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Human Airway Epithelia: Coxsackie-Adenovirus Receptor by Glycosyl-Phosphatidylinositol Modification Is Sufficient for Adenovirus-Mediated Gene

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Abstract

In well-differentiated human airway epithelia, the coxsackie B and adenovirus type 2 and 5 receptor (CAR) resides primarily on the basolateral membrane. This location may explain the observation that gene transfer is inefficient when adenovirus vectors are applied to the apical surface. To further test this hypothesis and to investigate requirements and barriers to apical gene transfer to differentiated human airway epithelia, we expressed CAR in which the transmembrane and cytoplasmic tail were replaced by a glycosyl-phosphatidylinositol (GPI) anchor (GPI-CAR). As controls, we expressed wild-type CAR and CAR lacking the cytoplasmic domain (Tailless-CAR). All three constructs enhanced gene transfer with similar efficiencies in fibroblasts. In airway epithelia, GPI-CAR localized specifically to the apical membrane, where it bound adenovirus and enhanced gene transfer to levels obtained when vector was applied to the basolateral membrane. Moreover, GPI-CAR facilitated gene transfer of the cystic fibrosis transmembrane conductance regulator to cystic fibrosis airway epithelia, correcting the Cl− transport defect. In contrast, when we expressed wild-type CAR it localized to the basolateral membrane and failed to increase apical gene transfer. Only a small amount of Tailless-CAR resided in the apical membrane, and the effects on apical virus binding and gene transfer were minimal. These data indicate that binding of adenovirus to an apical membrane receptor is sufficient to mediate effective gene transfer to human airway epithelia and that the cytoplasmic domain of CAR is not required for this process. The results suggest that targeting apical receptors in differentiated airway epithelia may be sufficient for gene transfer in the genetic disease cystic fibrosis.

INTRODUCTION

The first steps in adenovirus infection involve primarily two proteins in the viral capsid: fiber and penton base (9, 11, 12). The adenovirus fiber protein forms a trimer which binds to the cell via a high-affinity receptor, the coxsackie B and adenovirus type 2 and 5 receptor (CAR) (3, 29). Recent structural and genetic studies support a model in which the lateral cleft between two neighboring knob domains on fiber interact with the extracellular amino-terminal immunoglobulin V domain of CAR (4, 8, 26). Interestingly, adenovirus-meditated gene transfer to lymphocyte and CHO cell lines does not require the transmembrane or cytoplasmic domains of CAR, suggesting that the interaction between fiber-knob and CAR mediates primarily attachment to the cell surface (18, 30, 37). In addition to the fiber-CAR interaction, the penton base interacts with αvβ3 and αvβ5 integrins, facilitating receptor-mediated endocytosis of adenovirus (12, 21, 40). Thus, CAR is required for binding and infection, and αvβ integrins act as coreceptors.

Human airway epithelia are a target for gene transfer in the genetic disease cystic fibrosis (CF) (27, 38). Earlier works showed that adenovirus infection and adenovirus-mediated gene transfer to differentiated airway epithelia are inefficient due to lack of CAR and integrins in the apical membrane (2, 10, 13, 15, 23–25, 35, 41, 42). Thus, lack of fiber-knob binding to the apical membrane may be the rate-limiting step for adenovirus-mediated gene transfer to airway epithelia. Despite its absence on the apical membrane, CAR is present on the basolateral membrane (25, 35). Consequently, adenovirus infects airway epithelia from the basolateral surface

in a fiber-dependent manner (35).

These results raised the question of whether CAR localized in the apical membrane would be sufficient for adenovirus-mediated gene transfer from the apical surface. Answering this question is important for understanding the molecular mechanisms of adenovirus entry into human airway epithelia. The answer may also impact the development of targeted gene delivery of the cystic fibrosis transmembrane conductance regulator (CFTR) for CF. To address this question we studied adenovirus-mediated gene transfer in differentiated human airway epithelia expressing recombinant wild-type CAR and two modified CAR proteins: CAR lacking the cytoplasmic domain (Tailless-CAR) and CAR lacking the cytoplasmic and transmembrane domains but modified with a glycosyl-phosphatidylinositol (GPI) anchor signal sequence (GPI-CAR) to target the apical membrane (18, 30, 37). Recently, similar modifications in CAR (Tailless- and GPI-CAR) were found to localize to the apical membrane in a canine renal epithelial cell line (MDCK) (24). However, they did not facilitate adenovirus infection until the MDCK cells were treated with neuraminidase to remove sialic acid from the glycocalyx. To learn whether apically localized CAR facilitates gene transfer to the airways and to investigate the mechanisms involved, we studied primary cultures of well-differentiated human airway epithelia.

MATERIALS AND METHODS

Cells and culture

NIH 3T3 cells were cultured on 100-mm-diameter plates (Corning Costar, Corning, N.Y.) in Eagle's minimum essential medium (EMEM) (Sigma Chemical Co., St. Louis, Mo.) supplemented with 10% fetal calf serum (Sigma Chemical Co.), 1% nonessential amino acids, penicillin (100 U/ml), and streptomycin (100 μg/ml).

Airway epithelial cells were obtained from trachea and bronchi of lungs removed for organ donation. Cells were isolated by enzyme digestion as previously described (16, 43). Freshly isolated cells were seeded at a density of 5 × 105 cells/cm2 onto collagen-coated, 0.6-cm2 area Millicell polycarbonate filters (Millipore Corp., Bedford, Mass.). The cells were maintained at 37°C in a humidified atmosphere of 5% CO2 and air. Twenty-four hours after plating, the mucosal medium was removed and the cells were grown at the air-liquid interface (16, 43). The culture medium consisted of a 1:1 mix of DMEM-Ham's F-12, 5% Ultroser G (Biosepra SA, Cergy-Saint-Christophe, France), penicillin (100 U/ml), streptomycin (100 μg/ml), 1% nonessential amino acids, and insulin (0.12 U/ml). Airway epithelia reached confluence and developed a transepithelial electrical resistance, indicating the development of tight junctions and an intact barrier. Epithelia were allowed to differentiate by culturing for at least 14 days after seeding, and the presence of a ciliated surface was tested by scanning electron microscopy (43).

Flag-tagged CAR constructs and recombinant adenoviruses

cDNAs encoding three CAR constructs were kindly provided by J. M. Bergelson (Division of Immunologic and Infectious Diseases, Children's Hospital of Philadelphia, Philadelphia, Pa.): (i) full-length CAR (wt-CAR), (ii) CAR which lacks the cytoplasmic domain (Tailless-CAR), and (iii) CAR which has the decay-accelerating factor signal for GPI modification in place of the transmembrane and cytoplasmic domains (GPI-CAR) (37). All CAR constructs were modified with the Flag epitope tag consisting of amino acids DYKDDDDK, inserted downstream of the NH2-terminal hydrophobic leader signal sequence, as described previously (30).

We cloned the three Flag-tagged CARs into adenovirus vectors

Recombinant adenovirus vectors expressing the Flag-tagged CAR constructs (Ad5/wt-CAR, Ad5/Tailless-CAR, and Ad5/GPI-CAR), and β-galactosidase (β-Gal) (Ad2/βGal) were prepared by the University of Iowa Gene Transfer Vector Core at titers of ~1010 infectious units/ml (determined by plaque assay) as previously described (39). A recombinant adenovirus vector expressing green fluorescent protein (GFP), Ad2/GFP, and CFTR (Ad2/CFTR-16) were a gift of Sam Wadsworth (Genzyme, Framingham, Mass.).

Expression of CAR

NIH 3T3 cells, which normally express low levels of CAR, were infected with control adenovirus (Ad2/βGal), or adenovirus expressing either one of the three CAR constructs using Ad-CaPi coprecipiates. This method bypasses the need for the CAR receptor on target cells (6, 33). Briefly, Ad-CaPi coprecipitates were formed by adding CaCl2 to adenovirus particles in EMEM to achieve a final Ca2+ concentration of 5.8 mM. Cells were then infected with Ad-CaPi coprecipitates for 30 min, rinsed three times with EMEM, and evaluated for susceptibility to Ad2/GFP infection.

In airway epithelia, the CAR constructs were expressed by pretreating epithelia with 8 mM EGTA delivered in H2O to transiently disrupt the tight junctions. This technique results in reversible disruption of the tight junctions and allows apically administered adenovirus to access its endogenous receptor on the basolateral membrane (35, 36). Immediately after treatment, epithelia were infected

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with control adenovirus or adenovirus (multiplicity of infection [MOI], 10) expressing either of the three CAR constructs. Two days after infection with CAR-expressing adenoviruses, epithelial integrity was measured with an ohmmeter (EVOM; World Precision Instrument Inc., Sarasota, Fla.). The transepithelial resistance values for all infected epithelia were >300 Ω · cm2. Epithelia were then evaluated or studied as described below.

Analysis of Flag-tagged CAR protein expression

Expression of the adenovirus-encoded CAR constructs was evaluated by Western blot analysis of airway epithelia 2 days after infection with CAR-expressing adenoviruses. Protein was extracted from epithelia by incubation for 1 h at 4°C with lysis buffer (1% Triton X-100; 10 mM Tris-HCl, pH 7.4; 150 mM NaCl), supplemented with protease inhibitors (10 μg each of leupeptin, aprotinin, and pepstatin A per ml). The lysates were diluted in Laemmli sample buffer, and equal amounts were subjected to Western blotting. Flag-tagged CAR proteins on nitrocellulose membranes were detected by incubation with a 1:500 dilution of horseradish peroxidase-conjugated anti-Flag M2 monoclonal antibody (Sigma Chemical Co.) in 10 mM TBS (Tris-HCl, pH 7.4; 150 mM NaCl; 10 mM EDTA) containing 5% nonfat milk, and visualized after chemiluminescence by exposure for 1 to 5 min to X-Omat film (Eastman Kodak, Rochester, N.Y.).

RESULTS

GPI-CAR, Tailless, and wt-CAR mediate adenovirus gene transfer to 3T3 cells with similar efficiencies

Adenovirus vectors were generated to express three different Flag-tagged CAR constructs: (i) full-length CAR (amino acids [aa] 1 to 365), (ii) CAR lacking the cytoplasmic domain (aa 1 to 260), and (iii) CAR with the cytoplasmic and transmembrane domains replaced by a GPI anchor signal sequence (aa 1 to 235). Earlier studies showed that similar constructs were capable of mediating adenovirus infection in cells lacking CAR; however, it is unknown whether they have similar efficiencies. To address this issue, we transduced NIH 3T3 cells with various amounts of CAR-expressing adenovirus to vary the amount of CAR receptor. Then, we applied increasing concentrations of Ad2/GFP and assessed the percentage of GFP-positive cells as a measure of gene transfer. In addition, we studied varying amounts of CAR because we were limited by not knowing how levels of recombinant CAR compare to endogenous CAR. In cells infected with a high MOI (MOI, 50) of Ad-CAR vectors, we observed a dose-dependent increase in adenovirus-mediated GFP gene transfer regardless of which CAR molecule was expressed (Fig. (Fig.1A).1A). Moreover, the three CAR molecules seemed to function with similar efficiencies. Because differences in receptor efficiency may be more evident at lower levels of receptor (30), we also examined the dose-response of Ad2/GFP infection in cells expressing lower levels of CAR (Fig. (Fig.1B1B to D). As we reduced the amount of CAR expression by applying a lower MOI of the CAR-expressing virus, gene transfer with Ad2/GFP fell. However, we found similar reductions with all three CAR molecules. These observations are consistent with previous reports that all three CAR receptors can facilitate adenovirus-mediated gene transfer (18, 30, 37). In addition, these data suggest that their relative efficiencies are similar.

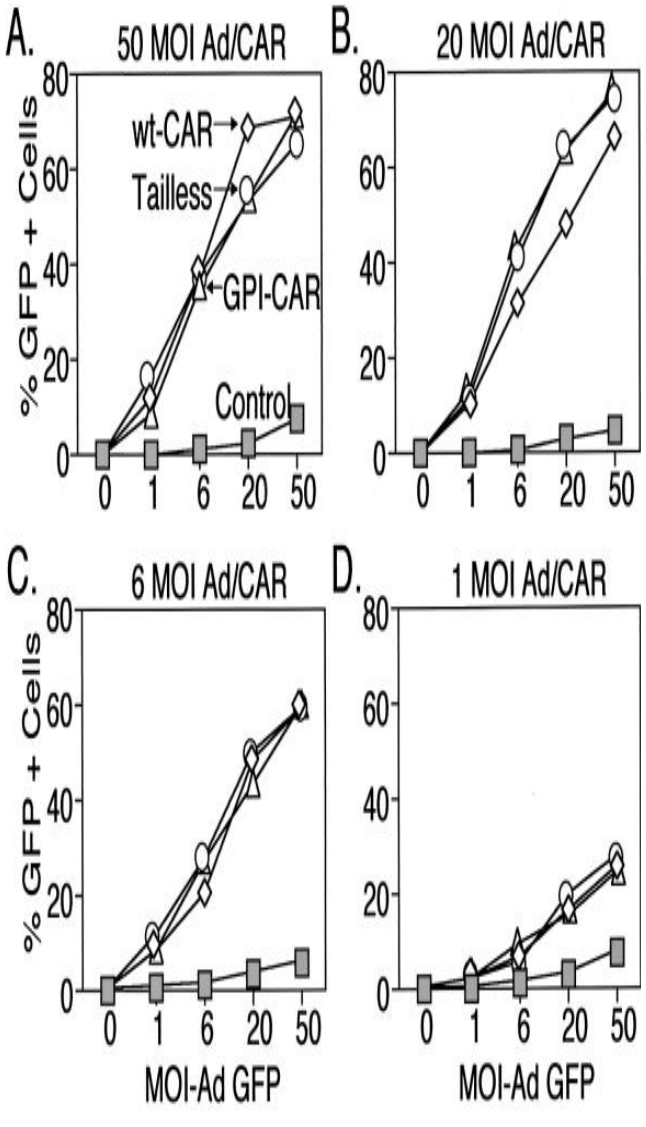

FIG. 1: Effect of CAR expression on adenovirus-mediated gene transfer to NIH 3T3 cells. Cells were infected with varying MOIs of Ad-CaPi coprecipitates encoding wt-CAR (◊). Tailless-CAR (○), GPI-CAR (▵), or CFTR (□) as a control. One day later cells were infected with varying MOIs of Ad2/GFP. Data are the percentage of GFP-positive cells for cells in

fected with the Ad/CAR vectors at MOIs of 50 (A), 20 (B), 6 (C), and 1 (D).

Expression of modified CAR molecules in human airway epithelia

Given that these three receptors function with similar efficiencies in a cell line, we studied their expression, localization, and function in primary cultures of well-differentiated airway epithelia. We delivered the CAR-expressing adenovirus vectors to the basolateral membrane by transiently disrupting the tight junctions, as previously reported (35). Western blot analysis showed specific expression of each Flag-tagged CAR construct at approximately similar amounts (Fig. (Fig.2).2). Naive epithelia and epithelia expressing β-Gal did not show a specific band at the predicted molecular weight range for any of the CAR constructs, confirming that the anti-Flag antibody specifically detects the CAR constructs in human airway epithelia.

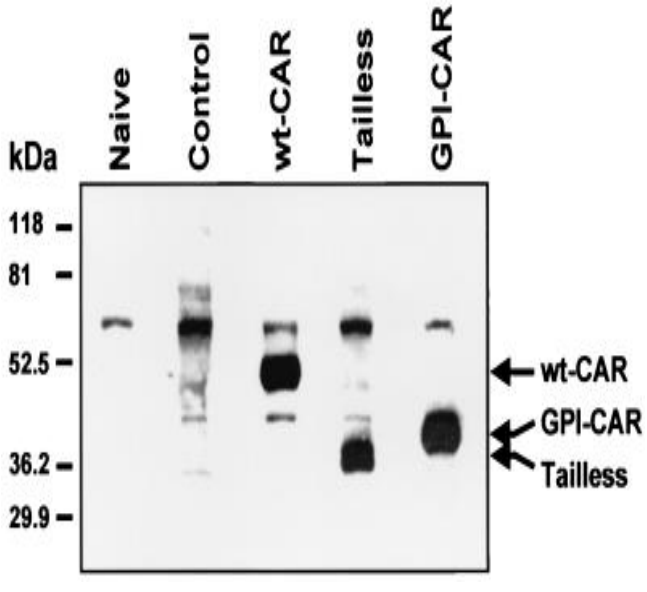

FIG. 2: Expression of adenovirus-encoded CAR constructs in primary cultures of human airway epithelia. Differentiated human airway epithelia were mock infected (Naive), infected with Ad2/GFP (Control), or infected with adenovirus vectors encoding wt-CAR, Tailless-CAR, or GPI-CAR. Two days after infection, cellular lysates were assessed for expression of Flag-tagged CAR proteins by Western blot analysis using anti-Flag M2-HRP monoclonal antibody. Arrows indicate the observed migration profiles of full-length CAR, Tailless-CAR, and GPI-CAR; migration of the three bands was consistent with the predicted molecular masses. The band at approximately 70 kDa was nonspecific as it was also observed in naive and mock-infected cells.

GPI-CAR, Tailless, and wt-CAR show distinct patterns of cell surface distribution in differentiated airway epithelia

We analyzed apical expression of CAR proteins by applying anti-Flag antibody to the apical surface followed by immunocytochemistry. Neither the control nor epithelia expressing wt-CAR presented Flag-tagged CAR on the apical membrane (Fig. (Fig.3A).3A). In contrast, epithelia expressing GPI-CAR showed substantial CAR on the apical membrane. Epithelia expressing Tailless-CAR showed a small amount of apical staining. These observations suggest the GPI modification targets CAR to the apical membrane, consistent with observations for GPI-anchored proteins in other epithelial cell types (20). In addition, the presence of Tailless-CAR on the apical surface suggests the cytoplasmic domain plays an essential role in exclusive basolateral localization of CAR in airway epithelia.

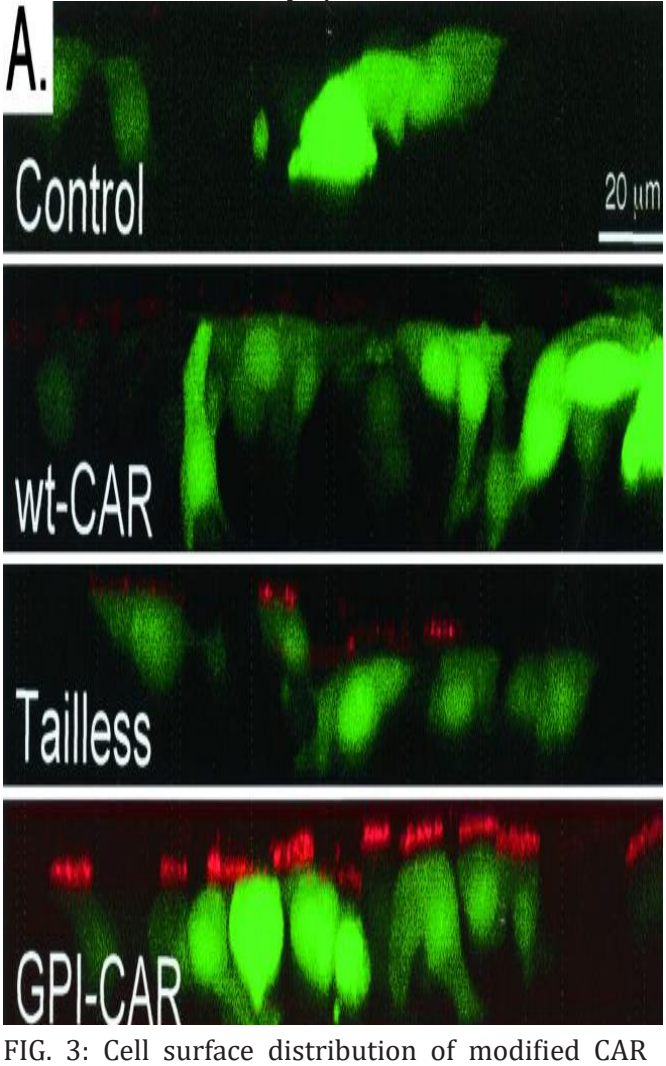

FIG. 3: Cell surface distribution of modified CAR proteins expressed in human airway epithelia. (A) Apical localization of CAR molecules was evaluated in airway epithelia with immunocytochemistry. GFP-positive cells are shown in green, and apical

Flag antibody binding is shown in red. Polarized surface distribution of CAR molecules was quantitated with a radioimmunoassay on the apical surface (B), or the basolateral surface (C). Data are means + standard errors of the means (error bars) (n = 6). ∗, P < 0.01 compared to control.

To obtain a more quantitative assessment of the polarized distribution of Flag-tagged CAR, we used a radioimmunoassay to measure specific binding of anti-Flag antibody to CAR-expressing airway epithelia. There was no specific binding of 125I-anti-Flag antibody to the apical surface of airway epithelia expressing wt-CAR (Fig. (Fig.3B).3B). This result is consistent with the lack of endogenous CAR at the apical surface (25, 35). Consistent with the immunocytochemical localization, there was a large amount of apical binding in epithelia expressing GPI-CAR and a small amount in epithelia expressing Tailless-CAR. In contrast, at the basolateral membrane we observed specific binding of 125I-anti-Flag antibody in epithelia expressing wt-CAR and Tailless-CAR, but not GPI-CAR (Fig. (Fig.3C).3C). Hence, airway epithelia specifically sequester wt-CAR in the basolateral membrane and GPI-CAR in the apical membrane. Tailless-CAR was distributed to both membrane domains.

Expression of GPI-CAR in airway epithelia enhances apical binding of adenovirus

We also studied binding of Cy3-labeled adenovirus to the apical membrane of CAR-expressing airway epithelia. Consistent with previous observations, adenovirus did not bind to control epithelia expressing β-Gal (Fig. (Fig.4)4) (35). Moreover, there was little or no apical binding of adenovirus to epithelia expressing recombinant wt-CAR. This is consistent with basolateral localization of the protein (Fig. (Fig.3).3). However, adenovirus bound to the apical surface of epithelia expressing GPI-CAR and, to a lesser extent, the epithelia expressing Tailless-CAR. These data indicate that adenovirus can bind to the extracellular domain of CAR when it is present on the apical surface of differentiated epithelia.

Apical localization of CAR is sufficient for adenovirus-mediated gene transfer from the apical surface

To determine if apical localization of CAR is sufficient for adenovirus infection, we investigated adenovirus-mediated gene transfer from the apical surface of epithelia expressing wt-CAR, Tailless-CAR, or GPI-CAR. Using Ad2/GFP we found minimal gene transfer in epithelia expressing wt-CAR and Tailless-CAR (Fig. (Fig.5A).5A). However, GPI-CAR expression substantially increased gene transfer.

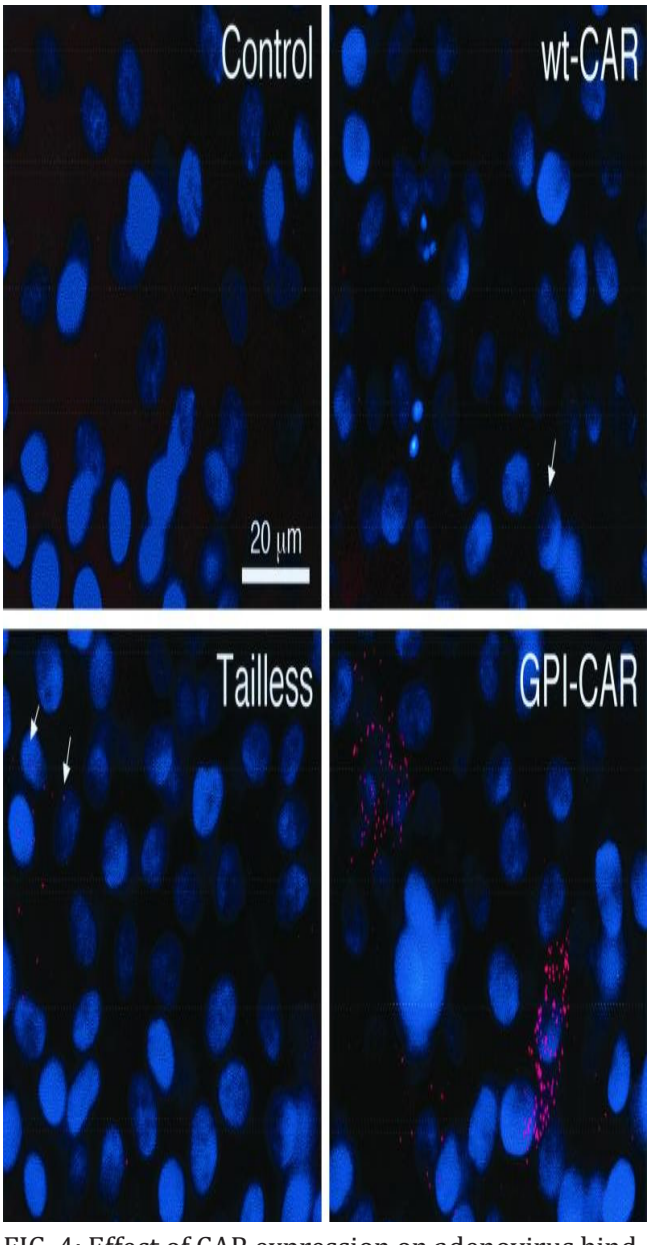

FIG. 4: Effect of CAR expression on adenovirus binding to the apical surface of CAR-expressing human airway epithelia. Data are en face projections of Cy3-labeled adenovirus (red) bound to the apical surface of control and CAR-expressing airway epithelia. DAPI-stained nuclei are blue.

In conclusion, expressing CAR on the apical surface by GPI modification rescues adenovirus binding and gene transfer from the apical surface of airway epithelia. These data suggest that targeting binding sites on the apical surface will enhance gene transfer. Thus, perhaps numerous different methods of increasing binding may be sufficient to improve gene transfer. However, we predict that targeting a high-affinity receptor which is capable of internalization will result in the most efficient gene transfer to the airway epithelia.

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presentation condition, suggests to us that these children relied primarily on visual-spatial encoding of the target sequence to perform the task. These results were obtained despite the fact that many of these cochlear implant children did well on the auditory WISC digit span task and on the auditory-only presentation condition of the memory game.

In summary, the present results suggest that even those cochlear implant children who are able to accurately identify speech signals in isolation, may not have phonological working memory mechanisms or processing strategies that are developed to a point equivalent to chronologically age-matched normal-hearing children. This outcome would not exactly be surprising, as many important milestones in the development of speech perception and memory are reached during the first 2 yr of life (Aslin, Jusczyk, & Pisoni, 1998; Jusczyk, 1997). Despite their prelingually deafened status, most of the cochlear implant users reported on in this paper received their implant at a point in time when the FDA did not permit implantation of children under 2 yr of age. Additionally, because the implantation procedure requires that candidates show a demonstrated failure to benefit from conventional hearing aids, we can be fairly certain that most of these 8- and 9-yr-old children had received only minimal auditory input for at least one quarter to one third of their lives. It should not be surprising, then, that the encoding strategies and working memory mechanisms of pediatric cochlear implant users seem to differ measurably from those of normal-hearing children.

Ongoing research in our lab is attempting to describe in more detail how these encoding/rehearsal mechanisms differ, and what kind of developmental changes can be observed or effected in these children. Increasingly, clinicians are beginning to see pediatric cochlear implant users that have reached ceiling levels of performance on the traditional standardized measures of speech perception and spoken word recognition that are typically used with this population—and yet these children are still clearly having problems with reading and other more advanced language skills that are based on listening, phonological encoding, and other metalinguistic abilities. Further investigation of how pediatric cochlear implant users engage in cognitive processing of information originating from this reintroduced sensory input modality may help us develop new assessment and treatment techniques (Pisoni, 2000). Eventually we would like to answer the question of whether individual differences in the function of particular components of working memory within the pediatric cochlear implant population might have a meaningful causal relation to the level of verbal language skill attained by individual children. The present research begins to address this important issue because it provides some of the first behavioral data on working memory in pediatric cochlear implant users involving tasks in which the potential contribution of each available sensory modality was varied.

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