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J Am Coll Surg. 2016;223(2):374–80.Article Google Scholar Li C, Liu P, Shao P, Pei J, Li Y, Pawlik TM, Martin EW, Xu RX. Handheld projective imaging device for near-infrared fluorescence imaging and intraoperative guidance of sentinel lymph node resection. J Biomed Opt. 2019;24(8): 080503.Article Google Scholar Zhu B, Rasmussen JC, Litorja M, Sevick-Muraca EM. Determining the performance of fluorescence molecular imaging devices using traceable working standards with si units of radiance. IEEE Trans Med Imaging. 2016;35(3):802–11.Article Google Scholar Page 2Fluorescence detection sensitivity and spatial resolution for detection characterized by ICG solution and resolution target. a Sensitivity is about 5 pM ICG solution, marked by red arrow. Excitation light power is about 20 mW focused at an area of a 200 μm diameter, with a power density of about 0.63 W/mm2. b Resolution test: Group -2 data. c Group -1 data. d Group 0 data. e Group 1 data. f FWHM calculation using Gaussian fit, spatial resolution defined by Sparrow criterion. Element 3 of group 1 is discernible, which indicates spatial resolution for detection is about 397 μm Combinatorial GxGxE CRISPR screen identifies SLC25A39 in mitochondrial glutathione transport linking iron homeostasis to OXPHOS Xiaojian Shi orcid.org/0000-0001-7456-29011,2 na1, Bryn Reinstadler orcid.org/0000-0001-6133-57853,4,5 na1, Hardik Shah orcid.org/0000-0001-8408-56863,4,5, Tsz-Leung To3,4,5, Katie Byrne1,2, Luanna Summer1,2, Sarah E. Calvo3,4,5, Olga Goldberger3,4, John G. Doench orcid.org/0000-0002-3707-98895, Vamsi K. Mootha orcid.org/0000-0001-9924-642X3,4,5 & Hongying Shen orcid.org/0000-0002-2115-70371,2 Nature Communications 13, Article number: 2483 (2022) Cite this article 3717 Accesses 33 Altmetric Metrics Cell biologyEnergy metabolismTransporters The SLC25 carrier family consists of 53 transporters that shuttle nutrients and co-factors across mitochondrial membranes. The family is highly redundant and their transport activities coupled to metabolic state. Here, we use a pooled, dual CRISPR screening strategy that knocks out pairs of transporters in four metabolic states — glucose, galactose, OXPHOS inhibition, and absence of pyruvate — designed to unmask the inter-dependence of these genes. In total, we screen 63 genes in four metabolic states, corresponding to 2016 single and pair-wise genetic perturbations. We recover 19 gene-by-environment (GxE) interactions and 9 gene-by-gene (GxG) interactions. One GxE interaction hit illustrates that the fitness defect in the mitochondrial folate carrier (SLC25A32) KO cells is genetically buffered in galactose due to a lack of substrate in de novo purine biosynthesis. GxG analysis highlights a buffering interaction between the iron transporter SLC25A37 (A37) and the poorly characterized SLC25A39 (A39). Mitochondrial metabolite profiling, organelle transport assays, and structure-guided mutagenesis identify A39 as critical for mitochondrial glutathione (GSH) import. Functional studies reveal that A39-mediated glutathione homeostasis and A37-mediated mitochondrial iron uptake operate jointly to support mitochondrial OXPHOS. Our work underscores the value of studying family-wide genetic interactions across different metabolic environments. The SLC25 family transporters play a critical role in shuttling metabolites into and out of mitochondria1,2,3. The protein family is evolutionarily conserved in nearly all eukaryotes, only missing in a few, highly diverged eukaryotes such as Giardia lamblia and Encephalitozoon cuniculi4. Among the 53 SLC25 proteins in human, the most well-characterized ones include adenine nucleotide carriers (ANTs) that exchange ADP for ATP to support cellular bioenergetics and UCP1 that is exclusively expressed in brown adipose tissue and dissipates proton motive force to generate heat. Despite the critical roles, approximately 20 members remain transporters of unknown functions.Elegant structural characterization of the well-known ANT enables structure-guided investigations on the SLC25 transporters of unknown functions. Each SLC25 transporter is a structural and functional monomer of approximately 300 amino acids with six transmembrane α-helices (3-fold pseudo-symmetrical repeats of the two transmembrane helices) surrounding the central cavity. The ANT crystal structures in both cytoplasmic-open (c-state) and matrix-open states (m-state) locked by two inhibitors bound at the solute binding site, carboxyatractyloside and bongkrekic acid respectively, highlighted a conserved alternating-access transport mechanism5 enabled by the conformational change upon solute binding at the central cavity6,7. The high-level sequence homology and structural similarity among the SLC25 transporters enable both identification of solute-binding residues and prediction of the transporting solute based on the putative chemical groups.A major challenge for the systematic interrogation of SLC25 transporter functions and their metabolic regulations lies in the high level of redundancy within the family. For instance, 36 members are part of paralogous subgroups8, including four ANT (exchanging ATP for ADP) and four calcium-binding mitochondrial carrier proteins SCaMCs (enabling net adenylate transport). Previously, in our genome-wide CRISPR screen in galactose, a low glucose condition designed to discover genes required for mitochondrial OXPHOS, none of the four ANTs scored as hits9. Yet, the ANT inhibitor, bongkrekic acid, induces cell death in low glucose10.Now, inspired by the mitochondria-focused genetic interaction map in Saccharomyces cerevisiae11 and the known influence of environment on genetic interactions12, we sought a dual genetic perturbation approach to probe the human SLC25 transporters under different metabolic states13. We applied a combinatorial CRISPR screening approach to interrogate SLC25 transporters in cellular physiology. By screening in four different media conditions, we uncovered their metabolic regulation, including the fitness defects in the mitochondrial folate transporter SLC25A32 KO cells that can be buffered in galactose condition due to substrate limitation in de novo purine biosynthesis. Amongst transporters of unknown function, our screen highlighted SLC25A39, in which SLC25A39 KO cells' growth defect is buffered by antimycin or by KO of the mitochondrial iron transporter SLC25A37. Follow-up studies combining mitochondrial metabolite profiling, organelle transport assay and structure-guided mutagenesis identified a critical role of SLC25A39 in mitochondrial glutathione uptake, a discovery that has also been independently reached by a recent report14. The buffering genetic interaction revealed from our CRISPR screen13 allowed further extending the finding by demonstrating a functional coordination of mitochondrial glutathione uptake (mediated by SLC25A39) and mitochondrial iron import (mediated by SLC25A37) in supporting OXPHOS.We utilized a dual Cas9 enzyme-based knockout strategy15 to probe all 53 human SLC25 family members in a pair-wise manner in pooled format. This dual Cas9 system takes advantage of different protospacer adjacent motif (PAM) sequences recognized by Streptococcus pyogenes Cas9 (SpCas9) versus Staphylococcus aureus Cas9 (SaCas9), enabling simultaneously knocking out two genes (Fig. 1a). To construct the pPapi-SLC25 library, SpCas9 and SaCas9 guides were designed to target 53 SLC25 carriers, seven additional SLC proteins present in MitoCarta 2.016, BCL2L1, MCL1 (the two paralogous anti-apoptotic proteins) and EEF2 (elongation factor 2, essential for protein translation) as positive controls, 8 non-cutting controls and 19 cutting controls that target olfactory receptors (ORs) as negative controls. This leads to a custom pPapi-SLC25 library of 273×273 = 74,529 plasmids for the pooled screen (Fig. 1b).Fig. 1: Combinatorial CRISPR screen of the SLC25 family transporters across four media conditions.a Schematic overview of the combinatorial CRISPR strategy. b SLC25-Papi library construction. c Growth rate of the pooled CRISPR screen. The batch 2 growth rate was shown and representative of the two batches. d positive control pair BCL2L1 and MCL1. Data shown are log2 fold changes from day 15 in the glucose condition. Gray, control-control pair; pink, BCL2L1 x Ctrl or Ctrl x BCL2L1; blue, MCL1 x Ctrl or Ctrl x MCL1; and purple, the double knockouts of BCL2L1 x MCL1 or MCL1xBCL2L1. The black lines indicate the median and the red line indicates the expected value for the double knockout based on the sum of the single knockouts when there is no genetic interaction. Statistical significance was calculated using two-tailed t test. Source data are provided as a Source Data file.We carried out a growth fitness screen in chronic myelogenous leukemia K562 cells across four media conditions (Fig. 1a): (1) standard high glucose media (25 mM glucose, glc), (2) galactose media in which the glucose is replaced by the same concentration of galactose (25 mM galactose, gal), (3) full media with 100 nM antimycin (antimycin), and (4) full glucose media but lacking pyruvate (−pyruvate). High glucose condition supports cellular bioenergetics using both glycolysis and OXPHOS. Galactose is an epimer of glucose, which only permits mitochondrial OXPHOS ATP production, due to slower kinetics to utilize galactose in glycolysis17. Antimycin is a known inhibitor of the mitochondrial electron transport chain (ETC) complex III inhibiting OXPHOS. Removing pyruvate in the media prevents the recycling of NADH into NAD + by the cytosolic LDH enzyme, forcing mitochondrial redox shuttle systems to support cytosolic redox balance18. All four media conditions are supplemented with uridine and pyruvate (except no pyruvate in –pyruvate condition), which are required for the cellular growth under OXPHOS inhibition19. In the screen, the cells grew exponentially with expected growth rates: glucose ~ −pyruvate > antimycin > galactose (Fig. 1c). The positive control pair BCL2L1 x MCL1 exhibited the expected synthetic sick genetic interaction as previously reported across all conditions (Fig. 1d)15.We quantified fitness in each condition as the log2-fold-change (LFC) of sgRNA abundance at fifteen days over plasmid DNA (Supplementary Data 1). After applying quality control filters (Supplementary Fig. 1 and Methods), we combined the data from two screening batches, and combined SaCas9 and SpCas9 targeting guides for the same genes. It is worth noting that we used cutting guides as the negative controls to also control for the deleterious effect during the double-stranded DNA cutting20 (see Methods). Together, we scored the genetic perturbation for 63 genes, giving a total of (632 – ½ (632 – 63) =) 2016 genetic perturbations, or a total of (2016 ×4 =) 8064 gene by environment conditions.We then proceeded to identify three categories of interactions: (i) GxE (Gene x Environment) interaction, wherein a single SLC25 gene KO differentially affects cellular fitness under certain metabolic states; (ii) GxG (Gene x Gene) interaction, wherein the loss of two genes leads to a fitness phenotype that is not the simple additive sum of two single KOs, and (iii) GxGxE (Gene x Gene x Environment) interaction, wherein the impact of the pairwise genetic interaction is dependent on the metabolic state.The results immediately revealed the value of screening pairs of knockouts across different metabolic conditions. Of 53 SLC25 family members, 6 genes scored significantly as essential in at least one of the four media conditions. They include SLC25A1 (citrate transporter), SLC25A26 (SAM transporter) and MTCH2 (unknown) in glucose; SLC25A1, SLC25A3 (phosphate transporter), SLC25A19 (thiamine pyrophosphoate transporter) and SLC25A26 in galactose; SLC25A1, SLC25A3 and SLC25A26 in antimycin; SLC25A1, SLC25A19, SLC25A26, SLC25A32 (folate transporter) and MTCH2 in -pyruvate condition. Importantly, directly comparing the single KO phenotype across four conditions highlighted 19 nutrient-dependent phenotypes that are otherwise mild in any single condition, which we termed GxE interactions (Fig. 2a and Supplementary Data 2). In glucose, 5 pairs of genes exhibited a pairwise GxG interaction, and 9 GxG interactions scored in at least one of the four conditions, including 8 GxG interactions that are condition-specific (Fig. 3a and see below). These observations indicate that SLC25 transporters exhibit considerable functional redundancy and that phenotypes can be unmasked only by combinatorial screening under different conditions.Fig. 2: Gene x Environment (GxE) mapping indicates that loss of mitochondrial folate metabolism can be buffered in galactose condition.a A heatmap depicts the fitness of single gene KOs across all four media conditions. Values are Z-scores of log fold change (LFC) value of the targeting guide abundance. Asterisks highlight the 19 significant "GxE" interactions, i.e., those knockouts that cause fitness phenotypes differentially across the conditions. Arrows indicate two hits that were experimentally validated and pursued in the current study: SLC25A32 and SLC25A19 (see Supplementary Fig 2). b SLC25A32 single KO phenotype across four conditions in the screen, showing the buffering effect in galactose. Gray, the control-control distribution; pink, SLC25A32 single KOs ("A32 x Ctrl" or "Ctrl x A32" combined). c Follow-up studies show growth fitness of SLC25A32 CRISPR KO cells generated by two different sgRNAs in glucose and galactose conditions. The dotted line denotes the expected LFC, based on an additive model, if there was no genetic interaction (n = 3). d de novo purine biosynthesis pathway. e LC-MS measurement of purine intermediates in SLC25A32 KO and control cells in glucose and galactose condition for 2 days (n = 3). f LC-MS measurement of tetrahydrofolate (THF) cofactors in SLC25A32 KO and control cells in glucose and galactose condition for 2 days (n = 3). g Growth fitness of wild type cells either cultured in low folate media (0.08 μM) or treated with DHFR inhibitor methotrexate at sub-IC50 dose (10 nM), in glucose and galactose condition. The dotted line denotes the expected LFC, based on an additive model, if there was no genetic interaction (n =3). Statistical significance was calculated using two-tailed t test. Significance level were indicated as *** p

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