

Litmus-Body: a Molecularly Targeted Sensor for Cell-Surface pH Measurements

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ABSTRACT: Precise pH measurements in the immediate environment of receptors is essential for elucidating the mechanisms through which local pH changes associated with diseased phenotypes manifest into aberrant receptor function. However, current pH sensors lack the molecular specificity required to make these measurements. Herein we present the Litmus-body, our recombinant protein-based pH sensor, which through fusion to an anti-mouse IgG nanobody is capable of molecular targeting to specific proteins on the cell surface. By normalizing a pH-dependent green fluorescent protein to a long-Stokes shift red fluorophore or fluorescent protein, we readily report pH independent of sensor concentration using a single 488-nm excitation. Our Litmus-body showed excellent responsiveness in solution, with a greater than 50-fold change across the physiological regime of pH. The sensor was further validated for use on live cells, shown to be specific to the protein of interest, and was able to successfully recapitulate the numerous pH changes along the endocytic pathway.

Acidification of the extracellular microenvironment is a hallmark of cancer progression^{1,2}. In response to an increased anabolic demand associated with uncontrolled proliferation, cancer cells upregulate glycolysis and consequently overproduce protons intracellularly³. This excess of protons is then expelled to maintain cellular homeostasis, lowering the pH of the extracellular space. The consequences of extracellular acidosis are diverse and profound: for example, mutant receptors may become permanently activated in a low pH environment⁴, and acid-adapted cells show a proclivity towards a more aggressive phenotype⁵. While these effects have been studied in the context of the bulk extracellular pH^{6,7}, work towards elucidating the precise relationship between localized acidity and aberrant cellular function has been limited by the ability to measure pH at precise locations.

Notably, this localized acidity is further exaggerated at the cancer cell surface⁸. It is suggested that cancer-associated proton secretion creates a concentration gradient of protons that is highest at the cell membrane⁹⁻¹⁰. In addition, negatively charged residues in the glycocalyx, a carbohydrate-enriched cell coat near the pericellular surface, have also been predicted to accumulate protons that lower the local pH¹¹. In concert with cancer-associated acidosis, the content of anionic moieties in the glycocalyx has been shown to increase¹², which could act synergistically with proton secretion to concentrate protons in the vicinity of cell surface receptors. These factors may lead to heterogeneity in the local pH that receptors experience, significantly impacting their functionality. Although cell surface pH can

be determined by recently developed pH sensitive fluorescent dyes conjugated to pH-low insertion peptides⁹ and cell penetrating peptides¹³, there remains an unmet need in the development of molecularly targeted sensors capable of reporting on the immediate environment of receptors.

Molecular targeting can be achieved by the diverse repertoire of antibody specificity¹⁴. Monoclonal primary antibodies that target specific cell surface receptors are clinically important for cancer therapies, such as Cetuximab for the cancer types that overexpress epidermal growth factor receptor (EGFR)¹⁵. Primary antibodies are conventionally detected by a secondary antibody, although its relatively large size (~150 kDa) can be disadvantageous in sample penetration and signal localization¹⁶. Recently, nanobodies, or single-domain antibodies, have emerged as attractive alternatives for specific binding and localisation to primary antibodies¹⁷. Specifically, Pleiner et al. have successfully expressed and validated a library for targeting rabbit IgG and all mouse IgG subclasses¹⁸. Their small size (~13 kDa), ease of labelling and consistent behaviour in recombinant protein fusions make nanobodies well-suited for fluorescence imaging¹⁹⁻²⁰.

Fluorescent protein-based biosensors are versatile tools that can be fused to nanobodies for specific targeting²¹. Through extensive protein engineering, derivatives of the green fluorescent protein (GFP) from *Aequorea victoria* have been selected for pH dependent fluorescence²²⁻²⁵. In particular, pHluorins have been widely used as genetically-encoded sensors for tracking the pH of intracellular compartments^{23,24}. Notably, the bright 488 nm excitable super-

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