and full-length proteins to lipid bilayers using total internal reflection fluorescence (TIRF) microscopy. In addition, we use TIRF to measure lateral diffusion of individual molecules in order to directly determine diffusion constants and gain information on specific protein-lipid interactions. Single-molecule techniques enable kinetic measurement under conditions in which equilibrium is not perturbed, as well as allowing resolution of multiple populations with distinct lateral diffusion properties. To our knowledge, this is the first single-molecule study using isolated proteins and supported lipid bilayers to probe molecular mechanisms of protein membrane docking. Both Ca^{2+}-regulated docking of C2 domains, and PIP_3-targeted docking of PH domains are being studied and the latest findings will be reported. Overall, we find that single molecule measurements complement and extend traditional measurements for the elucidation of protein-membrane docking mechanisms.

Lipids and Signaling on Membrane Surfaces

2900-Pos Lipid Raft Disruption Alters Both Local And Global IP_3-mediated Calcium Release In Human Neuroblastoma Cells

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Localized calcium signals such as calcium 'puffs' regulate physiological processes as varied as synaptic transmission and gene transcription, and arise because of the clustered distribution of inositol trisphosphate receptor (IP_3R) channels in the endoplasmic reticulum (ER) membrane. In light of growing evidence for the role of lipid rafts in spatially organizing membrane proteins, we sought to examine the possible role for lipid rafts in regulation of IP_3-mediated calcium signaling. Two-photon microscopy of laurdan fluorescence confirmed that the membrane order of SHSY-5Y cells increased when treated with methyl-beta-cyclodextrin (mβCD) for 10 minutes to remove membrane cholesterol, presumably disrupting lipid rafts, and subsequently decreased with replacement of cholesterol. Furthermore, we found that mβCD treatment reduced the amplitudes (but not wave velocity) of global intracellular $[Ca^{2+}]_i$ transients evoked by carbachol stimulation and by UV-flash photolysis of caged-IP_3, whereas these responses recovered following subsequent re- addition of cholesterol. The reduction in amplitude appears not to arise *via* calcium inhibition of IP_3R, because basal calcium levels remained unchanged after mβCD treatment. To then explore the effects of lipid environment on local calcium signals, we used short UV-flash photolysis durations to dissociate global rises of calcium into discrete puffs. We observed no changes in puff amplitudes or numbers of responding puff sites per cell following mβCD treatment, but the frequency of puffs was significantly reduced.

2901-Pos Endogenous Phosphatidylinositol 4, 5-bisphosphate Directly Regulates Cerebral Artery BK Channel Function

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Board B204

We have shown that exogenous application of phosphatidylinositol 4, 5- bisphosphate (PIP_2) increases BK channel activity (NPo) in cerebral artery myocytes and modifies cerebral artery myogenic tone (Liu et al., 2006; Vaithianathan et al., 2007). Here, we conducted a series of experiments to determine whether endogenous PIP_2 controls cerebral artery myocyte BK NPo and arterial tone. First, under physiological $Ca^{2+}{}_i$ (3 μM; Pérez et al., 1999), BK NPo ran down almost immediately after patch excision from the myocyte, becoming ~50% of initial values 30 min after. In the presence of 0.1 μ M okadaic acid, bath application of 0.5 mM Mg-ATP (Lin et al., 2005) totally rescued the rundown, which likely reflects channel activation by PIP_2 being regenerated *via* PI4KIIα (Yaradanakul et al., 2007). Moreover, PIP_2 monoclonal antibodies (1:1000) applied on top of Mg-ATP to the cytosolic side of the plasma membrane dropped NPo to <35% of control Second, co-transfection of HEK293 cells with BK-channel forming (cbv1)+smooth muscle-abundant (β_1) subunits and PI4kinaseIIα resulted in robust potentiation of NPo when compared with cbv1+ β_1 alone. This result is consistent with the idea that transfection of PI4KIIα leads to increased PIP_2 levels (Yaradanakul et al., 2007) and, thus, increased NPo. Third, perforated-patch recordings in freshly isolated myocytes under physiological conditions of voltage and Ca^{2+} demonstrated that inhibition of PLC under block of PKC and SR Ca^{2+}-ATPase (IP3 and DAG final targets) resulted in a dramatic increase in both activation slope and amplitude of total BK current, peak amplitude reaching 6,608.5±1,983.1% of control. Finally, PLC inhibition on top of block of PKC and SR Ca^{2+}-ATPase caused a robust increase in arterial diameter (+15.1±0.1%). We conclude that endogenous PIP_2 directly activates cerebrovascular myocyte BK channels and, thus, decreases vascular tone.

2902-Pos Conformational Manifold And Bilayer Insertion Of A Membrane-anchored Ganglioside, GM1

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Board B205

Specific recognition of membrane-bound gangliosides by proteins is critical for many biological processes including cell growth and maturation; however, little is known about the conformation and orientation of gangliosides in their biological environment. Here we report molecular dynamics (MD) simulations and NMR experi-

ments that resolve structural and dynamic properties of the ganglioside G_{M1} in membrane-like environments.

An all-atom, explicit solvent MD simulation of G_{M1} in a dimyristoylphosphatidylcholine lipid bilayer was run using the AMBER software package and the GLYCAM force field (recently extended to include parameters for lipids and glycolipids). The orientation and the immersion depth of G_{M1} from MD were compared with distance constraints from NMR paramagnetic induced relaxation enhancements. Perturbations on proton longitudinal relaxation rates of bicelle-anchored G_{M1} were monitored upon additions of a water soluble probe, Gd(DTPA) and a bicelle-embedded probe, 5-doxyl stearic acid. MD simulations were also validated via existing NMR data for the carbohydrate head group fragment of G_{M1}.

Our studies indicate the membrane environment can sterically restrict conformational space accessible to the glycolipid and significantly reduce solvent accessible surface area of the carbohydrate residue linked to the ceramide. Accessibility of the carbohydrate domain may affect glycolipid_protein recognition and binding, and as such, there are cases where carbohydrate fragments may be poor models for glycolipid_protein interactions that occur at the membrane surface. MD simulations, used in concert with NMR data, can provide realistic atomic-resolution structures of glycolipids in biologically relevant environments.

2903-Pos Dynamics Imaging of Membrane Nanostructural Changes Associated with Antigen-Mediated IgE Receptor Signaling in Mast Cells

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In mast cells, antigen-mediated crosslinking of the high-affinity IgE receptor (FcεRI) results in the movement of FcεRI into cholesterol-rich domains in the plasma membrane, where it is phosphorylated by the Src kinase, Lyn, to initiate the exocytotic release of histamine in the allergic response. Interrogating the molecular interactions occurring between the receptors and these functional domains in live RBL mast cells has remained challenging, particularly under physiological conditions where membrane domains are likely transient and sub-diffraction in size. Here, we use an integrated, multi-scale biophotonics approach that includes confocal microscopy, two-photon fluorescence lifetime imaging (FLIM), and fluorescence polarization anisotropy to image nanostructural changes within the plasma membrane (labeled with diI-C_{18}) that are associated with the stimulation of IgE-FcεRI in RBL mast cells using multivalent antigen (DNP-BSA) at 23°C. We find that the excited-state dynamics and localized membrane order of diI-C_{18} increase within 5 minutes of stimulation and plateau after 10 minutes, agreeing with the kinetics of tyrosine phosphorylation of FcεRI stimulated under the same conditions and assessed with immunoblotting. Our studies on living mast cells provide direct evidence that IgE-FcεRI associates with ordered cholesterol-rich domains that serve as functional platforms for IgE-FcεRI signaling.

2904-Pos Proton Hopping Along Lipid Bilayers Does Not Require Titratable Groups Or Charged Moities On The Membrane Surface

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Lateral proton diffusion along the membrane surface between proton pumping and proton consuming proteins is the most efficient pathway. The energetic barrier preventing proton escape into the bulk was hypothesized to arise from proton binding to titratable groups (e.g. ethanolamine) or electrostatic forces created by charged moieties (e.g. phosphate groups) on the membrane-water interface. We confirmed this hypothesis using planar lipid bilayers. However, upon removal of these groups from the membrane surface, a significant energetic barrier remained as indicated by experiments with glycerol monooleate bilayers. Proton diffusion along these bilayers was faster than diffusion along phosphatidylcholine (compare Serowy et. al, 2003) or phosphatidylethanolamine bilayers. The presence of structural proton diffusion was confirmed by experiments in D2O which revealed the largest isotope effect for glycerol monooleate membranes. Structured water layers most probably contribute significantly to the energetic barrier. By assuming a decreased dielectric constant for these water layers, we developed an analytical model that describes the combined network of two and three dimensional diffusion processes and chemical reactions. The consistency between experiment and theory suggests that interfacial structured water is crucial for the occurrence of high migration velocity, and that fixed proton binding sites act only to delay the proton transport process.

2905-Pos Phase Change of Sphingosine as a Function of pH

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Sphingosine is known to be an important biological mediator that affects many cell signaling targets, such as protein kinase C, protein kinase A type II, casein kinase, and so forth. Sphingosine is a basic building block of sphingolipids and its structure is described by the nomenclature, (2S,3R,4E)-2-amino-4-octadecene-1,3-diol. We have examined the phase changes of sphingosine as a function of pH, because the previously reported pK_a of this lipid was ambiguous, ranging from 6.7 to 9.1. Our pH titration of sphingosine

revealed that monomeric sphingosine has only one pK_a at 6.86 ± 0.10, but multimeric sphingosine has two distinguishable pK_as of 5.19 ± 0.08 and 8.19 ± 0.08 whereas only one amine exists in the molecule. pH titration curves of multimeric sphingosine collected at different salt concentrations also demonstrated that the lower pK_a around 5.2 does not change with salt concentration, whereas the higher pK_a, around 8.2, disappears at high salt concentrations. The nominal critical aggregation concentrations at pH = 3.5, 7.2, and 9.9, determined by dynamic light scattering, were 29.6 ± 2.1 μM, 0.71 ± 0.02 μM, and 5.77 ± 0.02 μM, respectively, indicating the existence of three different phases of sphingosine as a function of pH.

2906-Pos Capturing Hindered Diffusion on Nanopatterned Lipid Bilayers

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Board B209

Membrane proteins exhibit complex patterns of motion along the cell surface. In particular, molecules often undergo free diffusion within nanoscale compartments of the plasma membrane, occasionally crossing the boundaries between regions and giving rise to relatively slow long-range diffusion. As a platform for examining how this hindered diffusion modulates cell signaling, we created nanopatterned, glass-supported lipid bilayers containing arrays of parallel diffusion barriers spaced 125 or 250 nm apart, mimicking the spacing of cytoskeletal structures observed within living cells. These barriers were interspersed with gaps measuring 30, 40, or 50 nm in size and spaced 500 nm center-to-center, capturing the semipermeable nature associated with their in vivo counterparts. Titanium and chromium were explored as barrier materials. Supported lipid bilayers of egg phosphatidylcholine + 1% Texas Red-DHPE (TRPE) were formed on these surfaces by vesicle fusion. Long-range diffusion coefficients (tens of micrometers) of TRPE lipids parallel and perpendicular to the direction of the barriers were measured using an anisotropic fluorescence recovery after photobleach approach.

Long-range diffusion coefficients measured parallel to the barriers for all combinations of spacing, gap, and metal were similar to that on unpatterned glass, indicating that lipids undergo free diffusion between barriers.

Perpendicular to the barriers, long-range diffusion was reduced by up to a factor of 10 compared to that on unpatterned glass, capturing the fundamental property of hindered diffusion. Interestingly, TRPE diffusion on surfaces containing chromium barriers was consistent with a continuum diffusion model applied to a perforated plate. In contrast, diffusion across titanium barriers was higher than predicted by this model, and limited diffusion was observed over barriers with no gap. These results suggest a more complex interaction between titanium and supported lipid bilayers which only emerges at these scales.

2907-Pos Equilibrium Configurations for Planar Bilayer Lipid Membranes

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Board B210

Lipid bilayers constitute the dominant component of cell membranes. Their buildings blocks are amphiphilic molecules. These molecules are characterized by having hydrophilic head groups and hydrophobic tails. Therefore, when a specific concentration of lipid molecules is dissolved in an aqueous medium, planar bilayer lipid membranes (BLMs) are formed in which the hydrophobic heads become exposed to the watery solution whereas the hydrophilic tails constitute the core of the membranes.

Interest in research on BLMs is growing not only because they are the perfect model for studying the cell membranes but also because they demonstrated their potential as platforms for the development of many biologically inspired sensors and actuators. The actual use of BLMs is, however, hampered by their poor stability to environmental disturbances such as, for example, mechanical stresses. Because performing experiments on BLMs is challenging due to the small stresses and deformations involved, the formulation of reliable mathematical models becomes important for designing the experiments and interpreting their results.

A novel continuum model that illustrates the equilibrium configurations of BLMs is proposed. The model has been derived within the theoretical framework for nonlinear smectic A liquid crystals proposed by Stewart (2007). A unit vector, the so-called director, defines the local average orientation of the amphiphilic molecules in the smectic layers. Differently from previous studies, the energy density used in this study accounts for the elastic splay deformation of the director, the bending of the layers, the compression of the layers, and the coupling between the director and layer normal. Moreover, a surface energy is introduced to describe weak anchoring of the director to the boundary. The nonlinear differential equations that describe the equilibrium configurations of BLMs are solved numerically and their behavior is illustrated for different values of the material parameters.

2908-Pos Magic Angle Spinning ^{31}P NMR pH Titration of Fluid Phosphatidylinositol Polyphosphate/ Phosphatidylcholine Model Membranes

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Board B211

Phosphatidylinositol polyphosphates (PIPs) are only a minor pool of membrane phospholipids but are involved in many intracellular signaling processes. PIPs play key-roles in processes as diverse as membrane trafficking, cytoskeleton remodeling, receptor signal transduction and nuclear processes. Due to the multiple phosphomonoesters on their headgroups these lipids carry a high negative

charge density and many proteins have developed special binding domains that facilitate binding to PIPs. Initial recognition and binding of PIPs to proteins is likely mediated by the electrostatic properties of these highly charged lipids. However, very limited ionization data on PIPs in model lipid membranes is available. Here, we present for the first time, detailed ^{31}P NMR pH titration curves for all PIPs in the physiologically relevant pH range $4 < pH < 10$ dispersed in multilamellar dispersions of DOPC. We find for DOPI $(3,5)P_2$, where the two phosphomonoesters are separated by a hydroxyl group (at the 4 position), that the titration curves for both phosphomonoester groups can be fitted by a Henderson-Hasselbalch derived equation describing a simple ionization constant. However, for DOPI$(4,5)P_2$ and DOPI$(3,4)P_2$ (phosphomonoester groups next to each other), this is not the case. The respective titration curves cannot be fitted with a Henderson-Hasselbalch type equation, and the pKa's are higher than for DOPI$(3,5)P_2$. Most importantly, around physiological pH, additional peaks are observed in the MAS ^{31}P NMR spectra of DOPI$(4,5)P_2$, suggesting the formation of additional long lasting (on the NMR time scale) hydrogen bonded phosphoinositide species. These hydrogen bonds are likely to be intermolecular because 31P-NMR spectra obtained for inositol$(4,5)P_2$ did not show any of these additional peaks. These new NMR results will be discussed in light of recent findings showing enhanced mutual interaction of phosphoinositides around physiological pH.

2909-Pos The Binding To Membranes Of C2 Domains From Classical PKCs Is Specifically And Differentially Enhanced By PIP2

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C2 domains are conserved protein modules in many eukaryotic signalling proteins, including the protein kinase (PKCs). The C2 domains of classical PKCs bind to membranes in a Ca^{2+}-dependent manner and thereby act as cellular Ca^{2+} effectors. Recent findings suggest that the C2 domain of PKCα interacts specifically with phosphatidylinositols 4,5-bisphosphate (PIP_2) through its lysine rich cluster, for which it shows higher affinity than for POPS. In this work, we compared the three C2 domains of classical PKCs. Isothermal titration calorimetry revealed that the C2 domains of PKCα and β display a greater capacity to bind to PIP_2-containing vesicles than the C2 domain of PKCγ. Comparative studies using lipid vesicles containing both POPS and PtdIns(4,5)P2 as ligands revealed that the domains behave as PIP_2- binding modules rather than as POPS-binding modules, suggesting that the presence of the phosphoinositide in membranes increases the affinity of each domain. When the magnitude of PIP_2 binding was compared with that of other polyphosphate phosphatidylinositols, it was seen to be greater in both PKCβ and PKCγ-C2 domains. The concentration of Ca^{2+} required to bind to membranes was seen to be lower in the presence of PIP_2 for all C2 domains, especially PKCα. In vivo experiments using differentiated PC12 cells transfected with each C2 domain fused to ECFP and stimulated with ATP demonstrated that, at limiting intracellular concentration of Ca^{2+}, the three C2 domains translocate to the plasma membrane at very similar rates. However, the plasma membrane dissociation event differed in each case, PKCα persisting for the longest time in the plasma membrane, followed by PKCγ and, finally, PKCβ, which probably reflects the different levels of Ca2+ needed by each domain and their different affinities for PIP_2.

2910-Pos Ceramide Synthesized in the Endoplasmic Reticulum Can Be Rapidly Transferred to Mitochondria, Permeabilizing the Outer Membrane to Proteins

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Board B213

Elevated mitochondrial ceramide levels are associated with the initiation of apoptosis. There is evidence that ceramide is causal. Ceramide can initiate apoptosis by permeabilizing the mitochondrial outer membrane to apoptosis-inducing proteins. However, the mitochondria's ability to produce ceramide may be limited by its proteome. Here, we show that ceramide synthesized in isolated mammalian endoplasmic reticulum (E.R.) vesicles from either C_8-dihydroceramide (by the dihydroceramide desaturase) or sphingosine to produce long-chain ceramide (by the ceramide synthase), can transfer to isolated mitochondria. The rate of transfer is consistent with a simple collision model. The transfer of the long-chain ceramide is much faster than expected for an uncatalyzed process. Although the structure responsible for this apparent catalysis has not been identified, sufficient ceramide is transferred to reach the critical concentration required for ceramide to self-assemble into channels and permeabilize the outer membrane to cytochrome *c* and adenylate kinase. *In vivo*, special E.R. membranes, called mitochondria associated membranes, are in intimate contact with mitochondria and may be specialized to perform such transfer of ceramide. *In vitro*, we find that these membranes can produce and transfer enough ceramide to mitochondria to permeabilize the outer membrane, transiently, to proteins. This ceramide exchange between E.R. and mitochondria can act together with the activity of mitochondrial ceramide synthase and mitochondrial ceramidase to supply ceramide to mitochondria resulting in major functional changes.

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2911-Pos Structure Of Cer-1-p At The Air-Water Interface In The Absence And Presence Of Ca^{2+}

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Ceramide-1-phosphate (Cer-1-P), one of the simplest of sphingophospholipids, occurs in minor amounts in biological membranes. Yet recent evidence suggests this lipid is a second messenger with crucial roles in cell survival and inflammatory responses. In particular, during inflammation, PLC-α binds to cer-1-p in the presence of Ca^{2+} to facilitate the hydrolysis of structural membrane lipids. To get insight into the mechanism of cer-1-p function in cellular membranes and specifically its interaction with Ca^{2+}, we present a detailed structure of monomolecular layers of cer-1-p at the air-water interface. Combining surface-tension versus molecular area isotherms, Brewster angle microscopy and most importantly in-situ surface sensitive synchrotron diffraction techniques, we determined the morphology and structure at molecular length scales of cer-1-p in the monolayer on four different subphases. On water, 1mM Ca^{2+} and pH 7.2 buffer containing 1 mM Ca^{2+}, we find that cer-1-p forms solid like monolayers. Interestingly, considerable more Ca^{2+} is bound to cer-1-p on buffer containing 1 mM Ca^{2+} than pure water containing 1mM Ca^{2+}. Compared to water and the Ca^{2+} containing subphases, cer-1-p has a much more fluid like behavior on a buffered subphase at pH 7.2 without Ca^{2+}. These results can be qualitatively understood based on the molecular structure of cer-1-p and, in particular, the electrostatic/hydrogen-bond interactions of its phosphomonoester headgroup.

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2912-Pos Membrane Organization And Ionization Behavior Of The Minor But Crucial Lipid Ceramide-1-Phosphate

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Board B215

Ceramide-1-phosphate (Cer-1-P), one of the simplest of sphingophospholipids, occurs in minor amounts in biological membranes. Yet recent evidence suggests an important role of this lipid as a novel second messenger with crucial roles in cell survival and inflammatory responses. Here we present a detailed description of the physical chemistry of this hitherto little explored membrane lipid. At full hydration Cer-1-P forms a highly organized subgel (crystalline) bilayer phase (L_c) at low temperature, which transforms into a regular gel phase (Lβ) at ~45 °C, with the gel to fluid phase transition (L_β-L_α) occurring at ~65 °C. When incorporated at 5 mol % in a phosphatidylcholine bilayer, the pKa_2 of Cer-1-P, 7.39 ± 0.03, lies within the physiological pH range. Inclusion of phosphatidylethanolamine in the phosphatidylcholine bilayer, at equimolar ratio, dramatically reduces the pKa_2 to 6.64 ± 0.03. We explain these results in light of the novel electrostatic/hydrogen bond switch model recently described for phosphatidic acid. In mixtures with dielaidoylphosphatidylethanolamine, small concentrations of Cer-1-P cause a large reduction in the lamellar-to-inverted hexagonal phase transition temperature, suggesting that Cer-1-P induces, like PA, negative membrane curvature. These properties place Cer-1-P in a class more akin to certain glycerophospholipids (phosphatidylethanolamine, phosphatidic acid) than to any other sphingolipid. In particular, the similarities and differences between ceramide and Cer-1-P may be relevant in explaining some of their physiological roles.

2913-Pos Using Neutron Reflectometry to Study the Adhesion of Living Cells

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Board B216

The adhesion behavior of mouse fibroblast cells to a substrate has been examined using the surface sensitive technique of neutron reflectometry. Neutron reflectometry can provide density profiles in the range of 5 to 3000 angstroms from the substrate, yielding a better understanding of the length scales involved in the cell adherence. With this technique we are able to see adherence proteins at the interface, the first phospholipid membrane and its environment. Additionally, the separation of the cells from the substrate was seen upon introduction of both trypsin and distilled water.

Nucleocytoplasmic Transport

2914-Pos Conformational Changes in the Transport of Cargo through the Nuclear Pore Complex

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Board B217

Cargo that must pass through the nuclear pore complex (NPC) to complete biological processes within the cell are broad, varied, and of a large range of sizes. Experimental observations have revealed that the NPC can maintain high rates of transport throughput for most cargo, regardless of the actual shape or, to within a limit, size of the cargo as long as the cargo is bound to an NPC Importin molecule.