Myocardial infarction (MI) is highly heritable and multiple risk loci have been identified, yet the downstream effects of most MI risk variants on disease outcome remain poorly defined. Many MI risk genes have inflammatory roles, suggesting that a gene variant linked with MI incidence may also disrupt post-MI inflammation and fibrosis. Acute inflammatory response in the heart is required to initiate tissue repair and maintain ventricular function following MI. However, if left unresolved, chronic post-MI inflammation can lead to increased cardiac injury, fibrosis, dysfunction, and eventually heart failure (HF). We hypothesized that some MI risk variants might also cause deleterious post-MI inflammation and fibrosis, which would ultimately affect disease outcome. One such candidate is the MI risk variant rs3184504 [T] that resides in SH2B3 (also known as LNK), a master regulator of inflammatory signaling, but with unknown role(s) in post-MI inflammation and fibrosis.

**Background**—Genome-wide association studies are powerful tools for nominating pathogenic variants, but offer little insight as to how candidate genes affect disease outcome. Such is the case for SH2B3 adaptor protein 3 (SH2B3), which is a negative regulator of multiple cytokine signaling pathways and is associated with increased risk of myocardial infarction (MI), but its role in post-MI inflammation and fibrosis is completely unknown.

**Methods and Results**—Using an experimental model of MI (left anterior descending artery occlusion/reperfusion injury) in wild-type and Sh2b3 knockout rats (Sh2b3em2Mcwi), we assessed the role of Sh2b3 in post-MI fibrosis, leukocyte infiltration, angiogenesis, left ventricle contractility, and inflammatory gene expression. Compared with wild-type, Sh2b3em2Mcwi rats had significantly increased fibrosis (2.2-fold; P<0.05) and elevated leukocyte infiltration (>2-fold; P<0.05), which coincided with decreased left ventricle fractional shortening (~11%; P<0.05) at 7 days post left anterior descending artery occlusion/reperfusion injury. Despite an increased angiogenic potential in Sh2b3em2Mcwi rats (1.7-fold; P<0.05), we observed no significant differences in left ventricle capillary density between wild-type and Sh2b3em2Mcwi rats. In total, 12 genes were significantly elevated in the post left anterior descending artery occluded/reperfused hearts of Sh2b3em2Mcwi rats relative to wild-type, of which 3 (NLRP12, CCR2, and IFNγ) were significantly elevated in the left ventricle of heart failure patients carrying the MI-associated rs3184504 [T] SH2B3 risk allele.

**Conclusions**—These data demonstrate for the first time that SH2B3 is a crucial mediator of post-MI inflammation and fibrosis. (Circ Cardiovasc Genet. 2015;8:294-304. DOI: 10.1161/CIRCGENETICS.114.000527.)

**Key Words:** genetics • myocardial fibrosis • myocardial infarction • rats

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**Clinical Perspective on p 304**

In addition to inflammatory signaling, SH2B3 integrates multiple cytokine pathways involved in hematopoiesis and immune cell function. SH2B3 is an adaptor protein with 5 conserved functional domains: an N-terminal phenylalanine zipper for dimerization; a proline-rich region; a pleckstrin homology domain for binding phosphoinositides and membrane localization; a Src homology 2 (SH2) domain for interaction with phosphotyrosines; and a C-terminal recognition motif for the adaptor protein, CBL. SH2B3 has 20 known binding partners (see Table I in the Data Supplement for list) that interact predominantly through the pleckstrin homology domain and SH2 domains to activate major signaling pathways (eg, JAK/STAT and ERK1/2). Integrity of both domains is required for full SH2B3 activity, as demonstrated experimentally by site-directed mutagenesis and endogenously by clustering of rare loss-of-function mutations in both the pleckstrin homology.
domain and SH2 domains of SH2B3 in human lymphoma and leukemia. In these cases, all loss-of-function mutations in SH2B3 were prolymphomagenic, likely because SH2B3 is a negative regulator of cell signaling. The rs3184504 [T] allele causes an R262W substitution in the pleckstrin homology domain that is associated with leukocytosis, enhanced innate immunity, and increased susceptibility to multiple complex diseases with inflammatory components. Despite this, the functional role(s) and downstream target(s) of SH2B3 in complex disease settings (eg, MI) are completely unknown.

Our goal was to test the role of Sh2b3 in post-MI response, using an experimental model of MI (left anterior descending artery [LAD] occlusion/reperfusion injury) in wild-type (WT) and Sh2b3 mutant rats (Sh2b3mm2Mcwi). We assessed fibrosis, leukocyte infiltration, angiogenesis, left ventricular (LV) function, and Sh2b3-mediated gene expression in post-MI hearts of WT and Sh2b3mm2Mcwi rats. We also tested whether the MI-associated human rs3184504 [T] allele of SH2B3 was linked with similar changes in gene expression in LV tissues from genotyped end-stage HF patients. Our data demonstrate for the first time that Sh2b3 is a central mediator of post-MI cardiac inflammation and fibrosis and provide evidence of 3 novel downstream mediators of SH2B3 signaling in the heart.

Methods

Generation of the Sh2b3mm2Mcwi Mutant Rat

Zinc-finger nucleases constructs for the rat Sh2b3 gene (gene ID: 58838) were designed, assembled, and validated by Sigma-Aldrich to target exon 7 (target sequence 5′-ctcccccatccttgaatgtggagcagcctgtg-3′). mRNA encoding the Sh2b3 zinc-finger nucleases was diluted in microinjection buffer (1 mmol/L Tris, 0.1 mmol/L EDTA, pH 7.4) at a concentration of 2 ng/μL and injected into 1-cell SS/McwiHsd (SS) rat embryos. Fertilized 10-day embryos were then transferred to pseudopregnant Sprague–Dawley females, as described previously. Animals were screened for zinc-finger nuclease–induced mutations by PCR amplification using vendor-supplied primers: forward (5′-gtactgtgaggtttaaatgagtc-3′) and reverse (5′-ggaccacctaatcaggagca-3′). PCR products were analyzed by Sanger sequencing. One F1 animal resulted in a 1 bp frameshift mutation in exon 7, resulting in truncation to the normal amino acid sequence and disruption of the SH2 domain (also see http://rgd.mcw.edu/rgweb/report/gene/main.html?id=5509982). This founder was backcrossed to the SS parental strain, and multiple pairs of N mice were intercrossed to establish a breeding colony for phenotyping.

Model of Reperfused MI

All procedures were approved by the Medical College of Wisconsin Institutional Animal Care and Use Committee and performed in accordance with institutional guidelines. Male SS-Sh2b3mm2Mcwi and WT littermates at 8 to 10 weeks of age were anesthetized with 1.5% isoflurane (Phoenix Pharmaceutical Inc, St. Joseph, MO), inhaled via an anesthesia mask, and supplemented drinking water (0.125 mg/mL) for 2 days as postsurgical analgesia. Heart and blood tissues were collected from anesthetized animals that underwent LAD occlusion for 30 minutes and reperfusion for 2 hours and animals that underwent LAD occlusion for 30 minutes and reperfusion for 7 days.

Echocardiography

Echocardiographic assessments were performed on a GE Vivid 7 ultrasound machine (GE Healthcare, Waukesha, WI) equipped with a 10 MHz transducer. Rats were anesthetized with a ketamine cocktail (0.5 mL/kg): 10 mL Ketamine (100 mg/mL; Phoenix Pharmaceutical Inc)/0.6 mL Xylazine (100 mg/mL; Lloyd Laboratories, Shenandoah, IA)/1.4 mL Acetromazine (10 mg/mL; Boehringer Ingelheim Vetmedica, Inc, St. Joseph, MO). Echocardiographic images were recorded in the parasternal long axis and short axis views. M-mode in parasternal long axis views was used to measure interventricular septum thickness during diastole. The following measurements were assessed: interventricular septum during diastole; left ventricular posterior wall during diastole; left ventricular inner diameter during diastole; left ventricular inner diameter during systole; and fractional shortening.

Quantitative Histology Following LAD Occlusion for 2 Hours and Reperfusion for 2 Hours

Quantification of LV infarct size was performed as described previously. Briefly, to visualize the area-at-risk, the LAD was religated after 2 hours of reperfusion and hearts were retroperfused through the aorta first with 20 mL 0.9% saline then with 10 mL 10% wt/vol phthalocyanine dye (Golden Artist Inc, New Berlin, NY) suspended in 0.9% saline at 9 mL/min using a Minipulse 3 peristaltic perfusion pump (Gильson, Middleton, WI). After perfusion, hearts were excised, stored at −20°C for 45 min, sectioned into 10 to 12 slices, and completely immersed in 0.1 mol/L KH2PO4 buffered 1% wt/vol 2,3,5-triphenyltetrazolium chloride mixture for 30 minutes at 37°C to visualize the viable tissue (red) and infarcted tissue (white). Stained hearts were then fixed in formalin overnight. Images were captured at 6.3x magnification using a Leica MZ6 microscope (Meyer Instruments, Houston, TX) equipped with a Spot Insight camera (Diagnostic Instruments, Sterling Heights, MI). The area-at-risk (blue), viable tissue (red), and infarcted tissues (white) were quantified using Metamorph software (Molecular Devices, Sunnyvale, CA). The infarct size for each slice was calculated by taking the average of infarct/left ventricle from each side of the slice and correcting for the weight of the slice. The total infarct size of the heart was calculated by taking the mean of weight-corrected infarct size from all slices.

Quantitative Histology Following LAD Occlusion for 30 Minutes and Reperfusion for 7 Days

Hearts were excised, bifurcated at midventricle, and the top half snap-frozen in OCT (Tissue Tek, Torrance, CA). Tissues were cryosectioned at 8 μm thickness and stained with Gomori’s one-step Trichrome to visualize collagen fibrils, as described previously. High-powered fields of trichrome-stained hearts were acquired at 200x magnification using a Nikon E-400 with a Spot Insight camera (Nikon Instruments, Melville, NY), and low-powered fields were acquired at 1x (4000dpi) using a Nikon Coolscan VED (Nikon Instruments). Percent fibrosis was calculated from 1x images of...
the entire LV cross-section using Metamorph software (Molecular Devices). Data are presented as the percent area of fibrosis normalized to the total area of the LV.

Matrigel Plug Angiogenesis Assay
Male Sh2b3<sup>−/−</sup> mice and WT littermates at 8 to 10 weeks of age were anesthetized with 1.5% isoflurane and subcutaneously implanted with 500 μL of Matrigel (BD Biosciences, San Jose, CA) supplemented with 500 ng/mL of rat VEGF recombinant protein (R&D Systems, Minneapolis, MN). At 5 days postimplantation, matrigel plugs were excised, snap-frozen in OCT (Tissue Tek), and cryosectioned at 8 μm thickness. Blood vessels were visualized by anti-CD31 immunostaining as described below. Blood vessel density was calculated as the number of CD31<sup>+</sup> structures normalized to the total area of the cross-section.

Immunohistochemistry
All antibodies were diluted 1:100 in phosphate buffered saline with Tween (pH 7.4, 0.1% Tween-20) containing 5 mg/mL of BSA. Frozen sections were fixed with acetone for 10 minutes, rehydrated in phosphate buffered saline with Tween for 10 minutes, and incubated for 1 hour at 37°C with primary antibodies against Sh2b3 (HPA005483; Sigma-Aldrich, St. Louis, MO), CD31 (cat. 555025; BD Biosciences), Lyve1 (cat. AF2125; R&D Systems), cSm (cat. ab7817; Abcam, Cambridge, MA), and CD45 (cat. ab22636; Abcam). Slides were washed and incubated for 1 hour at 37°C with DyLight 488-, 549-, or horseradish peroxidase-labeled secondary antibodies (Jackson ImmunoResearch, West Grove, PA). For horseradish peroxidase staining, slides were developed using DAB (Vector Laboratories, Orton Southgate, UK). For double immunofluorescent staining, sections were incubated with primary and secondary antibodies at 37°C for 1 hour, respectively, with a 10 minute wash in phosphate buffered saline with Tween between steps. Slides were mounted in Vectashield medium containing 4,6-diamidino-2-phenylindole nuclear stain (Vector Laboratories). Images were acquired using a Nikon iE80 upright microscope equipped with a Qimaging QIClick CCD camera (Nikon Instruments) and MetaVue software (Molecular Devices).

RT-qPCR Analysis of Rat LV Tissues
Total RNA from the apical halves of post-MI hearts was extracted by Trizol (Life Technologies, Carlsbad, CA). cDNA was synthesized from 4 μg of total RNA using a RevertAid First Strand cDNA synthesis kit according to the manufacturer’s protocol (Fermentas, Burlington, Ontario, Canada). Gene expression was examined using multiple rat RT2 Profiler PCR Arrays (PARN-0952; PARN-03022) according to the manufacturer’s protocol (SABiosciences, Frederick, MD). RT-qPCR arrays were run on an ABI 7900 Real-Time (ABI, Foster City, CA). Target gene expression was normalized to a combination of 5 housekeeping genes: Actb, Hprt1, Ldha, Rpl13a, and Rplp1.

Quantitative RT-PCR was performed using GoTaq qPCR Master Mix (Promega) on an ABI 7900 Real-Time (ABI). A typical reaction consisted of an initial denaturation step at 95°C for 5 minutes followed by 40 cycles of denaturation at 95°C for 15 seconds and annealing, extension, and data acquisition at 60°C for 1 minute. A final melting curve for each primer was calculated by heating from 60°C to 90°C. Data were normalized to r18s, and relative mRNA expression was determined using the ΔΔC<sub>T</sub> method, as described previously.34,35

Western Blot Analysis
Cardiac blood endothelial cells were lysed in ice-cold RIPA buffer (Thermo Scientific, Rockford, IL) supplemented with 1:100 protease inhibitor cocktail (Sigma Aldrich) and 1:100 PMSF. Proteins were separated on 10% Tris-HCl Criterion Precast Gel (Bio-Rad, Hercules, CA) and then transferred onto nitrocellulose membranes, blocked for 1 hour at room temp with nonfat dry milk (Bio-Rad), and then overnight incubation with primary antibodies against Sh2b3 (Sigma Aldrich) or β-actin (Sigma Aldrich). The following day, blots were incubated for 1 hour at room temperature with horseradish peroxidase–conjugated secondary antibodies and developed with an Immun-star Western C kit (Bio-Rad). Protein bands were visualized using a Chemidoc XRS+ (Bio-Rad).

Profiling Serum MCP-1 Levels
Serum was collected from WT (n=4) and Sh2b3<sup>−/−</sup> (n=4) rats at 3 days post-LAD occlusion/reperfusion injury and was cleared of any cellular debris by centrifugation. Serum MCP-1 protein levels were assessed by a custom xMAP (Luminex) cytokine assay by Ocean Ridge Biosciences (Palm Beach Gardens, FL).

Human Variant Analysis
Linkage disequilibrium (LD; defined here as r<sup>2</sup>=0.6) for human single-nucleotide polymorphism (SNP) from the CEU cohort from the HapMap (http://hapmap.ncbi.nlm.nih.gov/) and 1000 genome (http://browser.1000genomes.org/index.html) projects were calculated using SNAP (http://www.broadinstitute.org/mpg/snp/ldsearch.php). SNPs associated with gene regulatory mechanisms were curated from the ENCODE study using the RegulomeDB database (http://www.regulomedb.org/).

Statistical Analysis
Data are presented as mean±SEM in the original scale unless otherwise indicated. Statistical analyses were performed using Sigma Plot 11.0 software and R 3.1.1 (http://www.R-project.org). Human expression data from the homozygous genotype groups were log-transformed to reduce the skewness of the distribution and to improve the homogeneity of variance. A Shapiro–Wilks test was performed on the human expression data to check for evidence of departure from a normal distribution, followed by a Bartlett test for evidence of variance heterogeneity before unpaired student’s t test. The Wilcoxon rank-sum test was used to perform 2-group comparison in comparisons with small sample size and those failing the Shapiro–Wilks test of normality. Unadjusted P values from the t test and the Wilcoxon rank-sum test were recorded. Multiple testing was controlled for by false discovery rate correction.

Results
Evidence That SH2B3 Is the MI Candidate Gene in the rs3184504 [T] Haplotype Block
The rs3184504 [T] allele ofSH2B3 resides in a 366 Kb haplotype block on human chromosome 12 (110318171–110684533 bp) that is associated by genome-wide association studies with increased incidence of MI. Because genome-wide association studies are unable to differentiate between the effects of other genes that are in LD,38 it is possible that
another gene (ATXN2, BRAP, or ACAD10) residing within the disease-associated LD block might be causative. We used the 1000 Genomes CEU population and ENCODE data to predict whether other likely causative SNPs reside in LD ($r^2>0.6$) with rs3184504 [T]. Of the 9 additional SNPs in LD ($r^2>0.6$) with rs3184504 [T] in the 366 Kb haplotype block, none were predicted to cause nonsynonymous changes or were associated with any expression quantitative trait locus or overlapped with transcriptionally active motifs, suggesting that **SH2B3** (rs3184504 [T]) is most likely the causative gene associated with increased MI incidence. However, the role(s) of **SH2B3** in the distinct pathophysiological processes involved in post-MI response are completely unknown.

**Sh2b3**em2Mcwi Rat Model

To test the role of Sh2b3 in post-MI response, we introduced a frame-shift mutation in Exon 7 of Sh2b3 by zinc-finger nucleases (ZFN) in the SS rat (Sh2b3em2Mcwi), which was predicted to produce a truncated protein. Western blot analysis of cardiac blood endothelial cells from wild-type (WT) and Sh2b3em2Mcwi rats showed complete ablation of the full-length Sh2b3 protein in the Sh2b3em2Mcwi rat (Figure 1 in the Data Supplement). Compared with wild-type (WT) littermates, homozygous Sh2b3em2Mcwi rats had significantly elevated circulating white blood cells under basal conditions (Table 1), including increased total lymphocytes (2.7-fold, $P<0.01$), monocytes (3.3-fold, $P<0.05$), and neutrophils (3.6-fold, $P<0.05$). Circulating white blood cells were also significantly elevated in individuals carrying the rs3184504 [T] risk allele, when compared with WT (Figure 1 in the Data Supplement). Compared with wild-type (WT) littermates, homozygous Sh2b3em2Mcwi rats had significantly elevated circulating white blood cells under basal conditions (Table 1), including increased total lymphocytes (2.7-fold, $P<0.01$), monocytes (3.3-fold, $P<0.05$), and neutrophils (3.6-fold, $P<0.05$). Circulating white blood cells were also significantly elevated in individuals carrying the rs3184504 [T] risk allele, when compared with WT (Figure 1 in the Data Supplement).

**Sh2b3 Mutation Does Not Affect Acute Myocardial Damage**

We first tested whether Sh2b3 mutation altered immediate response to acute LAD occlusion/reperfusion injury. The total mortality rates during LAD surgery were not significantly different between WT and Sh2b3em2Mcwi rat (data not shown), suggesting that Sh2b3 mutation does not disrupt immediate recovery from acute cardiac injury. Likewise, after 2 hours of reperfusion, no statistically significant difference in infarct size was observed between 2,3,5-triphenyltetrazolium chloride–stained infarcts of WT and Sh2b3em2Mcwi hearts (Figure 1). We examined whether the lack of immediate response to acute LAD occlusion/reperfusion injury could be as a result of distribution of Sh2b3 expression, that is, if Sh2b3 affects immediate response, one might expect Sh2b3 expression in cell-types that are most subject to damage at early timepoints (eg, cardiomyocytes). Using immunofluorescent staining of control WT hearts, we detected no expression of Sh2b3 in cardiomyocytes (Figure 2A and 2B). Sh2b3 was also absent from cardiac lymphatic vessels (Figure 2C), but was highly expressed by blood endothelial cells (blood endothelial cells; Figure 2D) and smooth muscle cells (SMCs; Figure 2E). After LAD occlusion/reperfusion injury, the localization of Sh2b3 expression was identical (Figure 2F–2O), with the addition of Sh2b3 positivity on subsets of CD45ra" leukocytes infiltrating the infarct, indicating that Sh2b3 might play a role in post-MI response through resident cell-types (blood endothelial cells and SMCs) or infiltrating leukocytes after MI.

**Sh2b3 Mutation Increases Pathological Remodeling in the Heart**

To test the role of Sh2b3 mutation in chronic post-MI response, WT (n=7) and Sh2b3em2Mcwi (n=12) rats were subjected to 30 minute LAD occlusion, followed by reperfusion for 7 days. At 7 days post-LAD occlusion/reperfusion injury, LV fibrosis was increased by 2.2±0.4-fold ($P<0.05$) in Sh2b3em2Mcwi hearts compared with WT, as indicated by trichrome staining (Figure 3A and 3B). At 7 days post-LAD occlusion/reperfusion injury, Sh2b3em2Mcwi had a greater sustained elevation of circulating white blood cells (3.2-fold versus WT; $P<0.001$), lymphocytes (2.8-fold versus WT; $P<0.001$), neutrophils (6.0-fold versus WT; $P<0.001$), and monocytes (4.5-fold versus WT; $P<0.001$; Table 1). Elevated circulating leukocytes in Sh2b3em2Mcwi rats coincided with increased LV infiltration of Ed1+ macrophages (2-fold versus WT; $P<0.05$; Figure 3C and 3D) and Ela2+ neutrophils (32-fold versus WT; $P<0.01$; Figure 3E, f) at 7 days post-LAD occlusion/reperfusion injury. Collectively, these data suggest that Sh2b3 mutation causes prolonged post-MI inflammation and remodeling in Sh2b3em2Mcwi rats, rather than the timely resolution of inflammation seen in the WT hearts.

Table 1. Analysis of Spleen Weight and Circulating PBMC Counts of WT and Homozygous Sh2b3em2Mcwi Rats

<table>
<thead>
<tr>
<th>Group</th>
<th>Spleen, g/kg BW</th>
<th>WBC</th>
<th>Lymphocyte</th>
<th>Neutrophil</th>
<th>Monocyte</th>
<th>n</th>
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<tbody>
<tr>
<td>Pre-LAD</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>WT</td>
<td>2.6±0.1</td>
<td>6.1±0.5</td>
<td>5.0±0.3</td>
<td>0.5±0.1</td>
<td>0.34±0.11</td>
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</tr>
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<td>Sh2b3em2Mcwi</td>
<td>7.0±0.4</td>
<td>&lt;0.001</td>
<td>16.6±1.7</td>
<td>&lt;0.001</td>
<td>13.4±1.4</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Post-LAD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>WT</td>
<td>3.5±0.1</td>
<td>8.3±1.1</td>
<td>7.2±0.9</td>
<td>0.9±0.3</td>
<td>0.2±0.1</td>
<td>4</td>
</tr>
<tr>
<td>Sh2b3em2Mcwi</td>
<td>9.2±0.1</td>
<td>&lt;0.001</td>
<td>26.7±1.2</td>
<td>&lt;0.001</td>
<td>20.1±1.4</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

Data are presented as the mean values±SEM. $P$-values were derived from a Student’s unpaired $t$-test. LAD indicates left anterior descending artery; WBC, white blood cells; and WT, wild type.
Sh2b3em2Mcwi Mutant Rats Have Increased Angiogenic Potential, but do not Have Increased Capillary Density Before or After LAD-Occlusion/Reperfusion Injury

The Sh2b3 knockout mouse has increased angiogenic potential, suggesting that the Sh2b3em2Mcwi mutant rat might also have increased angiogenic potential. To test the angiogenic potential of Sh2b3em2Mcwi rats, recombinant rat VEGF was implanted subcutaneously with 500 μL of matrigel supplemented with 500 ng/mL of recombinant rat VEGF. At 5 days postimplantation, matrigel plugs were excised and quantified for CD31+ blood vessels across the entire cross-section of the plug. Compared with WT (7.9±1.4 vessels per mm²), CD31+ blood vessel density was increased 1.7-fold (P<0.05) in Sh2b3em2Mcwi rats (13.0±2.0 vessels per mm²; Figure 4A and 4B), confirming that the mutation of Sh2b3 does increase angiogenic potential.

Myocardial angiogenesis (ie, collateral expansion of the coronary blood vessel network) typically occurs by 7 days post-LAD occlusion/reperfusion injury, prompting us to test whether capillary densities differed between WT (n=6) and Sh2b3em2Mcwi (n=6) hearts at 7 days post-LAD occlusion/reperfusion injury. Frozen sections from post-LAD occluded (30 minute occlusion; 7 days reperfusion) hearts were stained with anti-CD31 antibodies, and CD31+ capillary density was measured in 3 regions per LV: infarct, peri-infarct, and uninvolved. No significant differences in capillary density were observed between WT and Sh2b3em2Mcwi in the infarcted region (68±9 versus 75±7 vessels/field), the peri-infarct region (72±7 versus 67±7 vessels/field), or the adjacent uninvolved LV regions (280±20 versus 250±25 vessels/field; Figure 4C–4G). These data demonstrate that although Sh2b3 mutation enhances angiogenic response in some settings (Figure 4A and 4B), it had no effect on myocardial angiogenesis (Figure 4C–4G) and is therefore unlikely to improve outcome at later timepoints.

Decreased Fractional Shortening in Post-MI Hearts of Sh2b3em2Mcwi Rats

To test the effects of Sh2b3 mutation on post-MI cardiac function, we performed transthoracic echocardiography on WT (n=5) and Sh2b3em2Mcwi (n=8) at 7 days post-LAD occlusion/reperfusion injury. No significant differences in any echocardiography parameter were observed in the sham surgery animals. Compared with WT, no significant differences were observed in Sh2b3em2Mcwi hearts for interventricular septum during diastole (2.15±0.11 versus 2.33±0.20), left ventricular posterior wall during diastole (2.11±0.18 versus 1.93±0.11), left ventricular inner diameter during diastole (7.37±0.36 versus 7.67±0.12), and left ventricular inner diameter during systole (4.05±0.55 versus 4.69±0.25). In contrast, fractional shortening was significantly decreased in Sh2b3em2Mcwi hearts compared with WT (33.0±2.2% versus 44.2±3.4%; P<0.05) (Figure 5), suggesting that the increased LV damage caused by Sh2b3 mutation leads to decreased LV contractility.

SH2B3-Mediated Gene Expression in the Heart

Our data suggest that Sh2b3 mutation increases pathological inflammation and fibrosis in the post-MI heart (Figure 3), leading to decreased LV fractional shortening (Figure 5). The nonsynonymous SNP in SH2B3 (rs3184504 [T]) was linked with incidence of MI and inflammatory diseases, but the effects of rs3184504 [T] on inflammation and fibrosis in the heart are unknown. To identify downstream mediators that are affected.
by SH2B3 genotype, we compared cytokine mRNA expression in post-LAD occluded hearts of Sh2b3\textsuperscript{emmMcwi} and WT rats and then examined the subset of differentially expressed genes (>1.5-fold; \(P<0.05\)) in a cohort of end-stage HF patients (Table III in the Data Supplement). A subset of inflammatory mediators was examined by RT-qPCR in WT (n=6) and Sh2b3\textsuperscript{emmMcwi} (n=6) hearts at 7 days post-MI. Of the genes examined, expressions of 12 significantly differed >1.5-fold (false discovery rate <0.05) between Sh2b3\textsuperscript{emmMcwi} and WT hearts at 7 days post-LAD occlusion/reperfusion injury (Table 2; Table IV in the Data Supplement). Of the 12 differentially expressed genes, 3 (NLRP12, CCR2, and IFN\(\gamma\)) were also significantly different (false discovery rate <0.10) between HF patients with the rs3184504 [C] allele compared with those having the rs3184504 [T] risk allele compared with those having the rs3184504 [T] risk allele compared with those having the rs3184504 [T] risk allele compared with those having the rs3184504 [T] risk allele.

MCP-1 Serum Protein Levels

CCR2 and IFN\(\gamma\) are important mediators of the inflammatory (M1) monocyte subset recruitment to the injured myocardium. However, the transcripts of MCP-1, the ligand of CCR2 and main chemoattractant of inflammatory (M1) monocyte recruitment,\textsuperscript{39,40} were not elevated in the LV of Sh2b3\textsuperscript{emmMcwi} compared with WT at 7 days post-LAD occlusion/reperfusion injury. To test whether MCP-1 protein was elevated at another timepoint, we analyzed serum that had been collected from Sh2b3\textsuperscript{emmMcwi} (n=4) and WT (n=4) rats at 3 days post-LAD occlusion/reperfusion injury. This revealed a 2-fold (\(P<0.05\)) increase in MCP-1 protein levels in serum of Sh2b3\textsuperscript{emmMcwi} compared with WT rats after LAD occlusion/reperfusion injury (Figure 6). Collectively, these data suggest that multiple key mediators of the inflammatory M1 monocyte subset (MCP-1, CCR2, and IFN\(\gamma\)) are elevated by SH2B3 mutation.

Discussion

Multiple variants influence MI risk,\textsuperscript{2,4} but the potential role(s) of these variants in post-MI inflammation and fibrosis are largely unknown. Here we used an experimental model of MI (LAD occlusion/reperfusion injury) to test the role of the MI candidate risk gene, Sh2b3,\textsuperscript{7} in post-MI inflammation and fibrosis. We found that Sh2b3 mutation had limited (ie, unobservable) effects on acute post-MI damage (Figure 1), but exacerbated chronic inflammation and fibrosis at 7 days post-MI. At 7 days post-LAD occlusion/reperfusion injury, the Sh2b3\textsuperscript{emmMcwi} mutant rats had elevated leukocyte mobilization and LV infiltration (Table 1;Figure 2), increased LV fibrosis (Figure 2), and reduced LV contractility (Figure 5). Sh2b3 mutation also significantly elevated several key inflammatory mediators in LV tissues (NLRP12, CCR2, and IFN\(\gamma\)) that were similarly increased in the LV of human end-stage HF patients with the rs3184504 [C] allele compared with those having the rs3184504 [T] allele (Table 2). Collectively, these data suggest that NLRP12, CCR2, and IFN\(\gamma\) potentially mediate the effects of SH2B3 in the human and rat myocardium.

SH2B3 Is a Novel Mediator of Post-MI Inflammation and Fibrosis

Multiple factors contribute to post-MI transition to HF, including the extent of fibrotic and inflammatory damage in the LV.\textsuperscript{11–13} SH2B3 is an MI risk gene\textsuperscript{7} that is also associated with multiple risk factors for MI (eg, hypertension,\textsuperscript{49} thrombosis,\textsuperscript{47–49} and coronary artery disease\textsuperscript{50,51}), suggesting that individuals with the rs3184504 [T] allele are at higher risk of MI.\textsuperscript{7}
We propose that a gene (SH2B3) that increases MI incidence \(^7\) (the primary event leading to HF \(^5,2\)) and exacerbates post-MI chronic inflammation and fibrosis (negative correlates of HF \(^1,1–13\)) could potentially lead to worse post-MI outcome. This model fits with 2 other well-studied MI risk genes (ACE \(^5\) and the \(\beta_1\) receptor \(^1\)) that are also independently associated with increased risk of HF. \(^5,4,55\) Both genes can influence post-MI inflammation and fibrosis via the renin–angiotensin system \(^1,5,56\) and are primary post-MI therapeutic targets for attenuating the progression of HF. \(^1\) Of note, however, ACE inhibitors and \(\beta\)-blockers only delay progression of HF and eventually lose efficacy, \(^12\) suggesting that other genetic risk factors and pathways likely contribute to the post-MI response. Our data (Figure 1–6) and the reported associations of the rs3184504 [T] SH2B3 allele with MI incidence \(^7\) and multiple MI risk factors \(^26,46–48,50,51\) suggest that SH2B3 affects multiple levels of MI risk (eg, MI incidence and post-MI recovery).

**SH2B3-Mediated Gene Expression in the Heart**

SH2B3 is an intracellular mediator of 20 known pathways \(^14–16,18–20\) (see Table I in the Data Supplement for the full list) and is associated with 8 autoimmune and inflammatory diseases \(^26,27,29,30\) but the majority of SH2B3-mediated pathways have yet to be investigated in any disease setting. To our knowledge, only IL1\(\beta\) and IL6 expression were reported to be dependent on SH2B3 genotype (rs3184504 [T/C]), which was assessed in vitro from human PBMCs isolated from healthy individuals. \(^25\) Here, we examined the transcript expression of IL1\(\beta\), IL6, and the majority of other SH2B3-mediated pathways implicated in the literature (Table IV in the Data Supplement); however, none were significantly different between the Sh2b3\(^{em2Mcwi}\) and WT groups at 7 days post-MI (Table 2). Instead, we identified a subset of 12 genes that were differentially expressed between Sh2b3\(^{em2Mcwi}\) and WT hearts at 7 days post-MI (Table 2), 3 of which (NLRP12, CCR2, and IFN\(\gamma\)) were also significantly upregulated in HF patients with the rs3184504 [T] (Table 2).

Of the 3 genes upregulated in Sh2b3\(^{em2Mcwi}\) and HF patients with the rs3184504 [T] genotype (Table 2), 2 (CCR2 \(^4,42,43\) and IFN\(\gamma\) \(^4,45\)) were previously implicated in MI, whereas NLRP12 has yet to be tested in MI or any other cardiomyopathy. CCR2 (also known as C–C chemokine receptor 2) regulates...
leukocyte chemotaxis to inflammatory sites and is especially important for the early-phase recruitment of inflammatory M1 monocytes to cardiac infarcts. Moreover, the reduced monocyte/macrophage infiltration caused by Ccr2 knockout or Ccr2 inhibition correlates significantly with reduced post-MI damage and improves infarct healing in mouse LAD occlusion models, suggesting that elevated CCR2 expression in the LV of Sh2b3em2Mcwi rats and HF patients with the rs3184504 [T] genotype (Table 2) could potentially drive increased leukocyte infiltration and LV fibrosis. The observation that MCP-1 levels were elevated in the serum of Sh2b3 em2Mcwi mutant rats compared with WT rats further supports the potential role of SH2B3 in regulation of the inflammatory M1 monocyte subset.

IFNγ is a proinflammatory cytokine and the key stimulus activating inflammatory M1 monocytes/macrophages. Elevated IFNγ serum levels are predictive of increased post-MI risk of HF, and systemic overexpression of IFNγ in the SAP-IFNγ transgenic mouse model specifically caused chronic active myocarditis and decreased cardiac function. NRLP12 has not yet been directly implicated in MI, but is a likely candidate because of its role in the inflammasome pathways, which have been implicated in cardiac inflammation and remodeling. Collectively, our data suggest that MCP-1/CCR2, IFNγ, and NRLP12 are potential therapeutic targets for ameliorating post-MI response in patients with the rs3184504 [T] risk allele and should be explored further in future studies.

**Perspective: Heritable Immunity and MI**

In addition to the rs3184504 [T] SH2B3 risk allele, there are 32 other MI or CAD risk loci that have known roles in inflammation or fibrosis. The high prevalence of loci with these characteristics is likely as a result of immunity being a strong selective pressure and immune-associated genes...
often overlapping with inflammatory or fibrotic signaling. For example, the rs3184504 [T] SH2B3 risk allele was introduced de novo to Europe between the 5th and 9th centuries, coinciding with the emergence of the Bubonic plague. The rs3184504 [T] SH2B3 risk allele is associated with elevated circulating PBMCs and enhanced innate immunity, suggesting that rs3184504 [T] would enhance acute protection against bacterial infections, such as the plague. How- ever, because innate immune cells are also key effectors of chronic inflammation and fibrosis in the heart, an elevated innate immunity (ie, lowered threshold for response) likely increases susceptibility to pathological remodeling. Our data suggest that SH2B3 is likely one of the genes maintaining the inflammatory threshold that positively affect everyday immunity, but negatively affect chronic inflammatory and fibrotic diseases.

Acknowledgments

We thank J. Strande, L. Harmann, M. Tschannew, J. Wendt-Andrae, M. Grzybowski, S. Kalloway, J. Foeckler, and R. Schilling for excellent technical support.

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Disclosures

None.

References


Role of SH2B3 in Cardiac Inflammation and Fibrosis


The central role of inflammation and tissue remodeling in the development of heart failure is well recognized, but still poorly understood, and the genetic mechanisms underlying this relationship are even less understood. Acute inflammatory response initiates tissue repair and rapidly restores ventricular function after myocardial infarction (MI), the primary cause of heart failure. However, if left unresolved, chronic post-MI inflammation leads to increased cardiac injury, fibrosis, dysfunction, and eventually failure. Our goal is to characterize genetic variants that shift the balance in post-MI inflammatory response, which may also increase susceptibility to heart failure and affect post-MI treatment. One such variant is the rs318454 [T] allele of SH2B3, an important negative regulator of inflammation and immunity. The missense SNP (rs3184504 [T]; R262W) in SH2B3 (also known as LNK) is correlated by genome-wide association studies with MI, but the role of SH2B3 in post-MI response was unknown. Our data demonstrate for the first time that SH2B3 is a mediator of post-MI inflammation, fibrosis, and left ventricular function. Moreover, multiple proinflammatory mediators (NLRP12, IFNγ, and CCR2) were altered in the postinfarcted hearts of Sh2b3em2Mcwi mutant rats and heart failure patients with the human SH2B3 risk allele (rs318454 [T]) compared with their respective controls. Collectively, our data suggest that SH2B3 is likely one of the genes maintaining the inflammatory threshold that is important for everyday immunity, but negatively affects post-MI response.
SH2B3 Is a Genetic Determinant of Cardiac Inflammation and Fibrosis

Michael J. Flister, Matthew J. Hoffman, Angela Lemke, Sasha Z. Prisco, Nathan Rudemiller, Caitlin C. O'Meara, Shirng-Wern Tsaih, Carol Moreno, Aron M. Geurts, Jozef Lazar, Neeta Adhikari, Jennifer L. Hall and Howard J. Jacob

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**Supplementary Figure 1.** Western blot analysis of $Sh2b3$ protein expression in cardiac endothelial cells from wildtype (WT) and $Sh2b3^{em2Mcwi}$ (Mut) rats. HEK293 cells transfected with a $Sh2b3$ expression plasmid were used as a positive control (+).
Supplementary Table 1. Known *SH2B3*-mediated pathways.

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<th>Name</th>
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<tr>
<td>c-KIT</td>
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<td>Direct binding in mast cells in response to SCF (PMID: 11805142); Direct binding in BMMCs in response to SCF (PMID: 18753636); Direct binding in HEK293T cells following plasmid overexpression (PMID: 18588518).</td>
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<td>PDGFRA</td>
<td>RTK</td>
<td>Direct binding in HEK293T cells following plasmid overexpression and stimulation with PDGF (PMID: 21310211).</td>
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<tr>
<td>PDGFRB</td>
<td>RTK</td>
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<tr>
<td>FLT3</td>
<td>RTK</td>
<td>Direct binding in eosinophils and lymphocytic leukemia cells in response to FLT3 ligand (PMID: 22942183).</td>
</tr>
<tr>
<td>c-FMS</td>
<td>RTK</td>
<td>Direct binding in macrophages in response to M-CFS (PMID: 20571037).</td>
</tr>
<tr>
<td>JAK2</td>
<td>Kinase</td>
<td>Direct binding in myeloproliferative neoplasms in response to EPO or TPO (PMID: 20870899); Constitutive direct binding in myeloproliferative neoplasm that was enhanced by TPO (PMID: 18618018); Direct binding in BMMCs in response to SCF, TPO, and EPO (PMID: 19293402).</td>
</tr>
<tr>
<td>JAK3</td>
<td>Kinase</td>
<td>Direct binding in myeloproliferative neoplasms (PMID: 23045270).</td>
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<tr>
<td>PI3K</td>
<td>Kinase</td>
<td>Direct binding in lymph node lymphocytes in response to TCR activation (PMID: 8524815).</td>
</tr>
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<td>Kinase</td>
<td>Direct binding in COS cells following plasmid overexpression (PMID: 10799879).</td>
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<td>ILK</td>
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<td>Direct binding in HAEC cells following adenovirus overexpression (PMID: 22441983).</td>
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<td>SH2B1β</td>
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<tr>
<td>MPL</td>
<td>Cytokine Receptor</td>
<td>Direct binding in splenocytes in response to IL-11 (24297922). Constuitive direct binding in myeloproliferative neoplasm (PMID: 18618018); Direct binding in BMMCs to TPO (PMID: 17693582).</td>
</tr>
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<td>Binding Details</td>
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<td>PLCγ</td>
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<td>ABP-280</td>
<td>Actin Binding Protein</td>
<td>Direct binding in Jurkat T-cells in response to 5-ADC activation (PMID: 11163396).</td>
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<td>TNFα</td>
<td>Cytokine Receptor</td>
<td>Direct binding not known, but SH2B3 overexpression significantly decreased ERK1/2 phosphorylation and enhance AKT phosphorylation in TNFα-activated endothelial cells (PMID: 16644735).</td>
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### Supplementary Table 2. RT-qPCR primer sequences.

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<th>Name</th>
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Supplementary Table 3. Distribution of SH2B3 (rs3184504 [T]) genotypes in heart failure cohort.

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<td>Male</td>
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<td>Mean Age (range)</td>
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LVAD, left ventricular assist-device; HF, heart failure.
Supplementary Table 4. Gene expression in hearts WT and Sh2b3<sup>em2Mcwi</sup> rats at 7 days post-LAD occlusion

<table>
<thead>
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ND, Not Detected