Genetic Determinants of P Wave Duration and PR Segment

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Background—The PR interval on the ECG reflects atrial depolarization and atrioventricular nodal delay which can be partially differentiated by P wave duration and PR segment, respectively. Genome-wide association studies have identified several genetic loci for PR interval, but it remains to be determined whether this is driven by P wave duration, PR segment, or both.

Methods and Results—We replicated 7 of the 9 known PR interval loci in 16,468 individuals of European ancestry. Four loci were unambiguously associated with PR segment, while the others were shared for P wave duration and PR segment. Next, we performed a genome-wide analysis on P wave duration and PR segment separately and identified 5 novel loci. Single-nucleotide polymorphisms in KCND3 (P=8.3×10⁻¹¹) and FADS2 (P=2.7×10⁻⁵) were associated with P wave duration, whereas single-nucleotide polymorphisms near IL17D (P=2.3×10⁻⁸), in EFHA1 (P=3.3×10⁻¹⁰), and in LRCH1 (P=2.1×10⁻⁸) were associated with PR segment. Analysis on DNA elements indicated that genome-wide significant single-nucleotide polymorphisms were enriched at genomic regions suggesting active gene transcription in the human right atrium. Quantitative polymerase chain reaction showed that genes were significantly higher expressed in the right atrium and atrioventricular node compared with left ventricle (P=5.6×10⁻⁶).

Conclusions—Genetic associations of PR interval seem to be mainly driven by genetic determinants of the PR segment. Some of the PR interval associations are strengthened by a directional consistent effect of genetic determinants of P wave duration. Through genome-wide association we also identified genetic variants specifically associated with P wave duration which might be relevant for cardiac biology.

Key Words: aging ■ electrocardiography ■ genetics

Recent genome-wide association studies on PR interval, derived from the surface ECG, have been instrumental for gaining novel insight into the biology of underlying conduction traits. These analyses have led to the discovery of 9 genetic loci in Europeans,1,2 Asians,3 and blacks,4,5 some of which also confer an increased risk of atrial fibrillation. However, PR interval is the summation of P wave duration and PR segment, which are considered to reflect different aspects of the cardiac cycle. P wave duration reflects the electric signals that propagate through the atria and can indicate atrial enlargement.6 The PR segment corresponds to the period that electric signals are delayed at the atrioventricular node, before it travels through the ventricular branches to induce cardiac depolarization and may be prolonged during atrioventricular nodal dysfunction. It remains to be determined whether the previously identified PR-interval variants are driven by P wave duration, PR segment, or both. Understanding the origin of these genetic associations can further refine our understanding of atrial and atrioventricular node function. The aims of the current study are to (1) determine the association of the genetic variants identified by previous PR interval studies with P wave duration and PR segment and (2) determine whether genome-wide analyses of the subtraits (PR segment and P wave duration) can lead to the identification of novel single-nucleotide polymorphism associations.

Clinical Perspective on p 481

Study Samples
Participants of the Prevention of Renal and Vascular End-Stage Disease (PREVEND) study7 and the Lifelines study cohort8 were included. The primary objective of the PREVEND program was to prospectively investigate the natural course of increased levels of urinary albumin excretion as an indicator of increased cardiovascular and renal risk in the general population. LifeLines is a multidisciplinary prospective population-based cohort study examining in a unique 3-generation

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*A list of all LifeLines Cohort Study participants is given in the Data Supplement.

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design the health and health-related behaviors of 165,000 persons living in the North East region of the Netherlands. It uses a broad range of investigative procedures in assessing the biomedical, socio-demographic, behavioral, physical, and psychological factors which contribute to the health and disease of the general population, with a special focus on multimorbidity and complex genetics. Both are community-based cohort studies from the northern part of the Netherlands and have been approved by the review board of the University Medical Center Groningen. This study adheres to the principles expressed in the Declaration of Helsinki. All subjects provided written informed consent. Standard 12 lead ECGs in PREVEND and Lifelines were recorded using Cardio Perfect equipment (Welch Allyn Cardio Control, Delft, The Netherlands). Individuals were excluded from this analysis for the following reasons: atrial fibrillation, atrial flutter, electronic pacemaker rhythm, complete atrioventricular block, or Wolff–Parkinson–White syndrome. Also participants with extreme measurements (more than ±2 SD from the mean) were excluded on a per phenotype basis. Myocardial infarction and medication were not or minimally associated to durations of the P wave or PR segment in PREVEND; for this reason we did not adjust for these variables as previous analysis did.1 After exclusions, there were 3496 PREVEND and 12,972 Lifelines individuals with phenotype and genotype data contributing to the genotype-phenotype association analyses. Characteristics of participants are summarized in Table I in the Data Supplement.

Genotyping
Genotyping for PREVEND and Lifelines was performed on the Illumina CytoSNP12 v2 chip. Samples were excluded based on call rates below 0.95, sex mismatch, duplicate discordance, and genetic similarity (identity by state >0.2). Population stratification was assessed by principal component analysis over the sample correlation matrix, based on 16,842 independent (linkage disequilibrium [LD] pruned) single-nucleotide polymorphisms (SNPs). Samples were excluded when they diverged from the mean with ±3 standard deviations (Z-score>3) for the first 5 principal components. SNPs were excluded with a minor allele frequency of <0.01, call rate <0.95, or deviation from Hardy–Weinberg equilibrium (P<1×10−8). Genome-wide genotype imputation was performed using Beagle v. 3.1.0 using the National Center for Biotechnology Information (NCBI) build 36 of Phase II HapMap CEU data (release 22) as reference panel.

Statistical Analyses
Residuals of P wave duration and PR segment were calculated using general linear regression models to adjust for age, sex, and body mass index. Genome-wide association study analyses of imputed SNPs were performed on the standardized residuals using an additive genetic model in PLINK (v.1.07). Test statistics from each cohort were then corrected for their respective genomic control inflation factor to adjust for residual population substructure. Meta-analysis was performed using the inverse-variance method. SNPs with minor allele frequency <1% (weighted average across cohorts) were removed. The initial analysis considered variants to be independent if the pair-wise LD (r²) was less than 0.1 and if they were separated by ≥1 MB; this was defined a locus. To test if there were multiple SNPs in the same loci independently associated with P wave duration or PR segment we repeated the primary association analysis for each trait while adjusting on the trait-specific genome-wide significant sentinel SNPs by adding the SNP dosages as covariates in the regression analyses. We then combined the association results again for each study by inverse-variance weighting.

Similarly, to assess the association of selected SNPs (genome-wide significant SNPs from literature view) with PR interval, we performed association analyses in PREVEND and Lifelines and combined the results using the inverse-variance method.

Regulatory DNA
We used data available on DNase I hypersensitivity sites from 349 human tissues and cell lines (Gene Expression Omnibus accession numbers GSE29692 and GSE18927) of the Encyclopedia of DNA Elements (ENCODE) project9 and Roadmap Epigenomics Program.10 Hotspots were identified using the hotspot algorithm, and peaks were called at 5% false discovery rate in a uniform manner, as previously described.11 Aligned sequence reads (bed files) from 7 distinct histone modification assays in various human tissues were obtained from the Roadmap Epigenomics Project release 8. Only samples with matching input DNA samples were included. If replicate experiments were available we aggregated the sequence reads. MACS (v1.4) software was used to identify significant peaks (1×10−10) using a fixed DNA fragment size of 146.12 Three samples could not be called with MACS because of inconsistencies in the original data. As a result, this data set included aligned sequence reads of 323 samples (Table II in the Data Supplement).

For annotation of functional elements we included cardiac transcription factor data on Tbx3, Gata4, and Nkx2-5 from mouse heart13; p300 marks in human adult and fetal heart and RNA polymerase 2 from human fetal heart14; and Gata4, Mef2, Nkx2-5, Srf, and Tbx5 from the atrial HL-1 cell line.15 We used the called peak data from the Gene Expression Omnibus (GSE35151, GSE32587, and GSE21529). Peaks from mice were lift-over to human using the UCSC Genome Browser liftOver tool with the options --minMatch=0.1 – multiple after extending the regions by 1 kb.16 Conversion of hg18 to hg19 was also performed using the UCSC LiftOver tool when appropriate.

Quantitative Expression Analysis of Genes Associated With P Wave Duration and PR Segment
Wild-type FVB animals were euthanized at the age of 6 to 8 weeks. Left ventricles, right atria, and atrioventricular node tienenure junctions were dissected in sterile PBS and pooled per tissue type in 3 groups of 7 samples. Total RNA isolation was performed using the MagNA Lyser instrument (product no. 03358976001; Roche Applied Science) with MagNA Lyser Green Beads (product no. 03358941001, Roche Applied Science) and TRizol Reagent (catalog no. 15596-026; Invitrogen) according to the manufacturer’s protocol. After quantification, 400 ng of total RNA was treated with DNase I (18068-015, Invitrogen) to remove genomic DNA from the RNA sample. cDNA synthesis was performed using the SuperScript II Reverse Transcriptase kit (catalog no. 1806-014, Invitrogen). Expression of different genes was assayed with quantitative real-time polymerase chain reaction using the Roche LightCycler 480 system. Primer sequences are listed in Table III in the Data Supplement. Relative start concentration (N(0)) was calculated as previously described.17 Values were normalized to Gapdh expression levels, and differences in expression values were tested by 2-tailed t tests. All animal work was approved by the Animal Experimental Committee of the Academic Medical Center, University of Amsterdam, and was performed in compliance with the Dutch Government guidelines.

Results
We performed genome-wide association studies with 2.3 million imputed autosomal SNPs (HapMap 2 build 36 CEU panel) in the same individuals on P wave duration and PR segment. There was no evidence for inflation of test statistics at the final meta-analysis results, λP-duration=1.002, λP-PR-segment=1.019 (Figure I in the Data Supplement). Although PR segment is a smaller interval (≈44 ms) than P duration (≈113 ms) on the ECG, PR segment explains more of the PR interval (r²=0.66, P<10^-9) than P wave duration (r²=0.30, P<10^-9) because of greater variation in PR segment (Table I in the Data Supplement).

First, we looked up the association of the known PR interval SNPs in the P wave duration and PR segment association results (Table 1; Table IV in the Data Supplement). All previously identified PR interval loci that were significant in this study also showed an association signal with PR segment (P<0.004). Loci-containing genes SCN5A/SCN10A, CAV1 and SOX5 were also found to be associated with P wave duration;
Table 1. Seven of the Nine Known Genome-Wide PR Interval Loci1–5 Reached the Threshold of Significance for Replication (P<0.05/9) and Were Directionally Concordant With Previous Reports, as Indicated by P Values* and Effect Estimates

<table>
<thead>
<tr>
<th>Region</th>
<th>SNP</th>
<th>Coding (FRQ)/Noncoding Allele</th>
<th>P Wave Duration GWAS</th>
<th>PR Segment GWAS</th>
<th>PR Interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>FRQ</td>
<td>P</td>
<td>Value (β (SE))</td>
<td>P Value (β (SE))</td>
<td>Value (β (SE))</td>
<td>Reference</td>
</tr>
<tr>
<td>2p14</td>
<td>rs3891585</td>
<td>A (0.41)/G</td>
<td>0.024</td>
<td>0.29 (0.13)</td>
<td>2.30E-08</td>
</tr>
<tr>
<td>3p22.2</td>
<td>rs267567</td>
<td>A (0.47)/G</td>
<td>0.781</td>
<td>-0.04 (0.14)</td>
<td>0.320</td>
</tr>
<tr>
<td>3p22.2</td>
<td>rs3922844</td>
<td>T (0.33)/C</td>
<td>1.78E-08</td>
<td>-1.41 (0.25)</td>
<td>3.79E-04</td>
</tr>
<tr>
<td>3p22.2</td>
<td>rs6599222</td>
<td>T (0.84)/C</td>
<td>6.80E-08</td>
<td>-1.98 (0.37)</td>
<td>0.008</td>
</tr>
<tr>
<td>3p22.2</td>
<td>rs6763048</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>2p14</td>
<td>rs6801957</td>
<td>T (0.43)/C</td>
<td>8.44E-27</td>
<td>1.44 (0.13)</td>
<td>6.94E-41</td>
</tr>
<tr>
<td>4q12.23</td>
<td>rs7660702</td>
<td>T (0.70)/C</td>
<td>0.761</td>
<td>0.04 (0.14)</td>
<td>1.14E-14</td>
</tr>
<tr>
<td>5q35.2</td>
<td>rs251253</td>
<td>T (0.59)/C</td>
<td>0.078</td>
<td>0.22 (0.12)</td>
<td>3.56E-05</td>
</tr>
<tr>
<td>7q31.2</td>
<td>rs3807989</td>
<td>A (0.43)/G</td>
<td>3.50E-05</td>
<td>0.51 (0.12)</td>
<td>4.99E-12</td>
</tr>
<tr>
<td>11q13.5</td>
<td>rs4944092</td>
<td>A (0.76)/G</td>
<td>0.927</td>
<td>0.03 (0.33)</td>
<td>0.956</td>
</tr>
<tr>
<td>12q12.1</td>
<td>rs11047543</td>
<td>A (0.14)/G</td>
<td>4.93E-04</td>
<td>-0.65 (0.19)</td>
<td>1.57E-05</td>
</tr>
<tr>
<td>12q24.21</td>
<td>rs3825214</td>
<td>A (0.78)/G</td>
<td>0.031</td>
<td>-0.32 (0.15)</td>
<td>0.287</td>
</tr>
<tr>
<td>12q24.21</td>
<td>rs1896312</td>
<td>T (0.65)/C</td>
<td>0.231</td>
<td>0.19 (0.16)</td>
<td>1.17E-09</td>
</tr>
</tbody>
</table>

All loci that were significant for PR interval in this analysis were significantly associated with PR segment. However, SCNA5A/SCN10A, CAV1, and SOX5 also showed an association with P wave duration. PR interval statistics were obtained in Participants of the Prevention of Renal and Vascular End-Stage Disease (PREVEND) and Lifelines and combined using the inverse-variance method. Frequencies were calculated from the individuals of Lifelines and PREVEND that were included in the meta-analyses. SNPs were pruned on LD (r²>0.6, HapMap). Values* and Effect Estimates

*Significant values.

However, none of the known PR interval loci were specific for P wave duration. The association of the ARHGAP24 and TBX3 SNPs was higher for PR segment (P=1.1×10–14, P=1.2×10–9, respectively) compared with the association with PR interval (P=9.9×10–15 and P=5.0×10–9, respectively). All other PR interval associations decreased by separating PR interval into PR segment and P wave duration.

Second, the genome-wide meta-analysis identified a total of 93 SNPs in 3 loci to be significantly genome-wide associated (P<5.0×10–8) with P wave duration and 184 SNPs in 7 loci to be genome-wide associated with PR segment (Tables V and VI in the Data Supplement). Summary statistics of all 2.3 mol/L SNPs are provided in the Data Supplement. We identified a secondary signal (rs2253017) on chromosome 13 to remain genome-wide associated with PR segment while adjusting for rs2798269 (Table 2 and Figure 1; Figure II in the Data Supplement). One locus was shared among both phenotypes (the SCN10A locus). In total, we identified 10 independent

Table 2. Summary Statistics for the Sentinel SNPs That Were Identified in the Genome-Wide Association Study on P Wave Duration and PR Segment

<table>
<thead>
<tr>
<th>Region</th>
<th>SNP</th>
<th>Coding (FRQ)/Noncoding Allele</th>
<th>P Wave Duration</th>
<th>PR Segment</th>
</tr>
</thead>
<tbody>
<tr>
<td>FRQ</td>
<td>P</td>
<td>Value (β (SE))</td>
<td>P Value (β (SE))</td>
<td>Reference</td>
</tr>
<tr>
<td>1p13.2</td>
<td>rs2798334</td>
<td>T (0.29)/C</td>
<td>7.92E-11*</td>
<td>-0.92 (0.14)</td>
</tr>
<tr>
<td>2p14</td>
<td>rs11678354</td>
<td>A (0.36)/T</td>
<td>0.010</td>
<td>0.34 (0.13)</td>
</tr>
<tr>
<td>3p22.2</td>
<td>rs6801957</td>
<td>T (0.43)/C</td>
<td>8.44E-27*</td>
<td>1.44 (0.13)</td>
</tr>
<tr>
<td>4q21.23</td>
<td>rs13137008</td>
<td>T (0.70)/G</td>
<td>0.638</td>
<td>0.07 (0.14)</td>
</tr>
<tr>
<td>7q31.2</td>
<td>rs3807989</td>
<td>A (0.43)/G</td>
<td>3.50E-05</td>
<td>0.51 (0.12)</td>
</tr>
<tr>
<td>11q12.2</td>
<td>rs174577</td>
<td>A (0.33)/C</td>
<td>2.59E-08*</td>
<td>-0.73 (0.13)</td>
</tr>
<tr>
<td>12q24.21</td>
<td>rs10850949</td>
<td>A (0.27)/G</td>
<td>0.097</td>
<td>-0.23 (0.14)</td>
</tr>
<tr>
<td>13q12.11</td>
<td>rs2253017</td>
<td>T (0.15)/C</td>
<td>0.963</td>
<td>-0.01 (0.17)</td>
</tr>
<tr>
<td>13q12.11</td>
<td>rs2798269</td>
<td>T (0.40)/C</td>
<td>0.923</td>
<td>-0.01 (0.13)</td>
</tr>
<tr>
<td>13q14.13</td>
<td>rs9590974</td>
<td>A (0.65)/C</td>
<td>0.243</td>
<td>-0.15 (0.13)</td>
</tr>
</tbody>
</table>

*Significant values.

P values estimate the difference in duration in millisecond per copy of the coding allele, adjusted for the covariates in the model. FRQ indicates frequency; GWAS, genome-wide association studies; LD, linkage disequilibrium; NA, not available; and SNP, single-nucleotide polymorphism.

Significant associations.

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genetic variants to be genome-wide associated with P wave duration and PR segment. The variants explained on average 1.2% (P wave duration) and 3.1% (PR segment) of the phenotypic variation in Lifelines and PREVEND. All genome-wide top SNPs (sentinel SNPs) per independent locus were well imputed as shown in Table IV in the Data Supplement.

The Phenotype–Genotype Integrator at the National Center for Biotechnology Information (http://www.ncbi.nlm.nih.gov/gap/phegeni) was queried for literature on the significant SNPs and SNPs in LD ($r^2>0.6$, Hapmap). The FADS2 locus stands out, rs174577 (11q12), an SNP that has previously been associated with metabolic traits (Table VII in the Data Supplement).

SNPs in Regulatory DNA
To provide insight into tissue-specific regulatory DNA mechanisms influencing P wave duration and PR segment, we explored DNase I hypersensitivity sites and histone marks. We assigned the lowest $P$ value of P wave duration and PR duration to each of the 2.3 mol/L SNPs. We then compared the ratio of all SNPs with a $P$ value below $5\times10^{-8}$ in peaks of DNA elements to the ratio of all 2.3 mol/L SNPs in DNA elements. We considered all available tissues/experiments. Enrichment was defined if tissues passed the threshold of Q3+1.5 X interquartile range (Figure 2). SNPs in all available human heart tissues of interest (right atrium left ventricle, fetal heart), atria, and a few other nonheart tissues were overenriched for various DNA elements.

The genome-wide significant SNPs were annotated with various DNA elements that had been measured in the human or mouse heart. We found that all sentinel SNPs or SNPs in LD ($r^2>0.8$, 1000 genomes) overlap with ≥1 DNase I hypersensitivity site of human fetal heart. In Figure III in the Data Supplement we provide an overview of the sentinel SNPs in DNA elements to prioritize loci for experimental follow-up.

Candidate Genes and Gene Expression
We prioritized candidate genes by searching for (1) protein-coding gene nearest to the sentinel SNP and any other protein-coding gene within 10 kb (11 genes); (2) we also considered genes containing a coding SNP in high LD (1000G EUR, $r^2>0.8$) with the sentinel SNP (1 gene, SCN10A). This analysis identified 11 candidate genes (Table 2) for the 10 independent, genome-wide significant, SNPs.

To test the hypothesis that we identified regions actively transcribed in the right atrium and atrioventricular node, we performed quantitative polymerase chain reactions of the nearest gene to the sentinel SNP or any gene within 10 kb. Using carefully dissected tissue samples from adult mouse hearts, we analyzed the expression of the candidate genes in atrial, ventricular, and atrioventricular nodal components. From this analysis it is first noteworthy that Tbx3 expression was most highly expressed in the atrioventricular node tissue samples, thus acting as a validation for the dissection procedure. Using quantitative polymerase chain reaction, we observed that 10 of...
the 11 candidate genes were expressed in left ventricle, right atrium, and atrioventricular node in mice. Notably, SCN10A transcripts were not reproducibly detectable in mice, also in line with a recent study of atrial gene expression using RNAseq.\(^\text{18}\) All genes except N6AMT2 (lower expression) and ARHGAP24 showed significantly higher expression in atria or atrioventricular node compared with the left ventricle (\(P<0.05\), Figure 2). This number of genes (6) was also a significantly higher number than would be expected by chance (\(P_{\text{binomial}}=5.56\times10^{-4}\) at the 0.05 level of significance). N6AMT2 is annotated to rs2253017 (\(P=2.3\times10^{-4}\), PR segment), which is located between IL17D (+2.2 kb) and N6AMT2 (+2.2 kb). In contrast to N6AMT2, IL17D is expressed higher in the atrioventricular node and right atrium compared with the left ventricle, making it a more likely candidate gene.

### Discussion

The P wave and PR interval on the ECG are important traits that have proven relationship with and predictive value for normal and abnormal heart rhythm, supraventricular arrhythmias, and conduction disturbances. We replicated 7 out of 9 loci that were previously associated with PR interval and report that these are mainly driven by genetic variants affecting the PR segment and to a lesser extent P wave duration. We also observed that PR segment explains more of PR interval than P wave duration, in support of a genetic investigation of P wave duration. By studying the specific subtraits, we identified 5 novel independent genome-wide significant associations with PR segment or P wave duration. Variants near IL17D/N6AMT2, EFHA1, and LRCH1 were specifically associated with PR segment, whereas variants near KCND3 and FADS2 were specifically associated with PR duration.

We observed that genome-wide significant SNPs were specifically localized in chromatin marks and DNase I hypersensitive sites of the human fetal heart, compared with many other human tissues. This indicates that functionality of regulatory DNA elements may underlie some of the associations. The SNP in SCN10A (rs6801957) has already been studied and shown to affect a functional enhancer in the heart.\(^\text{14}\) Genome-wide SNPs were also overenriched in cell type-specific histone marks associated with active enhancers and promoters, H3K27ac and H3K4me1, of the human right atrium.\(^\text{19}\) The repressive-state associated mark H3K9ac in the right atrium contained no genome-wide SNPs and showed depletion compared with the other tissues. This finding suggests the regulatory mechanism to be mediated by gene activation and not repression.

Our expression analyses showed specific atrioventricular nodal expression of Tbx3, which is in line with the association of rs10850409 near Tbx3 with PR segment, reflecting the atrioventricular node-dependent duration on the ECG. Tbx3 is a well-characterized transcription factor that is required for the development of many tissues. In the heart it allows the cells to acquire pacemaker properties and is required for the specification of the atrioventricular conduction system.\(^\text{20}\)

We identified novel associations with P wave duration and PR segment in the genomic regions 1p13.2, 11q12.2, 13q12.11 (containing 2 independent signals), and 13q14.13. In locus 13q12.11, IL17D was a strong candidate based on the expression analysis. To date, there has only been one study on IL17D which described the protein to be preferentially expressed in skeletal muscle, brain, adipose tissue, heart, lung, and pancreas and to stimulate interleukin-6 and nuclear factor κ-light-chain-enhancer of activated B cells-dependent interleukin-8.
production relevant for heart function. Future studies should identify its potential role in the atria. In the same locus, we identified another independent signal containing EFHA1; the exact function of the protein remains to be determined, but a recent publication suggests a role in mitochondrial calcium handling. In locus 11q12.2, FADS2, a member of the fatty acid desaturases has been previously associated with a multitude of lipids, and a prominent role of lipid metabolism in the heart has been extensively studied. In locus 1p13.2, KCND3 encodes the Kv4.3 α-subunit that conducts the cardiac fast transient outward K+ current (Ito). This current is prominent in the repolarization phase of cardiac action potential. Several gain-of-function mutations have been recently associated with Brugada syndrome and early-onset lone atrial fibrillation. Finally, 13q14.13 contains LRCH1; no function has been assigned to the protein product of this gene.

Strengths and Limitations

This study is the first to investigate the differences in SNP associations between P wave duration and PR segment. The participants in this study are from the northern parts of the Netherlands, and measurements have been performed in the same center, which ensures a homogenous population and reduces variation in assays. The novel genotype–phenotype associations were highly statistically significant, but future efforts are required to understand the origin of these associations. Additionally, we note that the identified variants explained little of the phenotypic variation in the population but anticipate that the distinct genotype–phenotype associations with PR interval’s subtraits are more relevant to provide new biological insight into the heart’s function. In this study we were the first to combine as many as 672 experiments on histone modifications and DNase I hypersensitivity sites in human tissues for insight into the results of genome-wide analyses and thereby validating them. However, the analyses on DNA elements and gene expression in the right atrium might differ from the left atrial tissue which is thought to be the responsible tissue for AF vulnerability. It is unknown how the identified polymorphisms or which polymorphisms in LD have an effect on gene function causing the association. In-depth experimental studies are necessary to address the loci for their causal genes and the mechanisms on how genomic regions can affect the different aspects of P wave durations.

Conclusions

PR interval seems to be mainly genetically driven by PR segment, but some of the associations are further strengthened by a directional consistent effect of genetic determinants on P wave duration. By genome-wide association of the subphenotypes, we also identified 2 novel SNPs specifically associated with P wave duration which may be relevant for atrial biology and 3 novel SNP associations for PR segment. Analysis on DNA elements indicated that we identified regions actively transcribed in the right atrium, which was further validated by expression profiling of the candidate genes. In conclusion, analyzing subphenotypes of the ECG can lead to the identification of novel loci and genes and therefore might provide new insights into cardiac biology.

Sources of Funding

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Disclosures

None.

References


**CLINICAL PERSPECTIVE**

The PR interval on the electrocardiogram is an important predictor of normal and abnormal heart rhythm, supraventricular arrhythmias, and conduction disturbances. The PR interval reflects atrial depolarization and atrioventricular nodal delay, which can be partially differentiated by P wave duration and PR segment. Recent genome-wide association studies have identified common genetic variants associated with the PR interval. We investigated the relationship of these variants with P wave duration and the PR segment. In addition, we identified 2 novel signals influencing P wave duration, which may be relevant for atrial biology, harboring KCND3 and FADS2, and 3 novel signals influencing PR segment harboring IL17D, EFHA1, and LRCH1. Analyses of DNA elements suggested that the identified regions were actively transcribed in human atrial tissue, which was confirmed by showing that these candidate genes were more expressed in atrial and atrioventricular node tissue compared to the left ventricular tissue. Our findings highlight that appreciation of subphenotypes can provide new insight into atrial biology and lead to identification of novel genetic loci.
Genetic Determinants of P Wave Duration and PR Segment

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SUPPLEMENTAL MATERIAL

LifeLines Cohort Study Participants:

*LifeLines Scientific Protocol Preparation*

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*LifeLines GWAS Working Group:*

Behrooz Alizadeh, Marike Boezen, Marcel Bruinenberg, Noortje Festen, Lude Franke, Pim van der Harst, Gerjan Navis, Dirkje Postma, Harold Snieder, Cisca Wijmenga, Bruce Wolffenbuttel.

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**Table S1** Characteristics for P wave durations in PREVEND and Lifelines.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PREVEND (n=3496)</th>
<th>Lifelines(n=12,972)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Age (yrs)</td>
<td>49±12</td>
<td>48±11</td>
</tr>
<tr>
<td>Males %</td>
<td>48</td>
<td>42</td>
</tr>
<tr>
<td>BMI (kg/m2)</td>
<td>26±4</td>
<td>26±4</td>
</tr>
<tr>
<td>PR segment (ms)</td>
<td>41.9±18.1</td>
<td>44.0±18.1</td>
</tr>
<tr>
<td>P wave duration (ms)</td>
<td>117.0±12.7</td>
<td>113.4±12.3</td>
</tr>
<tr>
<td>PR interval (ms)</td>
<td>159.9±21.7</td>
<td>158.3±23.6</td>
</tr>
</tbody>
</table>
Table S2 Chromatin data of Roadmap epigenomics project evaluated, the number samples per experiment is indicated.

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<thead>
<tr>
<th>Sample Name</th>
<th>Chromatin mark</th>
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<td>H3K27ac</td>
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<td>Adipose Nuclei</td>
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</tr>
<tr>
<td>Adipose Tissue</td>
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</tr>
<tr>
<td>Adrenal Gland</td>
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</tr>
<tr>
<td>Adult Kidney</td>
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</tr>
<tr>
<td>Adult Liver</td>
<td>2</td>
</tr>
<tr>
<td>Aorta</td>
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</tr>
<tr>
<td>Bone Marrow Derived Mesenchymal Stem Cell Cultured Cells</td>
<td>4</td>
</tr>
<tr>
<td>Brain Anterior Caudate</td>
<td>1</td>
</tr>
<tr>
<td>Brain Cingulate Gyrus</td>
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<tr>
<td>Brain Hippocampus Middle</td>
<td>2</td>
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<tr>
<td>Brain Inferior Temporal Lobe</td>
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</tr>
<tr>
<td>Brain Mid Frontal Lobe</td>
<td>1</td>
</tr>
<tr>
<td>Brain Substantia Nigra</td>
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</tr>
<tr>
<td>Breast Luminal Epithelial Cells</td>
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</tr>
<tr>
<td>Breast Myoepithelial Cells</td>
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<tr>
<td>CD19 Primary Cells</td>
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<td>CD3 Primary Cells</td>
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<tr>
<td>CD34 Primary Cells</td>
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</tr>
<tr>
<td>CD4 Memory Primary Cells</td>
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<tr>
<td>CD4 Naive Primary Cells</td>
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<tr>
<td>CD4+ CD25- CD45RA+ Naive Primary Cells</td>
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<tr>
<td>CD4+ CD25- CD45RO+ Memory Primary Cells</td>
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<td>CD4+ CD25- IL17- PMA-Ionomycin stimulated MACS purified Th Primary Cells</td>
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<tr>
<td>CD4+ CD25- IL17+ PMA-Ionomycin stimulated Th17 Primary Cells</td>
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<tr>
<td>CD4+ CD25int CD127+ Tmem Primary Cells</td>
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<td>CD8 Naive Primary Cells</td>
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<td>Chondrocytes from Bone Marrow Derived</td>
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<td>Esophagus</td>
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<td>Fetal Brain</td>
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<td>Fetal Lung</td>
<td>1</td>
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<tr>
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<tr>
<td>Lung</td>
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<td>Mesenchymal Stem Cell Derived Adipocyte Cultured Cells</td>
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<td>Mobilized CD34 Primary Cells</td>
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<td>Muscle Satellite Cultured Cells</td>
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<td>Neurosphere Cultured Cells Ganglionic Eminence</td>
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<td>Penis Foreskin Keratinocyte Primary Cells</td>
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<tr>
<td>Penis Foreskin Melanocyte Primary Cells</td>
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<tr>
<td>Psoas Muscle</td>
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<td>Rectal Mucosa</td>
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<td>Right Atrium</td>
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<td>Tissue Type</td>
<td>Error 1</td>
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<td>-------------------------------</td>
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<tr>
<td>Right Ventricle</td>
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<tr>
<td>Sigmoid Colon</td>
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<td>Skeletal Muscle</td>
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<tr>
<td>Small Intestine</td>
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<tr>
<td>Spleen</td>
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<tr>
<td>Stomach Mucosa</td>
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<tr>
<td>Stomach Smooth Muscle</td>
<td>1</td>
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<tr>
<td>Th17 Primary Cells</td>
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<tr>
<td>Treg Primary Cells</td>
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<td><strong>Total Samples:</strong></td>
<td>41</td>
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**Table S3** Primer sequences used for the qPCR

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<tr>
<th>Name</th>
<th>Sequence</th>
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<td>Kcnd3_F</td>
<td>CCACACACCTGCCCCAICTCTAA</td>
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<tr>
<td>Kcnd3_R</td>
<td>CAGTCATCGCTGCTTTCAAAA</td>
</tr>
<tr>
<td>Meis1_F</td>
<td>TCTAAACTGACCAGCCTCTTTG</td>
</tr>
<tr>
<td>Meis1_R</td>
<td>TGGTATCCCACTGTGTGAAGT</td>
</tr>
<tr>
<td>Scn10a_F</td>
<td>CGGCAAGTATACCTCAACCAAGGGG</td>
</tr>
<tr>
<td>Scn10a_R</td>
<td>CAGACGCATACGCAGCGTAAGAG</td>
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<tr>
<td>Arhgap24_F</td>
<td>CTGAACGGACGATACAGCAACAAAC</td>
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<tr>
<td>Arhgap24_R</td>
<td>TGGAGGCTCAGCATTCCGTTTE</td>
</tr>
<tr>
<td>Cav1_F</td>
<td>CGAGGCACATCTCATACTCTGTT</td>
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<tr>
<td>Cav1_R</td>
<td>TGTGCGGCACATACACCTGCTT</td>
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<tr>
<td>Fads2_F</td>
<td>GTTCAGCGGCGGACCTCAATTT</td>
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<tr>
<td>Fads2_R</td>
<td>CAACGGCTCTCCTGGTATTC</td>
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<td>Tbx3_is2-4_F</td>
<td>GTCGTCACCTTCCACAAACTGA</td>
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<td>Tbx3_is2-4_R</td>
<td>GAGTTTAGTATAGTCTCGGTCC</td>
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<tr>
<td>Efha1_F</td>
<td>AAGACTTTGCTATGCGCTAGCA</td>
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<tr>
<td>Efha1_R</td>
<td>AGACGGTGCCGGAGATTTGTC</td>
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<tr>
<td>I17d_F</td>
<td>GGGCGTACAGGATTCCCTACGA</td>
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<tr>
<td>I17d_R</td>
<td>AGAAGACGGGTGCTGACTGCAAA</td>
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<tr>
<td>N6amt2_F</td>
<td>TCCAGTTTTCTGACTCGGGGCCAA</td>
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<td>N6amt2_R</td>
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</tr>
<tr>
<td>Lrch1_F</td>
<td>CCAAGACGGACCCAGTGCTTT</td>
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<tr>
<td>Lrch1_R</td>
<td>CGGATCGTAAACTGTGGGTCTA</td>
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</tbody>
</table>
**Table S4** full statistics and imputation quality metrics for the SNPs that were identified in this analysis and SNPs previously associated to PR interval.

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<tr>
<th>Region</th>
<th>SNP</th>
<th>Effect / non-effect allele</th>
<th>FRQ (Effect allele)</th>
<th>P wave duration Beta(se)</th>
<th>P PR segment Beta(se)</th>
<th>P PR interval Beta(se)</th>
<th>P</th>
<th>PREVEND Info(Plink 1.07) / $r^2$ (Beagle)</th>
<th>Lifelines Info(Plink 1.07) / $r^2$ (Beagle)</th>
</tr>
</thead>
<tbody>
<tr>
<td>11q12.2</td>
<td>rs174577</td>
<td>A/C</td>
<td>0.33</td>
<td>-0.73(0.13)</td>
<td>2.59E-08</td>
<td>-0.28(0.22)</td>
<td>2.03E-01</td>
<td>0.97/0.98</td>
<td>0.98/0.98</td>
</tr>
<tr>
<td>11q13.5</td>
<td>rs4944092</td>
<td>A/G</td>
<td>0.76</td>
<td>0.03(0.33)</td>
<td>9.27E-01</td>
<td>-0.03(0.53)</td>
<td>9.56E-01</td>
<td>0.18/0.11</td>
<td>0.2/0.10</td>
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<tr>
<td>12p12.1</td>
<td>rs11047543</td>
<td>A/G</td>
<td>0.14</td>
<td>-0.65(0.19)</td>
<td>4.93E-04</td>
<td>-1.32(0.31)</td>
<td>1.57E-05</td>
<td>0.93/0.88</td>
<td>0.91/0.90</td>
</tr>
<tr>
<td>12q24.21</td>
<td>rs10850409</td>
<td>A/G</td>
<td>0.27</td>
<td>-0.23(0.14)</td>
<td>9.66E-02</td>
<td>1.65(0.23)</td>
<td>7.62E-13</td>
<td>0.99/0.97</td>
<td>0.96/0.98</td>
</tr>
<tr>
<td>12q24.21</td>
<td>rs1896312</td>
<td>T/C</td>
<td>0.65</td>
<td>0.19(0.16)</td>
<td>2.31E-01</td>
<td>-1.60(0.26)</td>
<td>1.17E-09</td>
<td>0.65/0.64</td>
<td>0.64/0.62</td>
</tr>
<tr>
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<td>rs1895585</td>
<td>A/G</td>
<td>0.27</td>
<td>0.40(0.14)</td>
<td>5.05E-03</td>
<td>0.10(0.24)</td>
<td>6.66E-01</td>
<td>0.92/0.93</td>
<td>0.94/0.92</td>
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<tr>
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<td>0.78</td>
<td>-0.32(0.15)</td>
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<td>1.01/1.00</td>
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<td>1.58(0.28)</td>
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<td>T/C</td>
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<td>0.88/0.88</td>
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<td>-1.19(0.21)</td>
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<td>0.99/0.97</td>
<td>0.99/0.98</td>
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<td>0.95/0.96</td>
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<td>0.98/0.98</td>
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Table S5 All genome wide associated SNP for P wave duration. Beta values estimate the difference in duration in millisecond per copy of the coding allele (A1), adjusted for the covariates in the model. The direction column indicates the direction of effect in Lifelines and Prevend, respectively.

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Table S6 All genome wide associated SNP for PR segment. Beta values estimate the difference in duration in millisecond per copy of the coding allele (A1), adjusted for the covariates in the model. The direction column indicates the direction of effect in Lifelines and Prevend, respectively.

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Figure S1 QQ plots of the genome wide meta-analysis on A) P wave duration and B) PR segment. Meta-analysis by the inverse-variance method (IV) and weighted Z-score (WZ) were included for quality control.
Figure S2 Regional plots for the sentinel SNPs of P wave duration (left) and PR segment (right). At each region pairwise LD with the sentinel SNP is indicated.
P duration | PR segment
Figure S3 Functional annotation of genome wide associated SNPs.