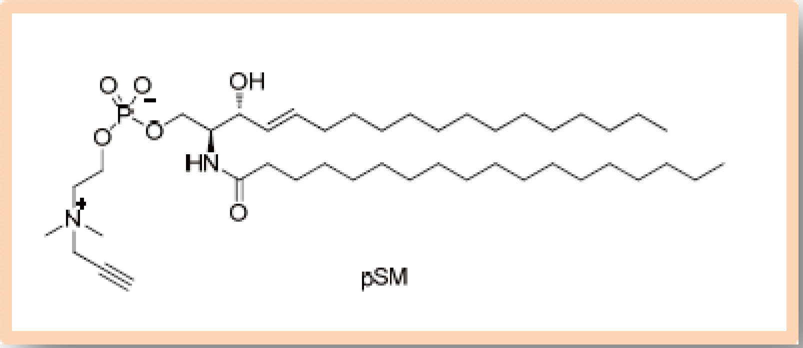


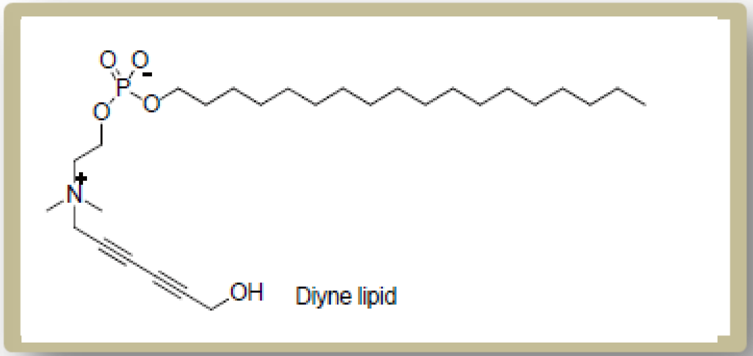
Figure 7. The partial molecuar area of chol in (blue) diyneSM/chol and (red) SSM/chol binary monolayers at 5 mN/m was estimated from Figure 5 c and d.

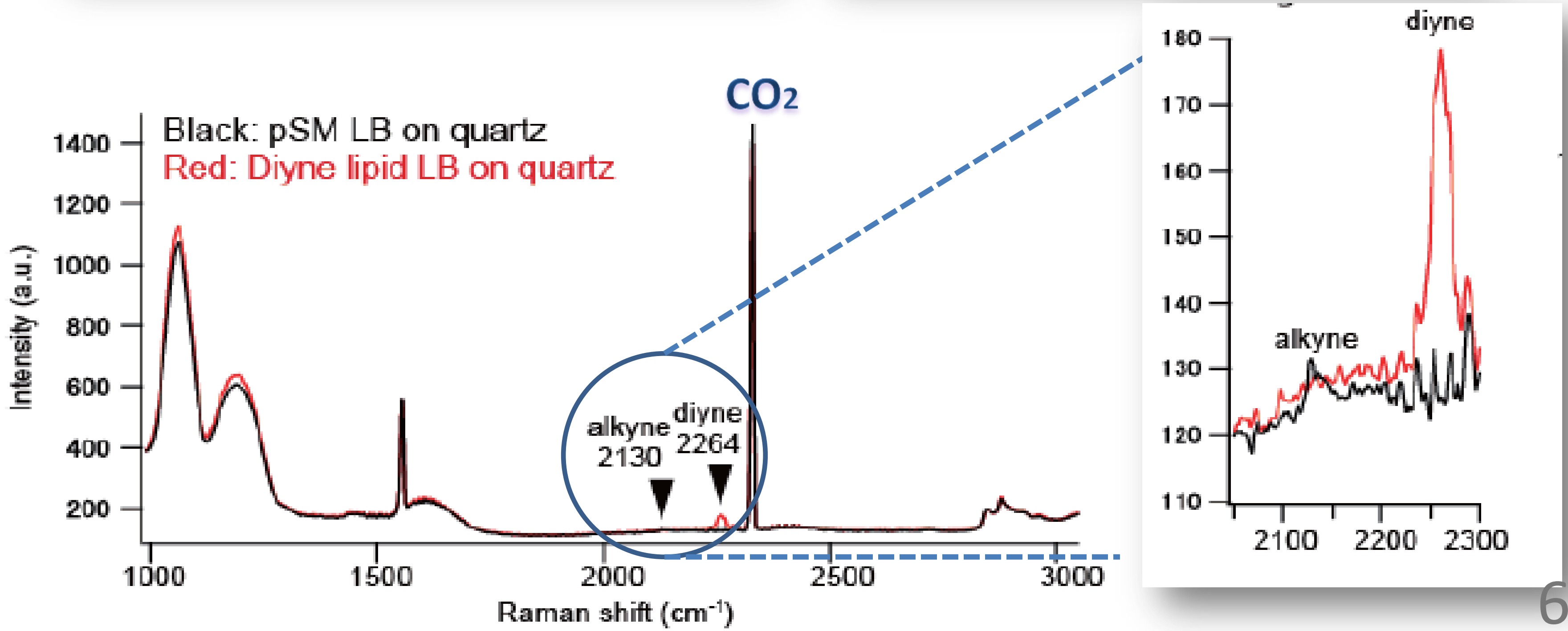
Table 1. Areal compressional modulus of SM C_{SM}^{-1} (mN/m) at 5 mN/m.

	x_{chol}=0 (LE phase)	$x_{chol} \geqq 0.5$ (ordered phase)
diyneSM	33±10	130±20
SSM	47±10	120±20

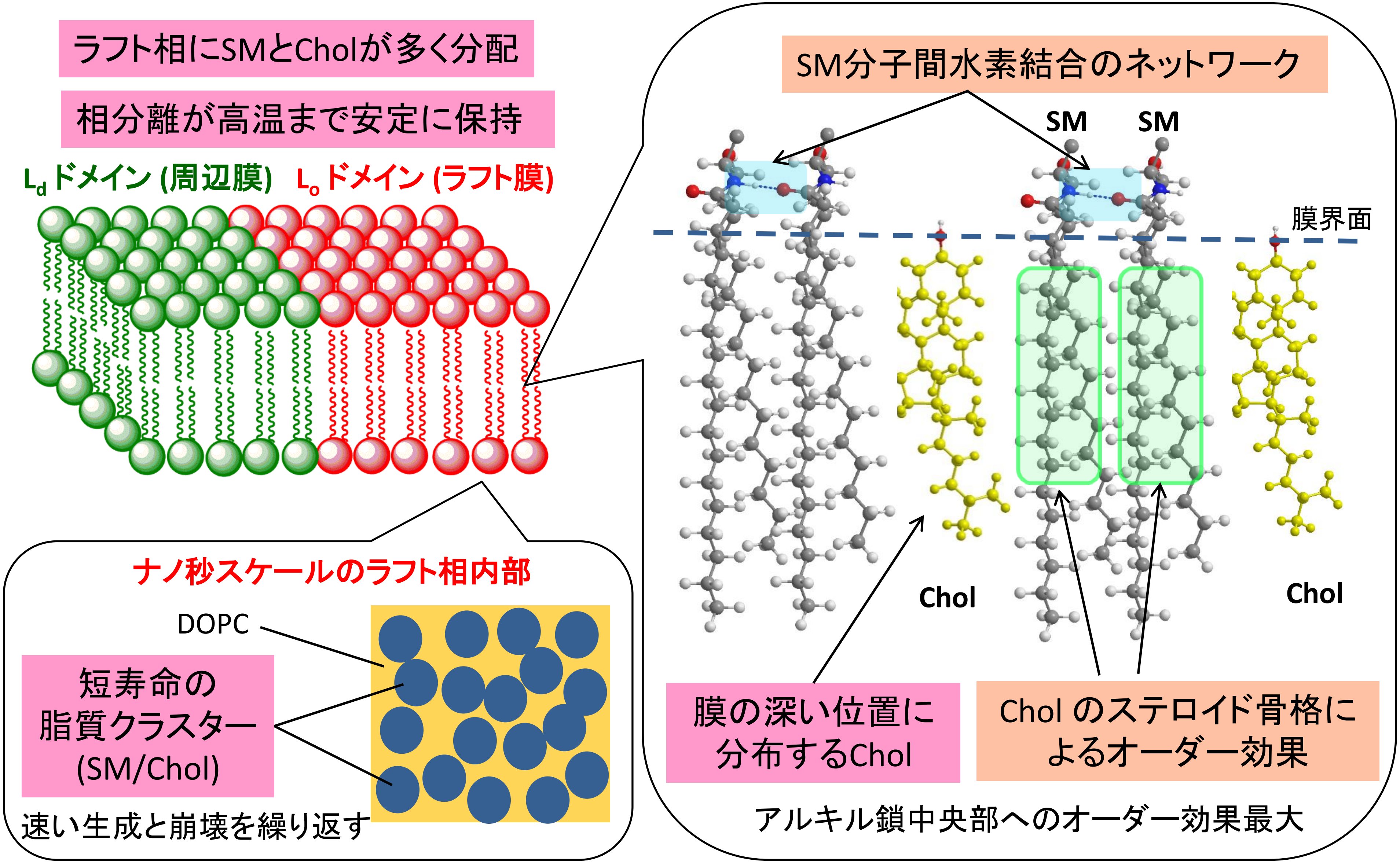
三重結合１つでは感度不足：共役ジインの強度は１０倍
－実際の膜で測定してみると－



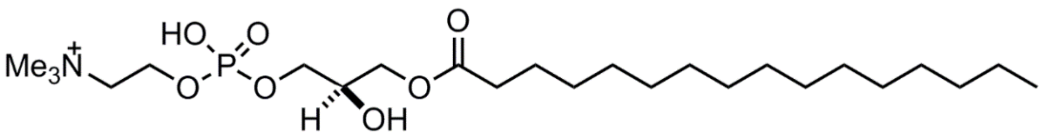




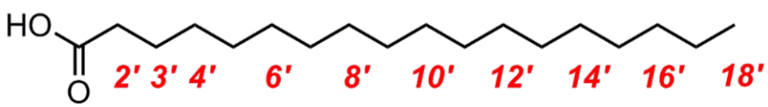
脂質ラフト形成モデル


ラフト相にSMとCholが多く分配
相分離が高温まで安定に保持
L_d ドメイン (周辺膜)
L_o ドメイン (ラフト膜)
ナノ秒スケールのラフト相内部
DOPC
短寿命の
脂質クラスター
(SM/Chol)
速い生成と崩壊を繰り返す
SM分子間水素結合のネットワーク
SM
SM
膜界面
Chol
Chol
膜の深い位置に
分布するChol
Chol のステロイド骨格に
よるオーダー効果
アルキル鎖中央部へのオーダー効果最大

位置選択的重水素標識PSPCの合成

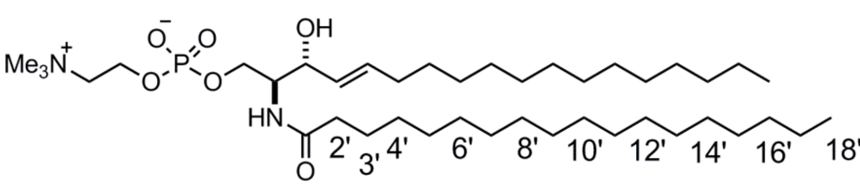


16:0 Lyso PC



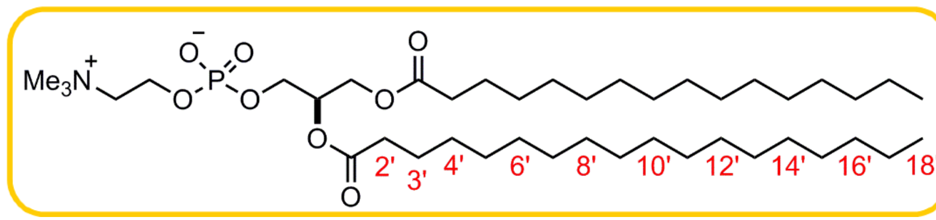
d_2- or d_3- stearic acid

MNBA, DMAP
CH_2Cl_2, rt, 16 h
49-90%



Stearoyl-sphingomyelin (SSM)

アシル鎖長 : C18
相転移温度(T_m) : 44 ℃



1-palmitoyl-2-stearoyl-*sn*-glycerol-3-phosphocholine (PSPC)

計10種類の標識体ライブラリー

アシル鎖長 : C18
相転移温度(T_m) : 48.8 ℃