Differential MERS-CoV Response in Different Cell Types

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SUMMARY
The ongoing COVID-19 pandemic piqued our interest in coronaviruses and prompted us to study MERS-CoV. While MERS-CoV has a low infection rate, it exhibits the highest mortality rate among the three known lethal coronaviruses. Thus, the potential for MERS-CoV to initiate a catastrophic pandemic remains a real threat. We decided to study MERS-CoV using online databases and analytical tools. We hypothesized that MERS-CoV infection elicits different responses in different types of host cells. We chose three data sets from Gene Omnibus Expression - GSE100504, GSE100509, and GSE86528, which represent MERS-CoV infection on human airway epithelial cells, primary human microvascular endothelial cells, and primary human fibroblasts, respectively. We performed RNA expression analysis on data collected 48 hours post-infection. Results indicated that human airway epithelial cells exhibited the most potent immune system response, suggesting that they are susceptible to pathogen infection, perhaps due to their location and exposure to the outside environment. We saw NRP1 and VEGFA upregulation in microvascular endothelial cells along with differential expression of angiogenesis and neural development processes. Given that NRP1 mediates SARS-CoV-2 entry into host cells, the infection mechanism for MERS-CoV on microvascular endothelial cells may be like that of SARS-CoV-2. In fibroblasts, we observed a positive regulation of the apoptotic process and negative regulation of cell proliferation. Together, our data supports our hypothesis and sheds light on the types of responses host cells elicit from MERS-CoV infection.

INTRODUCTION
Coronaviruses are a family of viruses known for the crown-shaped spike proteins that protrude from their outer membranes (1). There are three known coronaviruses that are lethal to humans: Severe Acute Respiratory Syndrome coronavirus (SARS-CoV), Middle East Respiratory Syndrome coronavirus (MERS-CoV), and Severe Acute Respiratory Syndrome coronavirus 2 (SARS-CoV-2) (2). While much attention has been directed towards SARS-CoV-2, the virus causing the ongoing pandemic, it is imperative that we learn about the other coronaviruses. Although SARS-CoV dissipated in 2004, MERS-CoV has continued to cause endemics since its appearance in Saudi Arabia in 2012 (2, 3, 4).

Both SARS-CoV-2 and MERS-CoV are Beta coronaviruses (2). MERS-CoV targets the same lung epithelial cells as SARS-CoV-2 and exhibits similar symptoms — acute respiratory and inflammatory issues post-infection (2). As illustrated by Kohli et al., MERS-CoV also targets the lower tract of the respiratory system and additional cells such as colon enterocytes, kidney proximal tubule cells, and urothelial bladder cells (5).

However, unlike SARS-CoV-2, which has a crude case fatality rate of around 10%, the crude case fatality rate of MERS-CoV ranges from 32.1% (2, 6, 7). Although the infection rate is lower for MERS-CoV than that of SARS-CoV-2, the potential for MERS-CoV to initiate a more catastrophic pandemic remains an undeniable reality. Realizing the potential danger of MERS-CoV, we decided to analyze the virus and examine how different cells in the human body may respond to its infection. Using publicly available online databases and analytical tools, we explored how human airway epithelial cells, microvascular endothelial cells, and fibroblasts responded to MERS-CoV at 48 hours post-infection.

We chose three cell types for this study based on their respective physiological importance. As outlined by Whitsett and Alenghat, airway epithelial cells construct the lining of the respiratory tract and serve several functions, such as producing surfactants and triggering immune responses (8). We chose airway epithelial cells in this study due to their location and proximity to pathogen infections. We also selected microvascular endothelial cells for this study due to their function and location. Microvascular endothelial cells are crucial for vessel homeostasis and inflammation and line the alveoli-capillary barrier of the lungs, thus, their susceptibility to infection makes it essential for this study (8,9). Finally, we considered fibroblasts as they are the most common cell type in the lung interstitium and maintain the extracellular matrix (10). While they are not the primary site of infection, Sirianni et al. demonstrate that fibroblasts directly link epithelial type 2 cells to capillary endothelial cells (11).
Overall, the susceptibility to MERS-CoV infection, location in the body, and entwined relationships with each other make these three cell types relevant to this study.

In this study, we hypothesized that MERS-CoV infection elicits different responses in different cell types. Our findings demonstrate apparent differences in the biological responses exhibited by the different cell types we studied. Both airway epithelial cells and fibroblasts had unique defense mechanisms against the virus. Additionally, responses in microvascular endothelial cells suggest that MERS-CoV elicits similar mechanisms to SARS-CoV-2. By analyzing RNA expressions in infected cells, we enhanced the understanding of cell type-specific host-pathogen responses of the MERS-CoV virus.

RESULTS

Differential RNA expression specific to cell type

To evaluate the transcriptional responses in human airway epithelial cells, primary human fibroblasts, and primary human microvascular endothelial cells 48 hours post MERS-CoV infection, we analyzed data set GSE100504, GSE86528, and GSE100509, respectively, via GEO2R (Table 1). With results from GEO2R independent samples T-test between 48 hours infection vs. mock infection (supplementary data), we took the top 2000 differentially expressed genes (p-values ranging from $1.13 \times 10^{-13}$ to $3.57 \times 10^{-3}$) to confirm differential RNA expression. We generated heat maps (Figure 1) for each data set to ensure differential expression between 48-hour infected and mock groups. We observed clear differential expression of genes between infected and mock-infected cells for primary human airway epithelial cells, microvascular endothelial cells, and human fibroblasts, respectively.

Enriched Gene Ontology (GO) biological processes

The top 2000 statistically significant differentially expressed genes from GEO2R analysis were placed into the Search Tool for the Retrieval of Interacting Genes (STRING), which allows the identification of enriched functions and biological processes from post-MERS-CoV infection (12). From the biological GO terms, we selected the top five mutually exclusive GO biological processes with their associated genes (Figures 2-4). STRING calculated the Log2 fold change (FC) for the genes concerning the uninfected cells (Log2 FC values ranged from -4 to +4). We color-coded the genes according to their Log2 FC values. Genes upregulated in MERS-infected cells are displayed in red, while genes downregulated are in green.

Human airway epithelial cells had several down regulated biological pathways, which included antigen processing, presentation of exogenous peptide antigen via MHC class I, TAP-independent and peptidyl-tyrosine dephosphorylation involved in the inactivation of protein kinase activity (GO:1990264), and few genes were associated with its biological pathways (Figure 2). Primary human microvascular endothelial cells had a mixed expression of its biological pathways, positive regulation of axon extension involved in axon guidance (GO:0048842) and interleukin-7-mediated signaling pathway (GO:0038111), and moderate genes associated with its biological pathways (Figure 3). Primary human fibroblasts had a mixed expression of their biological pathways, regulation of response to endoplasmic reticulum stress (GO:1905897) and negative regulation of translation (GO:0017148), and many genes associated with their biological pathways (Figure 4).

Strong Immune Responses in airway epithelial cells

When infected with MERS-CoV over 48 hours, airway epithelial cells demonstrated upregulation of the immune pathways.
Table 1: Gene expression data with ten samples from Primary Human Airway Epithelial Cells, Primary Human Microvascular Endothelial Cells, and Primary Human Fibroblasts.
system via three of its five selected biological processes (see methods for detailed description for selection) (Figure 2). The three differentially expressed immune processes included the upregulation of antigen processing and presentation of exogenous peptide antigen via MHC class I, TAP-independent (GO:0002480); the upregulation of negative regulation of natural killer cell-mediated cytotoxicity (GO:0045953); and the upregulation of cellular response to interferon-beta (GO:0035458). Compared to microvascular endothelial cells and fibroblasts, airway epithelial cells had a distinct and substantial upregulation of immune system biological processes.

#### NRP1 and VEGFA upregulation in microvascular endothelial cells

The genes NRP1 and VEGFA became interesting during our analysis due to their significant contribution to SARS-CoV-2 infections and their relationship to the biological processes of microvascular endothelial cells (Figure 3) (13, 14). We analyzed the expression across the three cell types and noted the log2FC values for each cell type (Figure 5). In airway epithelial cells, the log2FC value for NRP1 was 0.81, and VEGFA was 0.75. In microvascular endothelial cells, the log2FC values were 1.95 for NRP1 and 1.80 for VEGFA. In human fibroblast cells, the log2FC value for NRP1 was -0.68, and the log2FC value for VEGFA was 2.67. VEGFA was upregulated in all three infected cell lines (Figure 5) compared to mock-infected cells. However, NRP1 was only upregulated in infected airway epithelial and microvascular endothelial cells compared to the mock-infected cells. Ultimately, the expression levels of these two genes in this cell line were very different from the other two cell lines.

#### DISCUSSION

To initiate our analysis of differential pathway expression, we first confirmed differential RNA expression in airway epithelial cells, microvascular endothelial cells, and fibroblasts through R. By generating the heat maps, we were able to demonstrate varying RNA expression between the five control and five infected groups for all three cell lines. We then continued by investigating the differential expression of the biological processes using STRING. Airway epithelial cells seem to exhibit a more pronounced upregulation of immune system biological processes compared to microvascular endothelial cells and fibroblasts. Airway epithelial cells are the first line of defense against pathogens and, thus, are important in initiating both innate and adaptive immune responses (15). As observed from our data, airway epithelial cells exhibited upregulation of the biological response “Cellular Response to Interferon-

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**Figure 2:** Biological pathways and associated genes of airway epithelial cells. Gene expression data showing expressed biological processes (Antigen processing and presentation of exogenous peptide antigen via MHC class I, TAP-independent, Peptidyl-tyrosine dephosphorylation involved in inactivation of protein kinase activity, Negative regulation of natural killer cell mediated cytotoxicity, Cellular response to interferon-beta, and Branched-chain amino acid catabolic process) and their associated genes from Primary Human Airway Epithelial Cells with log2FC values (ranging from -4 to 4) color-coded for each gene.

**Figure 3:** Biological pathways and associated genes of microvascular cells. Gene expression data showing expressed biological processes (positive regulation of axon extension involved in axon guidance, interleukin-7-mediated signaling pathway, negative regulation of smooth muscle cell proliferation, sprouting angiogenesis, and neuron projection extension) and their associated genes from Primary Human Microvascular Endothelial Cells with log2FC values (ranging from -4 to 4) color-coded for each gene.
beta." Consequently, airway epithelial cells may have more pronounced immune responses than primary human microvascular endothelial cells and human fibroblasts.

In addition to the three immune processes, airway epithelial cells had a downregulation of the branched-chain amino acid catabolic process (GO:0009083), indicating the inhibition of amino acid breakdown. Contemporary studies reveal strong links between immune and metabolic functions. As illustrated by McGaha et al., amino acid availability determines the response of an immune system, especially for immune cells that require cell division, differentiation, and migration (16). Thus, the downregulation of amino acid metabolism may indicate a cellular mechanism that supports the immune system during infections.

The final biological process differentially expressed in airway epithelial cells was the upregulation of peptidyl-tyrosine dephosphorylation involved in the inactivation of protein kinase activity (upregulation of RNA transcripts from kinases). This indicates that the cell may have decreased its activation of protein kinases. As viruses acquire host kinases for their replication, the inactivation of kinases via dephosphorylation may be a strategy that cells use to defend against MERS-CoV effectively (17).

Primary human microvascular endothelial cells had less robust changes in the five selected biological processes we investigated. Nevertheless, NRP1 and VEGFA were found to be upregulated across the biological process of sprouting angiogenesis (GO:0002040). As illustrated by Gelfand et al., NRP1 promotes VEGFA by binding to it as a coreceptor, inducing angiogenesis in endothelial cells (13). Even though the correlation between angiogenesis and MERS-CoV infection is unclear, Meini et al. illustrated the role of intussusceptive angiogenesis in SARS-CoV-2 infection, which is achieved via the induction of chemokines and growth factors post-infection, inducing a pro-angiogenic microenvironment (14). Thus, we speculate that MERS-CoV may exhibit a pro-angiogenic mechanism during infection, notably in microvascular endothelial cells.

Unfortunately, there is limited research on the role of NRP1 in MERS-CoV infection. However, existing studies reveal the critical role of NRP1 in SARS-CoV. Cantuti-Castelvetri et al. have shown that NRP1 expression is abundant in respiratory endothelial cells and significantly potentiates SARS-CoV-2 infection (18). Additionally, Davies et al. have indicated the
manifestation of neurological symptoms via the expression of \textit{NRP1} in olfactory regions of the central nervous system (19). Like patients with SARS-CoV-2, patients with MERS-CoV have also reported neurological complications and respiratory symptoms (20). Ultimately, the upregulation of \textit{NRP1} in endothelial cells suggests its functional role in MERS-CoV infection.

Like that of \textit{NRP1}, the function of \textit{VEGFA} in MERS-CoV is unclear. Nevertheless, the upregulation of \textit{VEGFA} is complemented by the expression of positive regulation of axon extension involved in axon guidance and neuron projection extension (GO:1990138). Illustrated by Jin et al., \textit{VEGFA} induces not only angiogenesis but also neurotrophic and neuroprotective effects (21). As MERS-CoV patients experience neurological complications, \textit{VEGFA} and \textit{NRP1} may play a role in dysregulating the nervous system in MERS-CoV infection.

Like microvascular endothelial cells, human fibroblast cells did not exhibit apparent upregulation or downregulation of their biological processes. Nevertheless, we observe intriguing expressions of biological processes, notably the positive regulation of apoptotic processes (GO:0034249), the negative regulation of cell population proliferation (GO:0043065), the negative regulation of translation, and the regulation of response to endoplasmic reticulum stress. Thus, as fibroblasts may undergo apoptosis for wound healing (21) and infected cells undergo apoptosis for viral defense (22), we postulate that fibroblasts undergo apoptosis and inhibit protein synthesis as a defense mechanism when infected with MERS-CoV.

\section*{MATERIALS AND METHODS}
\subsection*{Analyzed Datasets}
We used publicly available datasets from GEO (Gene Expression Omnibus) under NCBI (National Center for Biotechnology Information) for RNA analysis of MERS-CoV. Specifically, we analyzed the super series GSE65575, a dataset published by the University of Wisconsin-Madison that aimed to model host responses under severe human viral infections. The options of MERS-CoV infection datasets were then limited by the super series.

\subsection*{Sample Selection}
We chose three datasets that explored host RNA via Microarray Analysis response to MERS-CoV infection from 0 to 48 hours. The first data set, GSE100504, investigated host RNA from human airway epithelial cells in response to MERS-CoV infection with a multiplicity of infection (MOI) of 5 Plaque Forming Units (PFU) per cell. The second data set, GSE86528, explored host RNA from primary human fibroblasts with an MOI of 5 PFU. Finally, the third data set, GSE100509, analyzed host RNA from microvascular endothelial cells in response to MERS-CoV infection with an MOI of 5 PFU. These three data sets included five mock samples and five wild-type MERS-CoV (iCMERS) infected cell samples. These data sets were generated using similar experimental pipelines: the same MERS-CoV, infection PFU, and sequencing technique.

\subsection*{Differential gene expression analysis}
We downloaded the series matrix file from GEO and GEO2R (the web analysis tool from GEO) to compare expression values. For GEO2R analysis, the 48-hour mock cells were compared with the 48-hour infected cells for each data set, and we downloaded the top differentially expressed genes table into a .txt file. We used R to make heatmaps for the top 2000 differentially expressed genes from GEO2R.

\subsection*{Enriched gene function analysis}
After generating the heat maps, the top differentially expressed genes table was placed into excel and sorted the genes by adjusted p-value. The 2000 lowest adjusted p-value genes, ranging from $1.13 \times 10^{-31}$ to $3.57 \times 10^{-3}$ were selected. The 2000 chosen genes were entered into the STRING Consortium Database of Protein-to-Protein Interaction Network (12).
ACKNOWLEDGEMENTS

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REFERENCES


20. Alshebri, Munirah Saad, et al. “Neurological Complications of SARS-COV, MERS-COV, and


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Supplemental Table 1: Dataset 100504 from human airway epithelial cells
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A_24_P21715 5.88E-08 1.72889731 RAD9A RAD9 homolog A (S. pombe)
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A_24_P379750 6.67E-08 1.39640609 MXD1 MAX dimerization protein 1
A_23_P77859 6.92E-08 1.07860908 TMEM88 transmembrane protein 88
A_23_P157495 6.92E-08 1.09362797 PPP3CC protein phosphatase 3, catalytic subunit, gamma isoform
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- **A_33_P3245937:** LOC100128402
- **A_33_P3327106:** LOC100129900
- **A_23_P159974:** kelch-like 13 (Drosophila)
- **A_23_P132515:** S1D1 transmembrane family, member 1
- **A_33_P3314192:** protein kinase C and casein kinase substrate in neurons 2
- **A_33_P3285032:** olfactory receptor, family 10, subfamily A, member 3
- **A_23_P210091:** suppressor of Ty 7 (S. cerevisiae)-like
- **A_33_P3233871:** coagulation factor XII (Hageman factor)
- **A_23_P22548:** chorioregemia (Rab escort protein 1)
- **A_24_P722:** synaptonemal complex protein 1
- **A_24_P260639:** histone cluster 1, H1d
- **A_33_P3574391:** nuclear transcription factor, X-box binding-like 1
- **A_33_P3251234:** |
- **A_33_P358082:** sestrin 2
- **A_33_P3358686:** |
- **A_33_P3404685:** |
- **A_23_P165380:** crystallin, gamma A
- **A_33_P3369567:** lymphocyte-specific protein 1
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- **A_33_P3789327:** small nucleolar RNA, C/D box 12B
- **A_33_P3307187:** neuronal PAS domain protein 3
- **A_23_P3417920:** A kinase (PRKA) anchor protein 4
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- **A_23_P101480:** microtubule associated serine/threonine kinase 1
- **A_33_P321533:** nuclear factor of activated T-cells, cytoplasmic, calcineurin-dependent 2
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**Notes:**
- **C12orf63** and **C11orf85** are located on chromosomes 12 and 11, respectively.
- **KIAA0586** is a gene on chromosome 11, and its role is not specified in the table.
- **C8orf37** and **C8orf31** are genes on chromosome 8, indicating regulatory or unknown functions.
- **PBX1** is associated with leukemia and transcription regulation.
- **CLMN** is involved in cell adhesion and signaling.
- **LAMP2** is a lysosomal protein that plays a role in membrane trafficking.
- **GALK1** is part of the galactokinase family, which catalyzes the conversion of glucose-1-phosphate to glucose-6-phosphate.
- **TIGD7** is associated with transposable elements, suggesting regulatory or functional roles.
- **MAGEB17** is related to melanoma antigens, indicating potential roles in immune response and cancer.
- **BBB4** is linked to Bardet-Biedl syndrome, a genetic disorder affecting multiple organ systems.
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**3-Mar**

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- Accession numbers are prefixed with A_ and P, indicating the database from which the gene information is derived.
- Gene names and symbols are provided.
- Descriptions include the gene's function or its involvement in cellular processes.
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**Histone Cluster 1, H2ac**

- **HIST1H2AC**: histone cluster 1, H2ac

**Gamma-Aminobutyric Acid (GABA) A Receptor, Epsilon**

- **GABRE**: gamma-aminobutyric acid (GABA) A receptor, epsilon

**Thrombospondin 3**

- **THBS3**: thrombospondin 3

** amidopetrulycytic myelin paranodal and inner loop protein**

- **OPALIN**: oligodendrocytic myelin paranodal and inner loop protein

**Gamma-Aminobutyric Acid (GABA) A Receptor, Epsilon**

- **GABRE**: gamma-aminobutyric acid (GABA) A receptor, epsilon

**Thrombospondin 3**

- **THBS3**: thrombospondin 3

**Surfactant Associated 3**

- **SFTA3**: surfactant associated 3

**Cappuccino Homolog (Mouse)**

- **CNO**: cappuccino homolog (mouse)

**Zinc Finger Protein 283**

- **ZNF283**: zinc finger protein 283

**Oligodendrocytic Myelin Paranodal and Inner Loop Protein**

- **OPALIN**: oligodendrocytic myelin paranodal and inner loop protein

**Gamma-Aminobutyric Acid (GABA) A Receptor, Epsilon**

- **GABRE**: gamma-aminobutyric acid (GABA) A receptor, epsilon

**Thrombospondin 3**

- **THBS3**: thrombospondin 3

**Surfactant Associated 3**

- **SFTA3**: surfactant associated 3

**Cappuccino Homolog (Mouse)**

- **CNO**: cappuccino homolog (mouse)

**Zinc Finger Protein 283**

- **ZNF283**: zinc finger protein 283
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**Gene Descriptions:**
- **STX2:** Syntaxin 2
- **MFAP1:** Microfibrillar-associated protein 1
- **DENR:** Density-regulated protein
- **C3:** Complement component 3
- **BMS1:** BMS1 homolog, ribosome assembly protein (yeast)
- **STX2:** Syntaxin 2
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