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Mapping genomic loci implicates genes and synaptic biology in schizophrenia

A full list of authors and affiliations appears at the end of the article.
[#] These authors contributed equally to this work.

SUMMARY

Schizophrenia has a heritability of 60–80%, much of which is attributable to common risk alleles. Here, in a 2-stage genome-wide association study of up to 76,755 people with schizophrenia and 243,649 controls, we report common variant associations at 287 distinct genomic loci. Associations were concentrated in genes expressed in CNS neurons, excitatory and inhibitory, but not other tissues or cell types. Using fine-mapping and functional genomic data, we identify 120 genes (106 protein-coding) as likely to underpin associations at some of these loci, including 16 genes with credible causal non-synonymous or UTR variation. We also implicate fundamental processes related to neuronal function, including synaptic organisation, differentiation, and transmission. Fine-mapped candidates were enriched for genes associated with rare disruptive coding variants in people with schizophrenia, including the glutamate receptor subunit *GRIN2A* and transcription factor *SP4*, and were also enriched for genes implicated by such variants in neurodevelopmental disorders. We identify biological processes relevant to schizophrenia pathophysiology, show convergence of common and rare variant associations in schizophrenia and neurodevelopmental disorders, and provide a rich resource of prioritised genes and variants to advance mechanistic studies.

Corresponding Author Contact Information Stephan Ripke: sripke@broadinstitute.org, James T. R. Walters: WaltersJT@cardiff.ac.uk, Michael C. O'Donovan: ODonovanMC@cardiff.ac.uk.
- These authors jointly supervised this work: Stephan Ripke, James T. R. Walters, Michael C. O'Donovan
- Deceased: Robert W. McCarley

AUTHOR CONTRIBUTIONS

The management group for this paper was led by MOD and JTRW with SR responsible for primary analytic matters supported by BMN and MJD. The management group was comprised of a subset of the PIs of the component studies, bioinformaticians, and analysts and were responsible for study design, conduct, management, primary and final interpretation and included OAA, BTB, SIB, ADB, DB, EB, SC, ACor, DCu, MJD, MDF, ED, HE, AHF, PVG, MGi, SJG, KSH, HHu, NI, RSK, KSK, JAK, JLe, TL, DFL, JLi, AMcI, AMcQ, VAM, DWM, BJM, BMN, MOD, RAO, MJO, AP, DPos, SQ, BPR, SR, DR, SGS, ASe, YS, EAS, PFS, MTT, MPV, JTRW, DRW, TW, NRW, XY, WY.

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INTRODUCTION

Schizophrenia typically manifests in late adolescence or early adulthood[1] and is associated with reduced life expectancy, elevated risk of suicide[2], serious physical illnesses[3], and substantial health and social costs. Treatments are at least partially effective in most people, but many have chronic symptoms, and adverse treatment effects are common[4]. There is a need for novel therapeutic target discovery, a process impeded by our limited understanding of pathophysiology.

Much of the between-individual variation in risk is genetic, involving large numbers of common alleles,[5] rare copy number variants (CNVs)[6], and rare coding variants (RCVs)[7,8]. A recent genome-wide association study (GWAS) reported 176 genomic loci containing common alleles associated with schizophrenia[9] but the causal variants driving these associations and the biological consequences of these variants are largely unknown. To increase our understanding of the common variant contribution to schizophrenia, we performed the largest GWAS of the disorder to date and analysed the findings to prioritise variants, genes and biological processes that contribute to pathogenesis.

RESULTS

Association Meta-Analysis

We carried out a primary GWAS in 74,776 cases and 101,023 controls followed by an Extended GWAS which included additional data for the most significant SNPs (Methods). In the primary GWAS, we combined by meta-analysis i) individual genotypes from a core PGC dataset of 90 cohorts of European (EUR) and East Asian (ASN) ancestry from the Psychiatric Genomics Consortium (PGC) totalling 67,390 cases and 94,015 controls. ii) summary-level data from 7,386 cases and 7,008 controls from 9 cohorts of African-American (AA) and Latino (LAT) ancestry[10]. We analysed up to 7,585,078 SNPs with MAF ≥ 1% in 175,799 individuals of whom 74.3% were EUR, 17.5% ASN, 5.7% AA, and 2.5% LAT (Supplementary Cohort Descriptions). This primary GWAS identified 313 independent SNPs (linkage disequilibrium (LD) r2 < 0.1) that exceeded genome-wide significance ($p<5\times10^{-8}$) (Extended Data Figure 1; Supplementary Table 1), spanning 263 distinct loci.

In the Extended GWAS, we meta-analysed the primary GWAS results with summary statistics from deCODE Genetics (1,979 cases, 142,626 controls) for index SNPs with $P<10^{-5}$ and identified 342 LD-independent significant SNPS (Supplementary Table 2) located in 287 loci (Supplementary Table 3; Supplementary Figures 1–2). Comparisons with the 128 associations (108 loci) we reported in 2014 are provided (Supplementary Note); one association (rs3768644; chr2:72.3Mb) is no longer supported[11].

Separate GWAS for males and females had a genetic correlation statistically indistinguishable from 1 (r_g=0.992, SE 0.024). These and other analyses (Supplementary Note) show that common variant genetic liability to schizophrenia is essentially identical in males and females despite reported sex differences in age at onset, symptom profile, course, and outcome[12].

SNP-based heritability and Polygenic Prediction

In the EUR sample, the SNP-based heritability (h^2_{SNP}) (i.e. proportion of variance in liability attributable to all measured SNPs) was estimated[13] to be 0.24 (SE 0.007). Using the all ancestry primary GWAS as the discovery sample, polygenic risk score (PRS) analysis explained a median of 0.073 of variance in liability (SNPs with GWAS $p<0.05$), and 0.024 when restricted to genome-wide significant SNPs. For almost all cohorts, PRS had more explanatory power based on risk alleles derived from the larger combined ancestry GWAS than from the matched ancestry GWAS; given the ancestry specific sample sizes, unsurprisingly[9], this effect was strongest for the non-EUR samples (Extended Data Figure 2 Supplementary Table 5).

PRS explained most variance in liability in cohorts of European ancestry (again a result of the ancestry composition of the GWAS[9]) and in samples which by ascertainment likely include the most severe cases (hospitalised patients or those treated with clozapine) (Supplementary Note). However, even in EUR cohorts, the median Area Under the Receiver Operating Characteristic Curve (AUC) is only 0.72, meaning the liability explained is insufficient for predicting diagnosis in the general population. Nevertheless, as a quantitative estimate of liability to schizophrenia, PRS has applications in research, and in those contexts, PRS can index substantial differences in liability between individuals in the primary GWAS. Compared to the lowest centile of PRS, the highest centile of PRS has an OR for schizophrenia of 39 (95% CI=29–53), and 5.6 (CI 4.9–6.5) when the top centile is compared with the remaining 99% of individuals (Supplementary Table 6). An extended discussion of heritability and polygenic prediction is provided in the Supplementary Note.

Post-GWAS processing

We next performed a number of secondary analyses in the core PGC dataset in which individual genotypes were available based on fully aligned QC and imputation procedures, and where the data in the HRC reference dataset allowed us to account for LD.

Gene Set Enrichments

Tissue and cell types—Genes with relatively high specificity for bulk expression in every tested region of human brain[14] were significantly enriched for associations (Extended Data Figure 3. Comparison with our earlier studies[11,15] shows increasingly clear contrast between the enrichments in brain and non-brain tissues. More strongly than in prior studies[16], from human single cell expression data[17], we found associations were enriched in genes with high expression in excitatory glutamatergic neurons from cerebral cortex and hippocampus (pyramidal CA1 and CA3 cells, and granule cells of dentate gyrus) and also human cortical inhibitory interneurons (Figure 4a). In mouse single-cell RNA-seq data[16], we found similar patterns of enrichments in genes with high expression in excitatory glutamatergic pyramidal neurons from the cortex and hippocampus (Figure 4b), and inhibitory cortical interneurons. We also found associations were enriched in inhibitory medium spiny neurons, the predominant cells of the striatum.

Supportive results were also obtained using a different dataset of 265 cell types in the mouse central and peripheral nervous system[18]. Very strong enrichments were again seen for genes expressed in excitatory glutamatergic neurons of the cortex (especially the deep layers) and hippocampus but also the amygdala (Supplementary Figure 3). Highly significant enrichments were also seen for other neuronal populations, including as above, inhibitory medium spiny neurones in striatum, but also both excitatory and inhibitory neurons from the midbrain, thalamus and hindbrain, and inhibitory cells from the hippocampus. There was little evidence for enrichment of genes with highly specific expression in glia or microglia. Overall, the findings across all the datasets are consistent with the hypothesis that schizophrenia is primarily a disorder of neuronal function, but do not suggest that pathology is restricted to a circumscribed brain region.

Associations enriched in Neuronal Ontologies—Of 7,315 gene ontology (GO) classifications 24 were associated with schizophrenia (Supplementary Table 7). All were relevant to neuronal function including development, differentiation, and synaptic transmission, and involved multiple cellular components including ion channels, synapses, and both axon and dendritic annotations. Using the expert-curated ontology of the SynGO consortium[19], we further examined the synaptic signal and found that conditionally significant annotations were mainly within postsynaptic terms (Supplementary Tables 8, 9), although enrichment was also found for genes involved in synaptic organisation and signalling.

Gene Prioritisation

To facilitate biological interpretation and laboratory follow up, we sought to prioritise specific variants and genes most likely to explain associations using a combination of fine-mapping, transcriptomic analysis, and functional genomic annotations. The initial steps in these procedures were necessarily based on 293 index SNPs (255 loci) that attained significance in the core PGC dataset (Methods, Supplementary Table 10), we then focussed on the loci that remained significant in the full Extended GWAS to maximise robustness (Figure 1).

Fine-mapping

We performed stepwise analyses (Supplementary Note), conditioning associations in loci on their index SNP (and any subsequent conditionally independent associations) to identify regions that contained independent signals (conditional $p<10^{-6}$). This analysis supported the existence of independent associations in ~10% of loci (Supplementary Table 10b).

We also employed the Bayesian fine-mapping method implemented in FINEMAP[20] to infer the most likely number of distinct causal variants driving our GWAS results. FINEMAP was based on 255 regions determined by the LD clumping procedure (Supplementary Table 11e), after merging clumps if their boundaries physically overlapped and excluding the extended MHC region (Methods). For regions predicted to contain 3 or fewer causal variants (N=249; Figure 1; Supplementary Tables 11a, 11b), we extracted from FINEMAP the posterior probabilities (PP) of being causal for every SNP across the region, and constructed credible sets of SNPs that cumulatively capture 95% of the regional PP (Supplementary Note).

For 33 regions, the 95% credible set contained 5 or fewer SNPs (Supplementary Table 11c) and for 9, only a single SNP. We highlight rs4766428 (PP>0.99) which is the only credible SNP in a locus that contains 25 genes and is located within *ATP2A2*. Mutations in *ATP2A2* cause Darier Disease[21], which co-segregates with bipolar disorder in several multiplex pedigrees and is associated with bipolar disorder and schizophrenia at a population level[22]. *ATP2A2* encodes a sarcoplasmic/endoplasmic reticulum calcium pump, suggesting that its role in schizophrenia pathogenesis may be through regulating neuronal cytoplasmic calcium levels. The likely relevance of calcium metabolism is also suggested by enrichment for associations in and around voltage-gated calcium channels (Supplementary Tables 3 and 7).

We denote as our broad fine-map set 628 genes (435 protein coding) that contained at least one credible SNP (Figure 1). To identify the most credible causal genes, we prioritised those mapping to the 287 loci that were genome-wide significant in our Extended GWAS that also contained a) at least one nonsynonymous (NS) or untranslated region (UTR) variant with a PP> 0.1 b) the entire credible set (Supplementary Tables 13, 14). These protein-coding genes had a greater than 3-fold enrichment for loss of function intolerance compared with other protein-coding genes within the loci that were not tagged by credible SNPs (Supplementary Table 15; Supplementary Note), supporting our strategy to delimit credible causal genes.

Among the 70 FINEMAP prioritised genes (64 protein-coding) were 16 genes (protein-coding by definition) based on NS or UTR variants (Supplementary Table 13). These include *SLC39A8* in which rs13107325, previously a moderately high credible SNP[23], is now strongly supported as causal (PP > 0.99). Other non-synonymous variants with high PP were found in genes with minimal functional characterization including *THAP8*, *WSCD2*, and in two E3 ubiquitin ligases *PJA1* and *CUL9.* Missense and UTR variants prioritised *interferon regulatory factor 3* (*IRF3* while *KLF6*, a transcription factor, was highlighted by three variants in the 3’ UTR. Finally, we identified 61 genes (55 protein-coding) in which the 95% credible set is restricted to a single gene (Supplementary Table 14).

Prioritisation by Gene Expression

To detect GWAS associations that are credibly explained by eQTLs, that is, variants that influence gene expression, we used summary-based Mendelian randomisation (SMR)[24] to find evidence that GWAS signals co-localise with eQTLs (from adult brain[25], fetal brain[26] or whole blood[27]) and the HEIDI test[24] to then reject co-localisations due to LD between distinct schizophrenia-associated and eQTL variants (Supplementary Table 16). To retain brain relevance, we considered only findings from blood that replicated in brain. After removing duplicates identified in multiple tissues (Supplementary Tables 17a–c), we identified 101 SMR-implicated genes (Supplementary Table 17d); the use of alternative methodologies supported the robustness of the SMR findings (Supplementary Note and Supplementary Table 17e).

We used three approaches to prioritise genes from these 101 candidates (Supplementary Note; Supplementary Tables 17f, 17g, 18). We identified (i) 32 genes as the single SMR-implicated gene at the locus or through conditional analysis of a locus containing multiple candidates: (ii) 16 genes where the putatively causal eQTLs captured 50% or more of the

FINEMAP posterior probability (iii) 29 genes where chromatin conformation analysis (Hi-C analysis of adult and fetal brain) suggested that a promoter of that gene interacted with a putative regulatory element containing a FINEMAP credible SNP[28].

After removing duplicates, there were 55 SMR/SMR-Hi-C prioritised genes (Supplementary Table 12) of which 46 were protein-coding. Genes where putatively causal eQTLs captured a particularly high FINEMAP PP (>95%) (Supplementary Table 17g) include *ACE* encoding angiotensin converting enzyme, the target of a major class of anti-hypertensive drugs (schizophrenia under-expression), *DCLK3* encoding a neuroprotective kinase[29](schizophrenia under-expression) and *SNAP91* (discussed below; schizophrenia over-expression).

Combining all approaches, FINEMAP and SMR, we prioritised 120 genes of which 106 are protein-coding (Figure 1; Extended Data Table 1).

Synaptic Location and Function of Prioritised Genes

Following the findings from the genome-wide enrichment tests, we examined prioritised genes in the context of synaptic location and function in the SynGO database[19] (Figure 3. Of the 106 proteins encoded, 15 have synaptic annotations (Supplementary Table 19); 7 postsynaptic, 5 both pre- and post- synaptic, 2 presynaptic, and 1 gene is not mapped to any specific compartment.

The results are consistent with the genome-wide enrichment tests pointing to postsynaptic pathology. However, many prioritised genes had additional locations suggesting that presynaptic pathology may also be involved. The encoded proteins map to 16 unique biological terms in the hierarchy (Supplementary Table 19), but there are specific themes. Multiple genes encode receptors and ion channels, including voltage-gated calcium and chloride channels (*CACNA1C*, *CLCN3*), metabotropic receptors (glutamate (*GRM1*) and GABA (*GABBR2*)), and the ligand-gated NMDA receptor subunit (*GRIN2A*). Others involve proteins playing a role in endocytosis (*SNAP91*), synaptic organisation and differentiation (*DLGAP2, LRRC4B*, *GPM6A, PAK6*), including *PTPRD* a receptor protein tyrosine phosphatase presynaptic organizer that trans-synaptically interacts with multiple postsynaptic cell adhesion molecules (e.g. *IL1RAPL1*), and modulation of chemical transmission (*MAPK3*, *DCC*, *CLCN3, DLGAP2*). The diversity of synaptic proteins identified in this study suggests multiple functional interactions of schizophrenia risk converging on synapses. It remains to be determined whether these interactions occur at a limited set of specific synapse types, or whether the diversity points to multiple types in different brain regions.

Convergence of Common and Rare Variant Associations

The Schizophrenia Exome Sequencing Meta-Analysis (SCHEMA) consortium (companion paper) identified 32 genes with damaging ultra-rare mutations associated with schizophrenia (FDR<0.05), including 10 at exome-wide significance. We found both sets of genes were enriched for common variant associations, as were more weakly associated SCHEMA genes down to uncorrected P<0.001 (Figure 2a, Supplementary Tables 20, 21). Moreover, within associated loci, protein coding genes containing one or more FINEMAP credible

SNPs were enriched for SCHEMA genes relative to other protein-coding genes (Figure 2b; Supplementary Table 21). There are rare variant overlaps in liability to schizophrenia, autism spectrum disorder (ASD) and developmental disorder (DD)[8,30,31]. We tested for and found that genes in which rare variants increase risk of ASD and DD[32,33] are also enriched for schizophrenia common variant associations. Moreover, they are also enriched among genes containing FINEMAP credible SNPs (Figure 2 Supplementary Tables 20, 21).

Convergences between rare variants and fine-mapped GWAS signals have been previously observed in other traits e.g.,[34,35], suggesting that genes most strongly implicated by fine-mapping and which have additional support from rare variant data are compelling candidates. Of the 10 exome-wide significant genes identified by SCHEMA[36], two were prioritised candidates from fine-mapping; *GRIN2A* encoding a glutamatergic NMDA receptor subunit, and *SP4*, a transcription factor highly expressed in brain and which is regulated by NMDA transmission, and also regulates NMDA receptor abundance[37]. Two other genes supported by SCHEMA at FDR<0.05 had strong support from fine-mapping: *STAG1,* which is involved in controlling chromosome segregation and regulating gene expression, and *FAM120A*, which encodes an RNA binding protein. SNPs mapping to these genes had cumulative FINEMAP PP of 0.88 and 0.72 respectively (Supplementary Table 11b). The prioritised fine-mapped set also contained 4 genes implicated in DD; a transcriptional regulator (*BCL11B*), the well-known *CACNA1C*[38], and genes mentioned elsewhere in this paper (*GRIN2A* and *SLC39A8*). Genes encoding additional transcriptional regulators are also of note; *RERE, FOXP1* and *MYT1L. RERE* was prioritised by SMR and is associated with *DD. FOXP1* and *MYT1L* are associated with both DD and ASD and met our fine-mapping prioritisation criteria in the core PGC dataset (Supplementary Table 12).

DISCUSSION

We have performed the largest GWAS of schizophrenia to date and in doing so, identify a substantial increase in the number of associated loci. We show that genes we prioritise within associated loci by fine-mapping are enriched for those with an increased burden of rare deleterious mutations in schizophrenia, and identify *GRIN2A*, *SP4*, *STAG1*, and *FAM120A* as specific genes where the convergence of rare and common variant associations strongly supports their pathogenic role in the disorder. Importantly, this convergence also implies that the pathogenic relevance of altered function of these genes extends beyond the small proportion of cases carrying rare mutations. We also demonstrate that common variant schizophrenia associations are enriched at genes implicated in neurodevelopmental disorders, opening the door for using the increasing power of rare variant studies of those disorders to further prioritise genes from GWAS studies. Exploiting this, in addition to *GRIN2A* we identify *BCL11B*, *CACNA1C*, *RERE*, *FOXP1*, *MYT1L* and *SLC39A8* as genes with strong support.

Enrichment of common variant associations was restricted to genes expressed in CNS neurons, both excitatory and inhibitory, and fundamental biological processes related to neuronal function. This points to neurons as the most important site of pathology in the disorder. We also show that genes with high relative specificity for expression in almost all tested brain regions are enriched for genetic association. This suggests that abnormal neuronal function in schizophrenia is not confined to a small number of brain structures, which in turn might explain its diverse psychopathology, association with a broad range of cognitive impairments, and lack of regional specificity in neuroimaging measures[1].

Disrupted neuronal function in schizophrenia is unlikely to be restricted to the synapse, but the concentration of associations in genes with pre- and post-synaptic locations, and with functions related to synaptic organisation, differentiation and transmission, point to the pathophysiological importance of these neuronal compartments and their attendant functions. This is further supported by studies showing substantial effects on schizophrenia risk of CNVs[39] and rare damaging coding variants in genes with similar functions, including some of the same genes (SCHEMA; companion paper). Genomic studies, therefore, converge in highlighting these areas of biology as targets for research aiming for a mechanistic understanding of the disorder; the large number of prioritised genes and variants identified here offer an unprecedented empirically-supported resource for that endeavour.

Ethics

The study protocols were approved by the institutional review board at each centre involved with recruitment. Informed consent and permission to share the data were obtained from all subjects, in compliance with the guidelines specified by the recruiting centres' institutional review boards. Genotyping of samples recruited in mainland China were processed and analysed by Chinese groups on Chinese local servers, to comply with the Human Genetic Resources Administrative Regulations.

ONLINE METHODS

Overview of Samples

Details of each of the samples (including sample size, ancestry, and whether included in the previous publication by the PGC) are given in Supplementary Cohort Descriptions. The core PGC dataset included 90 cohorts for which we had individual level genotype data fully processed under a uniform pipeline. This core dataset contains genotypes on 161,405 unrelated subjects; 67,390 schizophrenia/schizoaffective disorder cases and 94,015 controls, equivalent in power to 73,189 of each. A parent-proband trio is considered to comprise one case and one control. Approximately half (31,914 cases and 47,176 controls) of the samples were not included in the previous GWAS of the PGC[1]. Around 80% of the probands (53,386 cases and 77,258 controls) were of European Ancestry, and the remainder (14,004 cases and 16757 controls) were of East Asian ancestry[2]. We additionally included in the Primary GWAS summary statistics from 9 cohorts comprising African-American (AA; 6152 cases 3918 controls) and Latino (1234 cases, 3090 controls) participants; the combined sample is equivalent in power to 6,551 each of cases and controls. 1249 LD – independent ($r^2 > 0.1$) Variants showing evidence for association ($P < 1\times10^{-5}$) were further meta-analysed with an additional dataset of 1,979 cases and 142,626 controls of European ancestry obtained from deCODE genetics, thus the final analysis represents 320,404 diploid genomes.

Association Analysis

Technical Quality Control of the 90 cohorts comprising the primary PGC sample.—Technical Quality control was performed on the core PGC cohorts separately according to standards developed by the PGC[3] including SNP missingness < 0.05 (before sample removal); subject missingness < 0.02; autosomal heterozygosity deviation ($| F_{het} | < 0.2$); SNP missingness < 0.02 (after sample removal); difference in SNP missingness between cases and controls < 0.02; and SNP Hardy-Weinberg equilibrium (HWE: $P > 10^{-6}$ in controls or $P > 10^{-10}$ in cases). For family-based cohorts we excluded individuals with more than 10,000 Mendelian errors and SNPs with more than 4 Mendelian errors. For X-Chromosomal genotypes we applied an additional round of the above QC to the male and female subgroups separately.

Genomic Quality Control: Principal Component Analysis (PCA) and Relatedness Checking in the core PGC dataset—We performed PCA for all 90 cohorts separately using SNPs with high imputation quality (INFO >0.8), low missingness (<1%), MAF>0.05 and in relative linkage equilibrium (LD) after 2 iterations of LD pruning (r2 < 0.2, 200 SNP windows). We removed well known long-range-LD areas (MHC and chr8 inversion). Thus, we retained between 57K and 95K autosomal SNPs in each cohort. SNPs present in all 90 cohorts (N=7,561) were used for robust relatedness testing using PLINK v1.9[4]; pairs of subjects with PIHAT > 0.2 were identified and one member of each pair removed at random, preferentially retaining cases and trio members over case-control members.

To control for false positive associations due to inflated test statistics we evaluated the effectiveness of the primary technical and genomic quality control parameters on the genome-wide inflation of test statistics using the lambda GC (median)[5] and as necessary made the QC parameters more stringent until this value was between 1.0 and 1.4 (before inclusion of principal components as covariates) and/or between 1.0 and 1.15 after inclusion of PCA covariates. Additionally, we applied loose PCA filters for strongly stratified datasets even if we did not observe strong inflation of test statistics in order to retrieve reliable test statistics (see Supplementary Figure 4). Since the core PGC cohorts came from many distinct centres, countries, and continents, various measures (e.g., tightening of the technical QC parameters and/or genomic quality control) had to be taken in an iterative process to achieve this goal.

Supplementary Table 22 lists detailed per cohort exclusion numbers for individuals in the non-Asian samples. The Asian cohorts were sufficiently homogeneous as they did not show marked population structure in principal component analyses. The exclusion numbers for individuals during technical QC are in most cohorts low. For six cohorts (marked in yellow in Supplementary Table 22) it was necessary to exclude more than 100 cases during genomic QC so that Lambda GC fell within the window mentioned above. Supplementary Figure 4 gives details about this process and explains why the excluded cases could not be used with the presently available control cohorts for this manuscript.

Imputation of the core PGC dataset—Genotype imputation of case-control cohorts was performed using the pre-phasing/imputation stepwise approach implemented in EAGLE 2[6] / MINIMAC3[7] (with 132 genomic windows of variable size and default parameters). The imputation reference consisted of 54,330 phased haplotypes with 36,678,882 variants from the publicly available HRC reference, release 1.1[8] Chromosome X imputation was conducted using individuals passing quality control for the autosomal analysis. ChrX imputation and association analysis was performed separately for males and females. For trio-based cohorts, families with multiple (N) affected offspring were split into N parent-offspring trios, duplicating the parental genotype information. Trios were phased with SHAPEIT 3[9]. We created pseudo-controls based on the non-transmitted alleles from the parents. Phased case-pseudo-control genotypes were then taken forward to the IMPUTE4 algorithm[10] into the above HRC reference panel.

Association / Meta-analysis—In each individual cohort, association testing was based on an additive logistic regression model using PLINK[11]. As covariates we used a subset of the first 20 principal components (PCA), derived within each cohort. By default, we included the first 4 PCAs and thereafter every PCA that was nominally significantly associated ($p<0.05$) to case-control status. PCAs in trios were only used to remove extreme ancestry outliers. We conducted a meta-analysis of the results (including the 9 cohorts comprising African-American and Latino participants) using a standard error inverse-weighted fixed effects model. For chrX, gene dosages in males were scored 0 or 2, in females, 0/1/2. We summarised the associations as number of independently associated index SNPs. Index SNPs were LD independent and had $r2 < 0.1$ within 3 Mb windows. We recorded the left and rightmost variant with $r2<0.1$ to an index SNP to define an associated clump. To define loci, we added a 50kb window on each side of the LD clump and combined overlapping LD-clumps into a single locus.

Due to the strong signal and high linkage disequilibrium in the MHC, only one SNP was kept from the extended MHC region (chr6:25–35Mb).

We additionally examined the X chromosome for evidence of heterogeneity between the sexes and X chromosome dosage compensation using the methods described by Lee and colleagues[12,13] (Supplementary Note). To minimise possible confounding effects of ancestry on effect sizes by sex, we restricted this analysis to those of European ancestry.

We obtained summary association results from deCODE genetics for 1,228 index SNPs ($P < 1\times10^{-5}$) based on 1,979 cases and 142,626 controls of European ancestry. Genotyping was carried out at deCODE Genetics. We used this sample to establish that SNP associations from the primary GWAS replicated *en masse* in an independent sample (see Supplementary Note) by showing the directions of effect of index SNPs differed from the null hypothesis of randomly oriented effects and also comparing the expected number of same direction effects with those if all associations were true, taking into account the discovery magnitude of effect, and the replication effect-estimate precision (Supplementary Note).

The summary statistics from deCODE were combined with those from our primary GWAS dataset using an inverse variance-weighted fixed effects model. Similarly to the discovery meta-analysis (see above) we merged overlapping LD-clumps to a total of 287 distinct genomic regions (5 on the X-chromosome) with at least one genome-wide significant signal.

Polygenic Prediction

We estimated the cumulative contribution of SNPs to polygenic risk of schizophrenia using a series of leave-one-out polygenic prediction analyses based on LD-clumping and P-value thresholding (P+T)[14] (also known as C+T) using PLINK[11]. For calculating polygenic scores, we included the most significant SNP for any pair of SNPs within <500kb and with LD R^2 >0.1. We included only those with minor allele frequency >1%. We considered a range of P-value thresholds; 5×10^{-8}, 1×10^{-6}, 1×10^{-4}, 1×10^{-3}, 1×10^{-2}, 5×10^{-2}, 1×10^{-1}, 2×10^{-1}, 5×10^{-1} and 1.0. We performed logistic regression analysis within each case-control sample, to assess the relationship between case status and PRS (P+T) quantiles. The same principal components used for each GWAS were used as covariates for this analysis. Whenever the number of controls at a quantile was fewer than 5 times the number of covariates[15], or if the higher bound for the PRS Odds Ratio (OR) became infinity, Firth's penalised likelihood method was used to compute regression statistics, as implemented in the R package "logistf"[16]. ORs from these calculations were then meta-analysed using a fixed-effects model in the R package "metafor"[17]. To ensure stability of the estimates, meta-analysis was conservatively restricted to case-control samples which contained more than 10 individuals in the top 1% PRS, with at least one of them being a control. Analogous analyses were conducted to assess the ORs between individuals at the top and bottom quantiles. To assess the performance of PRS as a predictor of schizophrenia case status, we calculated liability R^2, Nagelkerke's R^2 following Lee et. al. 2012[18] and a combined area under the receiver operating characteristic curve (AUROC). Both liability R^2 and Nagelkerke's R^2 included any principal components marginally associated with the outcome within each cohort, in the baseline model. AUROC was estimated using the non-parametric meta-analysis implemented in the R package "nsROC"[19]. Polygenic score analysis of the African-American and Latino cohorts were conducted by the authors of the study reporting those datasets[20].

Secondary analyses in core PGC dataset

Some of the secondary analyses (Gene-set enrichments, conditional SNP association analyses, fine-mapping) necessitate access to individual level data, require identical QC and imputation procedures, and/or an accurate LD reference panel meaning these analyses could only be reliably performed in a subset of the dataset. The following analyses focussed on the core PGC dataset for which these conditions are met.

Gene Set Enrichments

Tissue and cell types: We collected bulk RNA-seq data across 53 human tissues (GTEx v8, median across samples)[21]; from a study of 19,550 nuclei from frozen adult human post-mortem hippocampus and prefrontal cortex representing 16 different cell types[22]; from a study of ~10,000 single cells from 5 mouse brain regions (cortex, hippocampus, hypothalamus, midbrain and striatum, in addition to specific enrichments for oligodendrocytes, dopaminergic neurons, serotonergic neurons and cortical parvalbuminergic interneurons) that identified 24 cell types[23]; from a study of~500,000 single cells from the mouse nervous system (19 regions) that identified 265 cell types[24].

Datasets were processed uniformly[25]. First, we calculated the mean expression for each gene for each type of data if these statistics were not provided by the authors. We used the pre-computed median expression (transcript per million (TPM)) across individuals for the GTEx tissues (v8). For the GTEx dataset, we excluded tissues with less than 100 samples, merged tissues by organ (with the exception of brain tissues), excluded non-natural tissues (e.g. EBV-transformed lymphocytes) and testis (outlier in hierarchical clustering), resulting in 37 tissues. Genes without unique names and genes not expressed in any cell types were excluded. We scaled the expression data to 1M Unique Molecular Identifiers (UMIs) or TPM for each cell type/tissue. After scaling, we excluded non-protein coding genes, and, for mouse datasets, genes that had no expert curated 1:1 orthologs between mouse and human (Mouse Genome Informatics, The Jackson laboratory, version 11/22/2016). We then calculated a metric of gene expression specificity by dividing the expression of each gene in each cell type/tissue by the total expression of that gene in all cell types/tissue, leading to values ranging from 0 to 1 for each gene (0: meaning that the gene is not expressed in that cell type/tissue, 1 that 100% of the expression of that gene is performed in that cell type/tissue). We selected the 10% most specific genes per cell type (or tissue) with an expression level of at least 1TPM, or 1 UMI per million, for downstream analyses and used MAGMA v1.08[26] to test whether they were enriched for genetic associations. We performed a one-sided test as we were only interested in enrichments for genetic associations (in contrast with depletions). We also applied partitioned LD score regression (LDSC) as described[27] to the top 10% genes for each cell type for heritability enrichment. We selected the one-sided coefficient z-score p-value as a measure of the association of the cell type/tissue with schizophrenia.

Ontology Gene sets: Gene set analyses were performed using MAGMA v1.08[26]. Gene boundaries were retrieved from Ensembl release 92 (GRCh37) using the "biomaRt" R package[28] and expanded by 35 kb upstream and 10 kb downstream to include likely regulatory regions[29]. Gene-wide p-values were calculated from European and Asian summary statistics separately using the SNP-wise "mean" Imhof method, and meta-analysed within the software. LD reference data files were from the European and East Asian populations of the Haplotype Reference Consortium[30]. Within each gene set analysis, p-values were corrected for multiple testing using the Bonferroni procedure. Specifically, we tested the following gene sets:

i. Gene ontology: 7,315 sets extracted from the GO database (http://geneontology.org/, accession date: 09/11/2020) curated to include only annotations with experimental or phylogenetic supporting evidence.

ii. SynGO ontology: Described elsewhere[31], this collection was analysed as two subsets; "biological process" (135 gene sets) and "cellular component" (60 gene sets). We controlled for a set of 10,360 genes with detectable expression in brain tissue measured as Fragments Per Kilobase of transcript per Million mapped reads (FPKM)[32] to detect synaptic signals above signals simply reflecting the property of brain expression. Exploiting the hierarchical structure of SynGO, gene sets were reconstructed using a “roll-up” method, in which parent categories contained all genes annotated to child categories. For stepwise conditional testing[33], we prioritised the most specific child annotations[34] (i.e. the lowest possible level) as regression covariates.

Conditional SNP Association Analyses—We performed stepwise conditional analyses of 248 loci that were genome wide significant in the core PGC dataset looking for independent associations. We performed association testing and meta-analysis across each locus, adding the allele dosages of the index SNP as a covariate. Where a second SNP had a conditional p-value of less than 1×10^{-6}, we considered this as evidence for a second signal and repeated the process adding this as an additional covariate. We repeated this until no additional SNPs in the region achieved $p<1\times10^{-6}$. We also searched for long range dependencies. Here we tested the all pairs of independent signals for conditional independence (Supplementary Note).

Fine-mapping—We used FINEMAP[35] to fine-map regions defined by LD clumps ($r^2>0.1$), excluding the MHC locus due to its complex LD structure. Clumps which overlapped (without adding the additional 50kb used to define physically distinct loci) were combined. As fine-mapping requires data from all markers in the region[36] we only performed fine-mapping on regions that attained genome-wide significance (GWS) in the core PGC GWAS. In total, we attempted to fine-map 255 non-overlapping regions (Supplementary Table 11e). Further details about the fine-mapping process are given in the Supplementary Note.

Summary-data-based Mendelian Randomization (SMR) analysis, FUSION and EpiXcan—We used SMR[37] as our primary method to identify SNPs which might mediate association with schizophrenia through effects on gene expression. The significance for SMR is set at the Bonferroni corrected threshold of 0.05/M where M is the number of genes with significant eQTLs tested for a given tissue. Significant SMR associations imply colocalization of the schizophrenia associations with eQTL. We applied the HEIDI test[37] to filter out SMR associations ($P_{\text{HEIDI}} < 0.01$) due to linkage disequilibrium between SCZ-associated variants and eQTLs. *cis*-eQTL summary data were from three studies: fetal brain (N=120)[38], adult brain (n = ~1,500)[39] and blood (n = ~32,000)[40]. Linkage disequilibrium (LD) data required for the HEIDI test[37] were estimated from the Health and Retirement Study (HRS)[41] (n = 8,557). We included only genes with at least one *cis*-eQTL at $P_{\text{eQTL}} < 5\times10^{-8}$, excluding those in MHC regions due to the complexity of this region. For blood, we included only genes with eQTLs in brain. This left 7,803 genes in blood, 10,890 genes in prefrontal cortex and 754 genes in fetal brain for analysis (see Supplementary Note for further details). SMR was performed using data from the primary GWAS. The results were then filtered to exclude significant SMR implicated genes where the eQTLs did not map within our definition of an associated locus in the Extended GWAS meta-analysis of our primary GWAS dataset and the dataset provided by deCODE genetics.

For genomic regions where there were multiple genes showing significant SMR associations, we attempted to resolve these with conditional analysis using GCTA-

COJO[42,43]. We selected the top-associated *cis*-eQTL for one gene (or a set of genes sharing the same *cis*-eQTL) ran a COJO analysis in the schizophrenia GWAS data and the eQTL data for each of the other genes conditioning on the selected top *cis*-eQTL. We then re-ran the SMR and HEIDI analyses using these conditional GWAS and eQTL results.

We used FUSION[44] and EpiXcan[45] as tests of robustness of the SMR results. Details are supplied in the Supplementary Note as are our approaches to prioritising SMR associated genes.

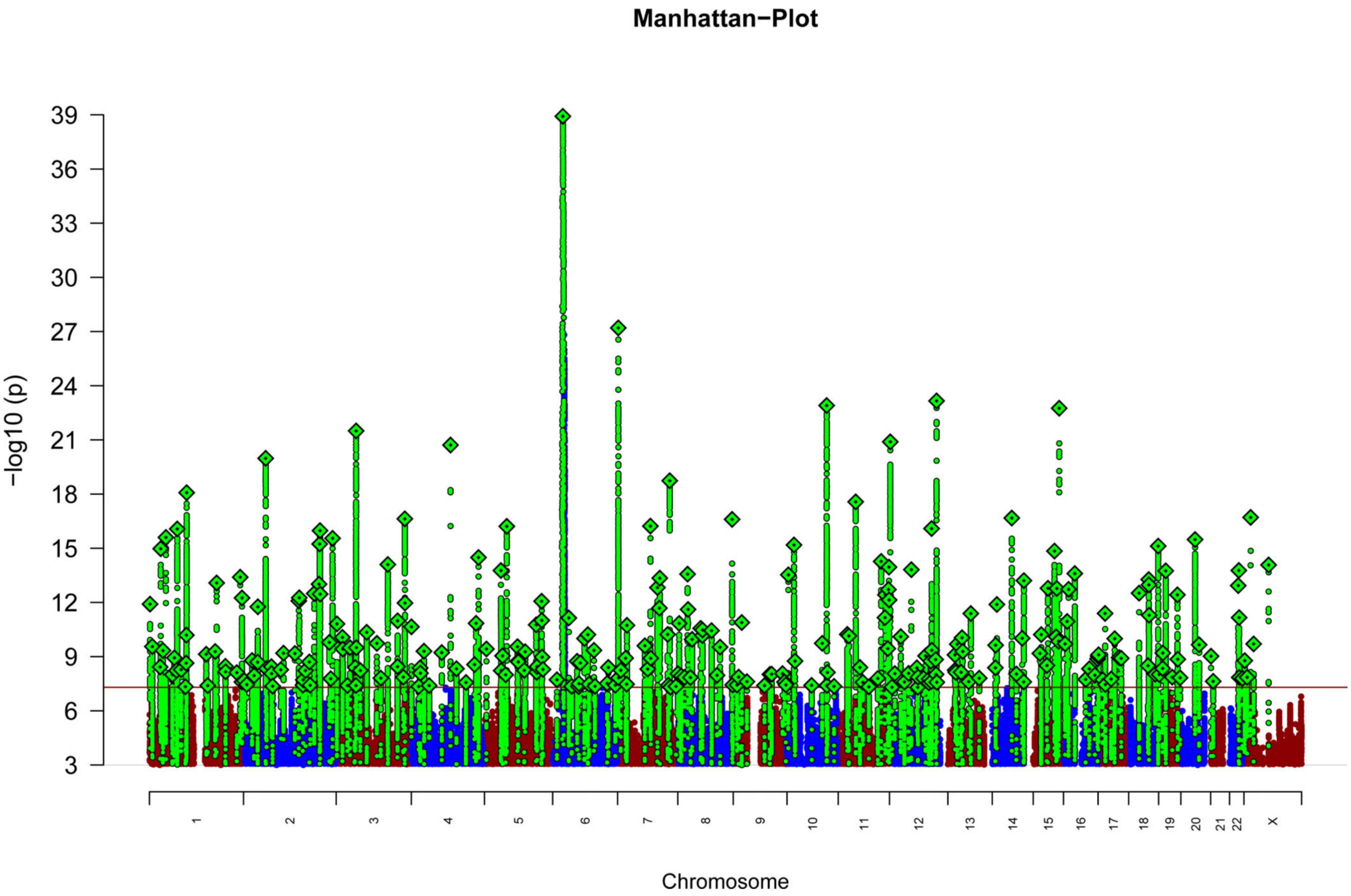
DATA AVAILABILITY

Summary statistics for the “Extended”, “Core”, ancestry specific and sex-stratified analyses is available at “https://www.med.unc.edu/pgc/download-results/scz/”. Genotype data are available for a subset of cohorts, including dbGAP accession numbers and/or restrictions, as described in the Supplementary Information section “Cohort Descriptions”.

CODE AVAILABILITY

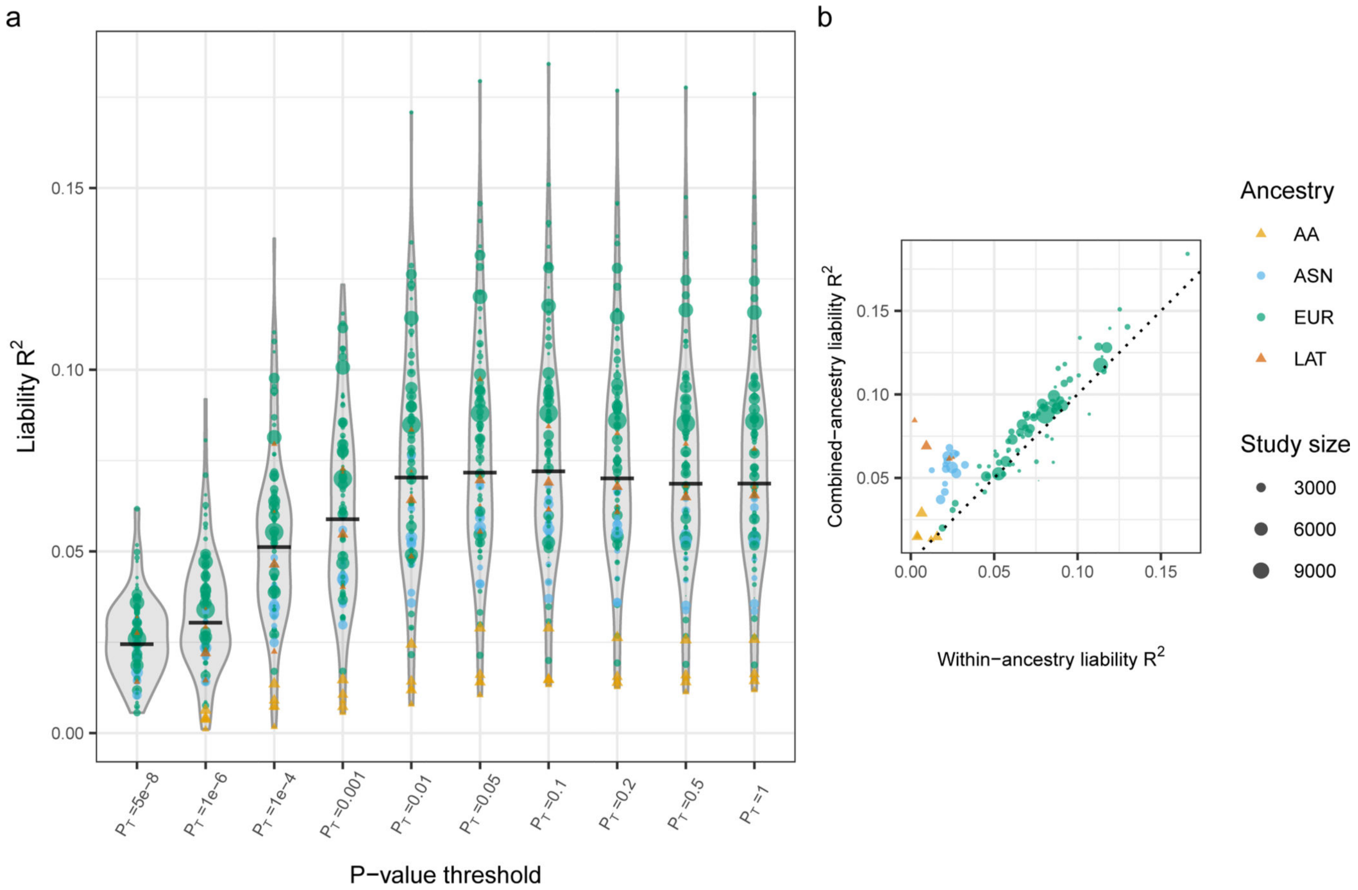
Core analysis code for RICOPILI can be found at “https://sites.google.com/a/broadinstitute.org/ricopili/”. This wraps PLINK (“https://www.cog-genomics.org/plink2/”), EIGENSOFT (“https://www.hsph.harvard.edu/alkes-price/software/”), EAGLE2 (“https://alkesgroup.broadinstitute.org/Eagle/”), MINIMAC3 (“https://genome.sph.umich.edu/wiki/Minimac3”), SHAPEIT3 (“https://mathgen.stats.ox.ac.uk/genetics_software/shapeit/shapeit.html”), METAL (“https://genome.sph.umich.edu/wiki/METAL_Documentation”), LDSR (“https://github.com/bulik/ldsc”). For downstream analyses, FINEMAP can be found at “http://christianbenner.com/”, and our utility for meta-analysing cohort-specific LD matrices can be found at https://github.com/Pintaius/LDmergeFM. MAGMA can be found at ”https://ctg.cncr.nl/software/magma” and the GO gene sets and automated curation pipeline are provided in https://github.com/janetcharwood/pgc3-scz_wg-genesets. SMR is available at “https://cnsgenomics.com/software/smr/” and SbayesS at “https://cnsgenomics.com/software/gctb/”.

Extended Data



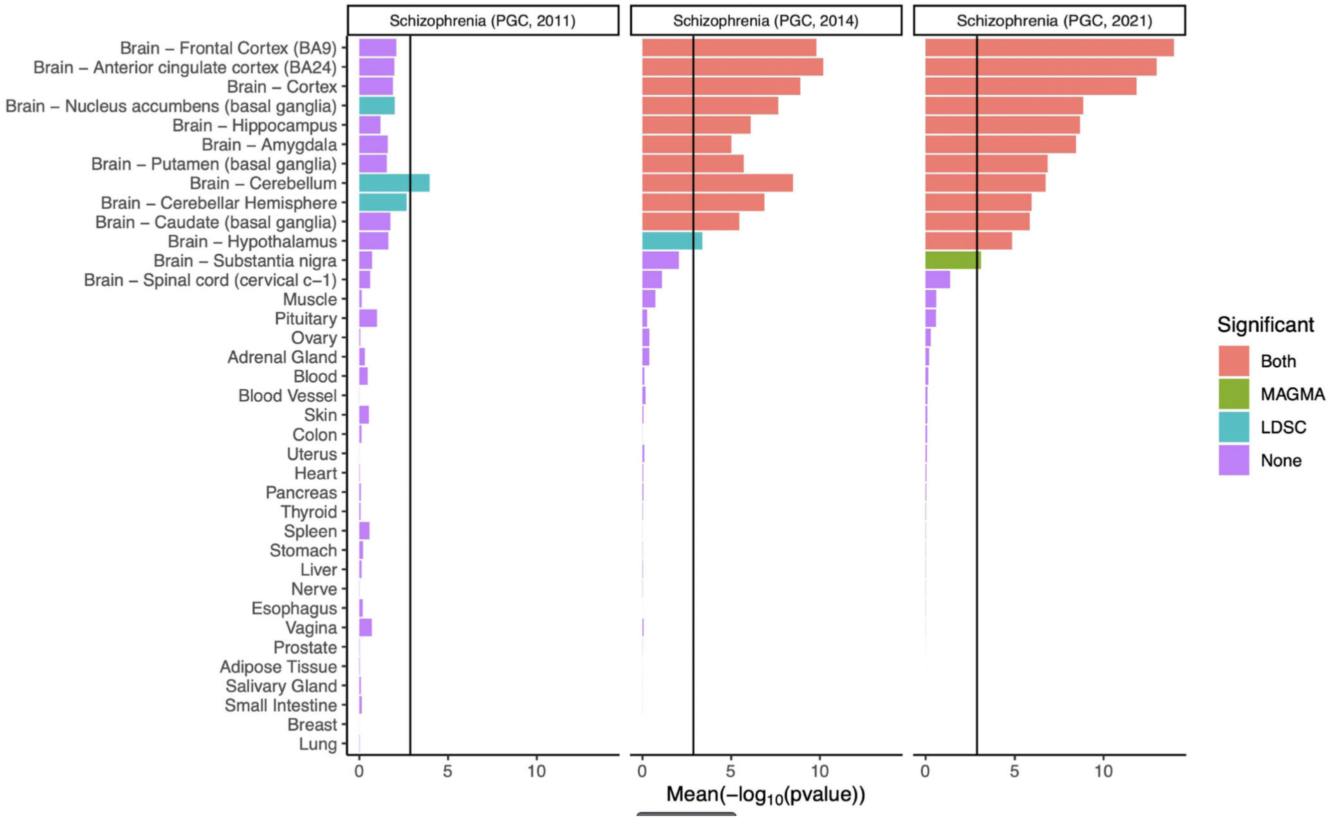
Extended Data Figure 1: Primary GWAS Manhattan plot

The x-axis indicates chromosomal position and the y-axis is the significance of association (−log10(P)). The red line represents genome-wide significance level (5×10−8). SNPs in green are in linkage disequilibrium (LD; R2 >0.1) with index SNPs (diamonds) which represent LD independent genome-wide significant associations.



Extended Data Figure 2: Polygenic risk prediction

A) Distributions of liability scale R^2 across 98 left-out-cohorts for polygenic risk scores built from SNPs with different p-value thresholds. Distributions of liability R^2 (assuming schizophrenia life-time risk of 1%) are shown for each p-value threshold, with point size representing size of the left-out cohort and colour representing ancestry. The median liability R^2 is represented as a horizontal black line. B) Liability R^2 of predicted and observed phenotypes in left-out cohorts using variants with p-value threshold p=0.05, from the fixed effect meta-analysis of variant effects, unadjusted for multiple comparisons. The polygenic risk scores are derived from two separate sets of leave-one-out GWAS meta-analyses: y-axis R^2 based on the results of primary GWAS including all ancestries; x axis R^2 based on cohorts of the same ancestry as the test samples. Circles denote core PGC samples. Triangles denote African American and Latino samples processed external to PGC by the providing author.



Extended Data Figure 3: Association between 37 human tissues and schizophrenia.

The mean of the evidence (-$\log_{10}$P) obtained from two methods (MAGMA, LDSC) for testing GWAS data for enrichment of association in genes with high expression in each tissue as determined from bulk RNA-seq[20]. The bar colour indicates whether gene expression in the tissue is significantly associated with both methods, one method or none. The black vertical line represents the significance threshold corrected for the total number of tissues tested in this experiment. We also analysed previous waves of PGC schizophrenia GWAS[11,21] for comparison.

Extended Data Table1:

List of prioritized genes

List of genes meeting prioritisation criteria summarised in Figure 1. Index SNP: index associated SNP for the locus from the GWAS. Ensembl ID: Ensembl gene identifier. Symbol ID: HGNC gene symbol. Gene Biotype: as classified by Ensembl. FINEMAP and SMR priority genes: genes meeting the prioritisation criteria described in the text. Rare priority genes: genes implicated by rare coding variants in schizophrenia, autism spectrum disorders or developmental disorder. Full details regarding the prioritisation criteria for each gene are given inSupplementary Tables 11–18.

Index SNP	Ensembl ID	Symbol ID	gene_biotype	FINEMAP priority gene	SMR priority gene	Rare priority gene
rs12712510	ENSG00000231200	AC068490.2	lincRNA	•		
rs6504163	ENSG00000159640	ACE	protein_coding		•	
rs7575796	ENSG00000115073	ACTR1B	protein_coding	•		
rs61833239	ENSG00000117020	AKT3	protein_coding		•	
rs6546857	ENSG00000163016	ALMS1P	pseudogene		•	
rs9925915	ENSG00000174939	ASPHD1	protein_coding		•	
rs12285419	ENSG00000175224	ATG13	protein_coding		•	
rs4766428	ENSG00000174437	ATP2A2	protein_coding	•		
rs1540840	ENSG00000127152	BCL11B	protein_coding	•		•
rs2304205	ENSG00000126453	BCL2L12	protein_coding	•		
rs3808581	ENSG00000104765	BNIP3L	protein_coding	•		
rs2649999	ENSG00000157895	C12orf43	protein_coding	•		
rs10774034	ENSG00000151067	CACNA1C	protein_coding	•		•
rs2944821	ENSG00000183166	CALN1	protein_coding	•		
rs6839635	ENSG00000145354	CISD2	protein_coding		•	
rs61405217	ENSG00000109572	CLCN3	protein_coding		•	
rs17194490	ENSG00000144619	CNTN4	protein_coding	•		
rs10127983	ENSG00000143578	CREB3L4	protein_coding		•	
rs2532240	ENSG00000120088	CRHR1	protein_coding		•	
8:4180090_T_A	ENSG00000183117	CSMD1	protein_coding	•		
rs715170	ENSG00000206129	CTD-2008L17.2	lincRNA	•		
rs113113059	ENSG00000112659	CUL9	protein_coding	•	•	
rs10957321	ENSG00000172817	CYP7B1	protein_coding		•	
rs61828917	ENSG00000117593	DARS2	protein_coding		•	
rs4632195	ENSG00000187323	DCC	protein_coding	•		
rs4678552	ENSG00000163673	DCLK3	protein_coding		•	
rs7816998	ENSG00000085788	DDHD2	protein_coding		•	
rs2600490	ENSG00000198010	DLGAP2	protein_coding	•		
rs8048039	ENSG00000103423	DNAJA3	protein_coding		•	
rs72728416	ENSG00000188641	DPYD	protein_coding	•		
rs8175378	ENSG00000170571	EMB	protein_coding		•	

Index SNP	Ensembl ID	Symbol ID	gene_biotype	FINEMAP priority gene	SMR priority gene	Rare priority gene
rs999494	ENSG00000135638	EMX1	protein_coding	•		
rs11619756	ENSG00000120658	ENOX1	protein_coding	•		
rs959071	ENSG00000262319	ENSG00000262319	antisense		•	
rs4073003	ENSG00000072134	EPN2	protein_coding	•		
rs6925079	ENSG00000188107	EYS	protein_coding	•		
rs815609	ENSG00000055147	FAM114A2	protein_coding		•	
rs4766428	ENSG00000204856	FAM216A	protein_coding		•	
rs1006945	ENSG00000101447	FAM83D	protein_coding		•	
rs58120505	ENSG00000122687	FTSJ2	protein_coding		•	
rs4702	ENSG00000140564	FURIN	protein_coding	•	•	
rs10985811	ENSG00000136928	GABBR2	protein_coding	•		
rs1858999	ENSG00000167491	GATAD2A	protein_coding		•	
rs12498839	ENSG00000150625	GPM6A	protein_coding	•		
rs12188094	ENSG00000164199	GPR98	protein_coding	•		
rs77502336	ENSG00000023171	GRAMD1B	protein_coding	•		
rs9926049	ENSG00000183454	GRIN2A	protein_coding	•		•
rs2206956	ENSG00000152822	GRM1	protein_coding	•		
rs11210892	ENSG00000178922	HYI	protein_coding		•	
rs1378559	ENSG00000169306	IL1RAPL1	protein_coding	•		
rs38752	ENSG00000184903	IMMP2L	protein_coding	•		
rs3814883	ENSG00000169592	INO80E	protein_coding		•	
rs2304205	ENSG00000126456	IRF3	protein_coding	•		
rs2532240	ENSG00000120071	KANSL1	protein_coding		•	•
rs10243922	ENSG00000122778	KIAA1549	protein_coding	•		
rs17731	ENSG00000067082	KLF6	protein_coding	•		
rs459391	ENSG00000224924	LINC00320	lincRNA	•	•	
rs9545047	ENSG00000227676	LINC01068	lincRNA		•	
rs28454198	ENSG00000249307	LINC01088	antisense	•		
rs2387414	ENSG00000131409	LRRC4B	protein_coding	•		
rs59498392	ENSG00000175324	LSM1	protein_coding		•	
rs58120505	ENSG00000002822	MAD1L1	protein_coding	•		
rs35164357	ENSG00000112893	MAN2A1	protein_coding	•		
rs9925915	ENSG00000102882	MAPK3	protein_coding		•	
rs2532240	ENSG00000186868	MAPT	protein_coding		•	
rs143116451	ENSG00000175727	MLXIP	protein_coding		•	
rs2914983	ENSG00000115540	MOB4	protein_coding		•	
rs4793888	ENSG00000153944	MSI2	protein_coding	•		
rs11263770	ENSG00000141140	MYO19	protein_coding		•	
rs324017	ENSG00000166886	NAB2	protein_coding	•		
rs9545047	ENSG00000102471	NDFIP2	protein_coding		•	

Index SNP	Ensembl ID	Symbol ID	gene_biotype	FINEMAP priority gene	SMR priority gene	Rare priority gene
rs2119242	ENSG00000078114	NEBL	protein_coding	•		
rs1121296	ENSG00000172260	NEGR1	protein_coding	•		
rs5943629	ENSG00000146938	NLGN4X	protein_coding	•		
rs9975024	ENSG00000180530	NRIP1	protein_coding	•		
rs11972718	ENSG00000122584	NXPH1	protein_coding	•		
rs1939514	ENSG00000183715	OPCML	protein_coding	•		
rs56205728	ENSG00000137843	PAK6	protein_coding	•		
rs7432375	ENSG00000114054	PCCB	protein_coding		•	
rs10069930	ENSG00000204969	PCDHA2	protein_coding		•	
rs246024	ENSG00000204962	PCDHA8	protein_coding		•	
rs35734242	ENSG00000185619	PCGF3	protein_coding	•		
rs58950470	ENSG00000197136	PCNXL3	protein_coding	•		
rs6588168	ENSG00000184588	PDE4B	protein_coding	•		
rs2929278	ENSG00000167004	PDIA3	protein_coding		•	
rs34539323	ENSG00000181191	PJA1	protein_coding	•		
rs6673880	ENSG00000149527	PLCH2	protein_coding	•		
rs3813567	ENSG00000041357	PSMA4	protein_coding		•	
rs2890914	ENSG00000153707	PTPRD	protein_coding	•		
rs61937595	ENSG00000179912	R3HDM2	protein_coding	•		
rs11121172	ENSG00000142599	RERE	protein_coding		•	•
rs11227250	ENSG00000172922	RNASEH2C	protein_coding		•	
rs13107325	ENSG00000246560	RP11–10L12.4	antisense		•	
rs6479487	ENSG00000227603	RP11–165J3.6	antisense		•	
rs505061	ENSG00000234840	RP11–399D6.2	lincRNA	•		
rs1198588	ENSG00000259946	RP11–490G2.2	lincRNA		•	
rs35351411	ENSG00000259616	RP11–507B12.2	lincRNA	•		
rs10035564	ENSG00000272335	RP11–53O19.3	lincRNA		•	
rs1915019	ENSG00000253553	RP11–586K2.1	antisense		•	
rs10873538	ENSG00000256500	RP11–73M18.2	protein_coding		•	
rs154433	ENSG00000103037	SETD6	protein_coding		•	
rs2914983	ENSG00000115524	SF3B1	protein_coding		•	
rs12652777	ENSG00000170624	SGCD	protein_coding	•		
rs13107325	ENSG00000138821	SLC39A8	protein_coding	•		•
rs2909457	ENSG00000144290	SLC4A10	protein_coding	•		
rs6839635	ENSG00000164037	SLC9B1	protein_coding		•	
rs2022265	ENSG00000065609	SNAP91	protein_coding	•	•	
rs7811417	ENSG00000105866	SP4	protein_coding	•		•
rs3810450	ENSG00000161277	THAP8	protein_coding	•		
rs704364	ENSG00000163634	THOC7	protein_coding		•	
rs7312697	ENSG00000133687	TMTC1	protein_coding	•		

Index SNP	Ensembl ID	Symbol ID	gene_biotype	FINEMAP priority gene	SMR priority gene	Rare priority gene
rs1924377	ENSG00000133107	TRPC4	protein_coding	•		
rs13262595	ENSG00000171045	TSNARE1	protein_coding	•		
rs10861176	ENSG00000198431	TXNRD1	protein_coding	•		
rs10238960	ENSG00000185274	WBSCR17	protein_coding	•		
rs2929278	ENSG00000092470	WDR76	protein_coding		•	
rs3764002	ENSG00000075035	WSCD2	protein_coding	•		
rs11693094	ENSG00000170396	ZNF804A	protein_coding	•		
rs72986630	ENSG00000197933	ZNF823	protein_coding	•	•	
rs758749	ENSG00000127903	ZNF835	protein_coding	•		

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Authors

Vassily Trubetskoy[#],
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Georgia Panagiotaropoulou,
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Swapnil Awasthi,
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Alice Braun,
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Julia Kraft,
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Nora Skarabis,
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Henrik Walter,
Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Stephan Ripke,

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Antonio F. Pardiñas[#],
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Charlotte A. Dennison,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Lynsey S. Hall,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Janet C. Harwood,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Alexander L. Richards,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Sophie E. Legge,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Amy Lynham,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Nigel M. Williams,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Nicholas J. Bray,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Valentina Escott-Price,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

George Kirov,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Peter A. Holmans,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Andrew J. Pocklington,

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Michael J. Owen,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

James T. R. Walters,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Michael C. O'Donovan,
MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Ting Qi,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Julia Sidorenko,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Yang Wu,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Jian Zeng,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Jacob Gratten,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Peter M. Visscher,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Jian Yang,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Naomi R. Wray,
Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Ting Qi,
School of Life Sciences, Westlake University, Hangzhou, China

Jian Yang,
School of Life Sciences, Westlake University, Hangzhou, China

Tim B. Bigdeli,
Department of Psychiatry and the Behavioral Sciences, SUNY Downstate Medical Center, New York, NY, USA

Department of Psychiatry, Veterans Affairs New York Harbor Healthcare System, New York, NY, USA

Institute for Genomic Health, SUNY Downstate Medical Center, New York, NY, USA

Ayman H. Fanous,
Department of Psychiatry, Veterans Affairs New York Harbor Healthcare System, New York, NY, USA

Julien Bryois,
Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Sarah E. Bergen,
Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Anna K. Kähler,
Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Patrik K. E. Magnusson,
Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Christina M. Hultman,
Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Patrick F. Sullivan,
Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Chia-Yen Chen,
Biogen, Cambridge, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Psychiatric and Neurodevelopmental Genetics Unit, Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA

Elizabeth G. Atkinson,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Jacqueline I. Goldstein,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Daniel P. Howrigan,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Alicia R. Martin,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Mark J. Daly,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Hailiang Huang,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Benjamin M. Neale,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Stephan Ripke,
Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Tian Ge,
Psychiatric and Neurodevelopmental Genetics Unit, Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA

Max Lam,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Tian Ge,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Elizabeth G. Atkinson,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Richard A. Belliveau,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Kimberley D. Chambert,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Giulio Genovese,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Phil H. Lee,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Alicia R. Martin,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Olli Pietiläinen,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Steven A. McCarroll,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Jennifer L. Moran,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Jordan W. Smoller,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Tyler C. Brown,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Guoping Feng,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Steven E. Hyman,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Morgan Sheng,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Steven E. Hyman,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Hailiang Huang,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Benjamin M. Neale,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Max Lam,
Research Division, Institute of Mental Health, Singapore, Republic of Singapore

Siow Ann Chong,
Research Division, Institute of Mental Health, Singapore, Republic of Singapore

Mythily Subramaniam,
Research Division, Institute of Mental Health, Singapore, Republic of Singapore

Max Lam,
Division of Psychiatry Research, Zucker Hillside Hospital, Glen Oaks, NY, USA

Todd Lencz,
Division of Psychiatry Research, Zucker Hillside Hospital, Glen Oaks, NY, USA

Anil K. Malhotra,
Division of Psychiatry Research, Zucker Hillside Hospital, Glen Oaks, NY, USA

Kyoko Watanabe,
Department of Complex Trait Genetics, Center for Neurogenomics and Cognitive Research, Amsterdam Neuroscience, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

Oleksandr Frei,
NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

Ingrid Agartz,
NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

Lavinia Athanasiu,
NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

Ingrid Melle,
NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

Ole A. Andreassen,
NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

Oleksandr Frei,
Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Lavinia Athanasiu,
Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Ingrid Melle,
Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Nils Eiel Steen,
Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Ole A. Andreassen,
Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Oleksandr Frei,
Center for Bioinformatics, Department of Informatics, University of Oslo, Oslo, Norway

Tian Ge,
Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Lynn E. DeLisi,
Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Raquelle I. Mesholam-Gately,
Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Larry J. Seidman,
Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Frank Koopmans,
Department of Molecular and Cellular Neurobiology, Center for Neurogenomics and Cognitive Research, Faculty of Science, Amsterdam Neuroscience, Vrije Universiteit, Amsterdam, The Netherlands

Sigurdur Magnusson,
deCODE Genetics, Amgen, Reykjavik, Iceland

Hreinn Stefánsson,
deCODE Genetics, Amgen, Reykjavik, Iceland

Kari Stefansson,
deCODE Genetics, Amgen, Reykjavik, Iceland

Jakob Grove,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Esben Agerbo,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

National Centre for Register-based Research, Aarhus University, Aarhus, Denmark

Thomas D. Als,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Jonas Bybjerg-Grauholm,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Ditte Demontis,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

David M. Hougaard,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Ole Mors,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Preben B. Mortensen,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

National Centre for Register-based Research, Aarhus University, Aarhus, Denmark

Merete Nordentoft,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Anders D. Børglum,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Jakob Grove,
Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Thomas D. Als,
Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Ditte Demontis,
Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Manuel Mattheisen,
Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Anders D. Børglum,
Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Jakob Grove,
Center for Genomics and Personalized Medicine, Aarhus, Denmark

Thomas D. Als,
Center for Genomics and Personalized Medicine, Aarhus, Denmark

Ditte Demontis,
Center for Genomics and Personalized Medicine, Aarhus, Denmark

Anders D. Børglum,
Center for Genomics and Personalized Medicine, Aarhus, Denmark

Minsoo Kim,
Department of Psychiatry, Semel Institute, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Michael J. Gandal,
Department of Psychiatry, Semel Institute, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Zhiqiang Li,
Affiliated Hospital of Qingdao University and Biomedical Sciences Institute of Qingdao University (Qingdao Branch of SJTU Bio-X Institutes), Qingdao University, Qingdao, China

Yongyong Shi,
Affiliated Hospital of Qingdao University and Biomedical Sciences Institute of Qingdao University (Qingdao Branch of SJTU Bio-X Institutes), Qingdao University, Qingdao, China

Yongyong Shi,
Affiliated Hospital of Qingdao University and Biomedical Sciences Institute of Qingdao University (Qingdao Branch of SJTU Bio-X Institutes), Qingdao University, Qingdao, China

Zhiqiang Li,
Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Wei Zhou,
Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Shengying Qin,
Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Yongyong Shi,
Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Yongyong Shi,
Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Georgios Voloudakis,
Department of Psychiatry, Pamela Sklar Division of Psychiatric Genomics, Friedman Brain Institute, Department of Genetics and Genomic Science and Institute for Data

Science and Genomic Technology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Wen Zhang,
Department of Psychiatry, Pamela Sklar Division of Psychiatric Genomics, Friedman Brain Institute, Department of Genetics and Genomic Science and Institute for Data Science and Genomic Technology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Panos Roussos,
Department of Psychiatry, Pamela Sklar Division of Psychiatric Genomics, Friedman Brain Institute, Department of Genetics and Genomic Science and Institute for Data Science and Genomic Technology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Wen Zhang,
Department of Genetics and Genomic Sciences and Institute for Genomics and Multiscale Biology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Mark Adams,
Division of Psychiatry, Centre for Clinical Brain Sciences, University of Edinburgh, Royal Edinburgh Hospital, Edinburgh, UK

Andrew McIntosh,
Division of Psychiatry, Centre for Clinical Brain Sciences, University of Edinburgh, Royal Edinburgh Hospital, Edinburgh, UK

Ingrid Agartz,
Department of Psychiatric Research, Diakonhjemmet Hospital, Oslo, Norway

Ingrid Agartz,
Centre for Psychiatry Research, Department of Clinical Neuroscience, Karolinska Institutet and Stockholm Health Care Services, Stockholm Region, Stockholm, Sweden

Erik Söderman,
Centre for Psychiatry Research, Department of Clinical Neuroscience, Karolinska Institutet and Stockholm Health Care Services, Stockholm Region, Stockholm, Sweden

Erik G. Jönsson,
Centre for Psychiatry Research, Department of Clinical Neuroscience, Karolinska Institutet and Stockholm Health Care Services, Stockholm Region, Stockholm, Sweden

John J. McGrath,
National Centre for Register-based Research, Aarhus University, Aarhus, Denmark

Mariam Al Eissa,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Nicholas J. Bass,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Alessia Fiorentino,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Niamh Louise O’Brien,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Jonathan Pimm,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Sally Isabel Sharp,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Andrew McQuillin,
Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Margot Albus,
Comedicum Lindwurmhof, Munich, Germany

Madeline Alexander,
Center for Depression, Anxiety and Stress Research, McLean Hospital, Belmont, MA, USA

Behrooz Z. Alizadeh,
University Medical Center Groningen, University Center for Psychiatry, Rob Giel Research Center, University of Groningen, Groningen, The Netherlands

Richard Bruggeman,
University Medical Center Groningen, University Center for Psychiatry, Rob Giel Research Center, University of Groningen, Groningen, The Netherlands

Behrooz Z. Alizadeh,
Department of Epidemiology, University Medical Center Groningen, University of Groningen, Groningen, The Netherlands

Köksal Alptekin,
Department of Psychiatry, Dokuz Eylül University School of Medicine, Izmir, Turkey

Köksal Alptekin,
Department of Neuroscience, Dokuz Eylül University Graduate School of Health Sciences, Izmir, Turkey

Farooq Amin,

Department of Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA, USA

Volker Arolt,
Department of Psychiatry, University of Münster, Münster, Germany

Rebecca Lencer,
Department of Psychiatry, University of Münster, Münster, Germany

Matthias Rothermundt,
Department of Psychiatry, University of Münster, Münster, Germany

Bernhard T. Baune,
Department of Psychiatry, University of Münster, Münster, Germany

Manuel Arrojo,
Servizo de Psiquiatría, Complexo Hospitalario Universitario de Santiago de Compostela, Servizo Galego de Saúde (SERGAS), Santiago de Compostela, Spain

Maria Helena Azevedo,
Institute of Medical Psychology, Faculty of Medicine, University of Coimbra, Coimbra, Portugal

Silviu A. Bacanu,
Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Bradley T. Webb,
Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Brandon K. Wormley,
Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Brien P. Riley,
Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Kenneth S. Kendler,
Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Martin Begemann,
Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Marina Mitjans,
Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Agnes A. Steixner-Kumar,

Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Hannelore Ehrenreich,
Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Judit Bene,
Department of Medical Genetics, Medical School, University of Pécs, Pécs, Hungary

Beben Benyamin,
Australian Centre for Precision Health, University of South Australia Cancer Research Institute, University of South Australia, Adelaide, South Australia, Australia

Beben Benyamin,
UniSA Allied Health and Human Performance, University of South Australia, Adelaide, South Australia, Australia

Beben Benyamin,
South Australian Health and Medical Research Institute, Adelaide, South Australia, Australia

Giuseppe Blasi,
Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Antonio Rampino,
Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Silvia Torretta,
Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Alessandro Bertolino,
Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Julio Bobes,
Área de Psiquiatría-Universidad de Oviedo, Hospital Universitario Central de Asturias (HUCA), Asturias, Spain

Julio Bobes,
Instituto de Investigación Sanitaria del Principado de Asturias (ISPA), Oviedo, Asturias, Spain

Julio Bobes,
Centro de Investigación Biomédica en Red de Salud Mental, Oviedo, Asturias, Spain

Stefano Bonassi,
Unit of Clinical and Molecular Epidemiology, IRCCS San Raffaele Roma and San Raffaele University, Rome, Italy

Rodrigo Affonseca Bressan,
Department of Psychiatry, Universidade Federal de São Paulo, São Paulo, Brazil

Ary Gadelha,
Department of Psychiatry, Universidade Federal de São Paulo, São Paulo, Brazil

Cristiano Noto,
Department of Psychiatry, Universidade Federal de São Paulo, São Paulo, Brazil

Rodrigo Affonseca Bressan,
Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Ary Gadelha,
Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Cristiano Noto,
Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Vanessa Kiyomi Ota,
Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Marcos Leite Santoro,
Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Sintia Iole Belangero,
Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Evelyn J. Bromet,
Department of Psychiatry and Behavioural Health, Stony Brook University, Stony Brook, NY, USA

Richard Bruggeman,
Department of Clinical and Developmental Neuropsychology, University of Groningen, Groningen, The Netherlands

Peter F. Buckley,
Health Science Center, University of Tennessee, Memphis, TN, USA

Randy L. Buckner,
Department of Psychology, Harvard University, Cambridge, MA, USA

Jonas Bybjerg-Grauholm,

Center for Neonatal Screening, Department for Congenital Disorders, Statens Serum Institut, Copenhagen, Denmark

David M. Hougaard,
Center for Neonatal Screening, Department for Congenital Disorders, Statens Serum Institut, Copenhagen, Denmark

Wiepke Cahn,
University Medical Center Utrecht, Department of Psychiatry, Rudolf Magnus Institute of Neuroscience, Utrecht, The Netherlands

René S. Kahn,
University Medical Center Utrecht, Department of Psychiatry, Rudolf Magnus Institute of Neuroscience, Utrecht, The Netherlands

Wiepke Cahn,
Altrecht, General Menthal Health Care, Utrecht, The Netherlands

Murray J. Cairns,
School of Biomedical Sciences and Pharmacy, University of Newcastle, Newcastle, New South Wales, Australia

Rodney J. Scott,
School of Biomedical Sciences and Pharmacy, University of Newcastle, Newcastle, New South Wales, Australia

Paul A. Tooney,
School of Biomedical Sciences and Pharmacy, University of Newcastle, Newcastle, New South Wales, Australia

Murray J. Cairns,
Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Ulrich Schall,
Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Rodney J. Scott,
Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Paul A. Tooney,
Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Murray J. Cairns,
Centre for Brain and Mental Health Research, University of Newcastle, Newcastle, New South Wales, Australia

Paul A. Tooney,
Centre for Brain and Mental Health Research, University of Newcastle, Newcastle, New South Wales, Australia

Monica E. Calkins,
Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Raquel E. Gur,

Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Ruben C. Gur,
Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Bruce I. Turetsky,
Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Vaughan J. Carr,
School of Psychiatry, University of New South Wales, Sydney, New South Wales, Australia

Vaughan J. Carr,
Department of Psychiatry, Monash University, Melbourne, Victoria, Australia

Vaughan J. Carr,
Neuroscience Research Australia, Sydney, New South Wales, Australia

David Castle,
Department of Psychiatry, University of Melbourne, Parkville, Victoria, Australia

Carol Harvey,
Department of Psychiatry, University of Melbourne, Parkville, Victoria, Australia

David Castle,
St Vincent’s Hospital, Melbourne, Victoria, Australia

Stanley V. Catts,
Brain and Mind Centre, The University of Sydney, Sydney, New South Wales, Australia

Stanley V. Catts,
School of Medicine, University of Queensland, Herston, Queensland, Australia

Raymond C. K. Chan,
Institute of Psychology, Chinese Academy of Science, Beijing, China

Raymond C. K. Chan,
Department of Psychology, University of Chinese Academy of Sciences, Beijing, China

Boris Chaumette,
INSERM U1266, Institute of Psychiatry and Neuroscience of Paris, Université de Paris, GHU Paris Psychiatrie & Neurosciences, Paris, France

Oussama Kebir,
INSERM U1266, Institute of Psychiatry and Neuroscience of Paris, Université de Paris, GHU Paris Psychiatrie & Neurosciences, Paris, France

Marie-Odile Krebs,
INSERM U1266, Institute of Psychiatry and Neuroscience of Paris, Université de Paris, GHU Paris Psychiatrie & Neurosciences, Paris, France

Boris Chaumette,

Department of Psychiatry, McGill University, Montreal, Québec, Canada

Wei Cheng,
Department of Computer Science, University of North Carolina, Chapel Hill, NC, USA

Eric F. C. Cheung,
Castle Peak Hospital, Hong Kong, China

Siow Ann Chong,
Saw Swee Hock School of Public Health, National University of Singapore, Singapore, Republic of Singapore

Mythily Subramaniam,
Saw Swee Hock School of Public Health, National University of Singapore, Singapore, Republic of Singapore

David Cohen,
Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Angèle Consoli,
Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Marianna Giannitelli,
Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Claudine Laurent-Levinson,
Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

David Cohen,
Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Angèle Consoli,
Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Marianna Giannitelli,
Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Claudine Laurent-Levinson,
Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

David Cohen,
Institut des Systèmes Intelligents et de Robotique (ISIR), CNRS UMR7222, Faculté des Sciences et Ingénierie, Sorbonne Université, Paris, France

Quirino Cordeiro,
Department of Psychiatry, Irmandade da Santa Casa de Misericórdia de São Paulo, São Paulo, Brazil

Javier Costas,
Instituto de Investigación Sanitaria (IDIS) de Santiago de Compostela, Complexo Hospitalario Universitario de Santiago de Compostela (CHUS), Servizo Galego de Saúde (SERGAS), Santiago de Compostela, Spain

Charles Curtis,
Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Diego Quattrone,
Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Gerome Breen,
Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

David A. Collier,
Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Marta Di Forti,
Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Evangelos Vassos,
Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Charles Curtis,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Valeria Mondelli,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Diego Quattrone,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Therese van Amelsvoort,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Marta Di Forti,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Robin M. Murray,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Evangelos Vassos,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Therese van Amelsvoort,
National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

Michael Davidson,
University of Nicosia Medical School, Nicosia, Cyprus

Kenneth L. Davis,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Vahram Haroutunian,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Dolores Malaspina,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Abraham Reichenberg,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Larry J. Siever,

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Jeremy M. Silverman,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Joseph D. Buxbaum,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

René S. Kahn,
Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Lieuwe de Haan,
Department of Psychiatry, Academic Medical Centre, University of Amsterdam, Amsterdam, The Netherlands

Lieuwe de Haan,
Department of Psychiatry, Academic Medical Centre, University of Amsterdam, Amsterdam, The Netherlands

Lieuwe de Haan,
Arkin, Institute for Mental Health, Amsterdam, The Netherlands

Lieuwe de Haan,
Arkin, Institute for Mental Health, Amsterdam, The Netherlands

Franziska Degenhardt,
Institute of Human Genetics, University of Bonn, Bonn, Germany

Andreas Forstner,
Institute of Human Genetics, University of Bonn, Bonn, Germany

Markus M. Nöthen,
Institute of Human Genetics, University of Bonn, Bonn, Germany

Lynn E. DeLisi,
Cambridge Health Alliance, Cambridge, MA, USA

Faith Dickerson,
Sheppard Pratt Health System, Baltimore, MD, USA

Dimitris Dikeos,
First Department of Psychiatry, Medical School, National and Kapodistrian University of Athens, Eginition Hospital, Athens, Greece

George N. Papadimitriou,
First Department of Psychiatry, Medical School, National and Kapodistrian University of Athens, Eginition Hospital, Athens, Greece

Timothy Dinan,

Department of Psychiatry and Neurobehavioural Sciences, University College Cork, Cork, Ireland

Timothy Dinan,
APC Microbiome Ireland, University College Cork, Cork, Ireland

Srdjan Djurovic,
NORMENT Centre, Department of Clinical Science, University of Bergen, Bergen, Norway

Srdjan Djurovic,
Department of Medical Genetics, Oslo University Hospital, Oslo, Norway

Jubao Duan,
Center for Psychiatric Genetics, NorthShore University HealthSystem, Evanston, IL, USA

Pablo V. Gejman,
Center for Psychiatric Genetics, NorthShore University HealthSystem, Evanston, IL, USA

Alan R. Sanders,
Center for Psychiatric Genetics, NorthShore University HealthSystem, Evanston, IL, USA

Jubao Duan,
Department of Psychiatry and Behavioral Neurosciences, The University of Chicago, Chicago, IL, USA

Pablo V. Gejman,
Department of Psychiatry and Behavioral Neurosciences, The University of Chicago, Chicago, IL, USA

Alan R. Sanders,
Department of Psychiatry and Behavioral Neurosciences, The University of Chicago, Chicago, IL, USA

Giuseppe Ducci,
Department of Mental Health, ASL Rome 1, Rome, Italy

Frank Dudbridge,
Department of Health Sciences, University of Leicester, Leicester, UK

Johan G. Eriksson,
Department of General Practice and Primary Health Care, University of Helsinki and Helsinki University Hospital, Helsinki, Finland

Johan G. Eriksson,
Folkhälsan Research Center, Helsinki, Finland

Johan G. Eriksson,
Department of Obstetrics and Gynecology, Yong Loo Lin School of Medicine, National University of Singapore, Singapore, Republic of Singapore

Lourdes Fañanás,
Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain

Lourdes Fañanás,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Javier González Peñas,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Ana González-Pinto,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

María Dolores Molto,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Carmen Moreno,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Mara Parellada,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Julio Sanjuan,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Benedicto Crepo-Facorro,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Ignacio Mata,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Celso Arango,
Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Stephen V. Faraone,
Departments of Psychiatry and Neuroscience and Physiology, SUNY Upstate Medical University, Syracuse, NY, USA

Andreas Forstner,
Centre for Human Genetics, University of Marburg, Marburg, Germany

Josef Frank,

Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Fabian Streit,
Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Stephanie H. Witt,
Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Marcella Rietschel,
Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Nelson B. Freimer,
Department of Human Genetics, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Roel A. Ophoff,
Department of Human Genetics, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Nelson B. Freimer,
Department of Psychiatry and Biobehavioral Sciences, University of California Los Angeles, Los Angeles, CA, USA

Menachem Fromer,
Division of Psychiatric Genomics, Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Eli A. Stahl,
Division of Psychiatric Genomics, Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Alessandra Frustaci,
Barnet, Enfield and Haringey Mental Health NHS Trust, St Ann’s Hospital, London, UK

Elliot S. Gershon,
Departments of Psychiatry and Human Genetics, University of Chicago, Chicago, IL, USA

Ina Giegling,
Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Annette M. Hartmann,
Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Bettina Konte,

Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Dan Rujescu,
Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Paola Giusti-Rodríguez,
Department of Genetics, University of North Carolina, Chapel Hill, NC, USA

Jin P. Szatkiewicz,
Department of Genetics, University of North Carolina, Chapel Hill, NC, USA

Patrick F. Sullivan,
Department of Genetics, University of North Carolina, Chapel Hill, NC, USA

Stephanie Godard,
Departments of Psychiatry and Human and Molecular Genetics, INSERM, Institut de Myologie, Hôpital de la Pitiè-Salpêtrière, Paris, France

Javier González Peñas,
Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Carmen Moreno,
Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Mara Parellada,
Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Celso Arango,
Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Ana González-Pinto,
BIOARABA Health Research Institute, OSI Araba, University Hospital, University of the Basque Country, Vitoria, Spain

Srihari Gopal,
Neuroscience Therapeutic Area, Janssen Research and Development, Titusville, NJ, USA

Adam Savitz,
Neuroscience Therapeutic Area, Janssen Research and Development, Titusville, NJ, USA

Qingqin S. Li,
Neuroscience Therapeutic Area, Janssen Research and Development, Titusville, NJ, USA

Jacob Gratten,
Mater Research Institute, University of Queensland, Brisbane, Queensland, Australia

Michael F. Green,
Department of Psychiatry and Biobehavioral Sciences, Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Keith H. Nuechterlein,
Department of Psychiatry and Biobehavioral Sciences, Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Catherine A. Sugar,
Department of Psychiatry and Biobehavioral Sciences, Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Michael F. Green,
VA Greater Los Angeles Healthcare System, Los Angeles, CA, USA

Tiffany A. Greenwood,
Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Gregory A. Light,
Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Neal R. Swerdlow,
Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

David Braff,
Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Olivier Guillin,
INSERM, Rouen, France

Dominique Campion,
INSERM, Rouen, France

Olivier Guillin,
Centre Hospitalier du Rouvray, Rouen, France

Dominique Campion,
Centre Hospitalier du Rouvray, Rouen, France

Olivier Guillin,
UFR Santé, Université de Rouen Normandie, Rouen, France

Sinan Gülöksüz,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Jurjen J. Luykx,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Bart P. F. Rutten,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Therese van Amelsvoort,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Ruud van Winkel,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Therese van Amelsvoort,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Ruud van Winkel,
Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Sinan Gülöksüz,
Department of Psychiatry, Yale School of Medicine, New Haven, CT, USA

Blanca Gutiérrez,
Department of Psychiatry, Faculty of Medicine and Biomedical Research Centre (CIBM), University of Granada, Granada, Spain

Eric Hahn,
Department of Psychiatry, Charité - Universitätsmedizin, Berlin, Germany

Hakon Hakonarson,
Children's Hospital of Philadelphia, Leonard Madlyn Abramson Research Center, Philadelphia, PA, USA

Renata Pellegrino,
Children's Hospital of Philadelphia, Leonard Madlyn Abramson Research Center, Philadelphia, PA, USA

Vahram Haroutunian,
Department of Neuroscience, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Vahram Haroutunian,
Mental Illness Research Clinical and Education Center (MIRECC), JJ Peters VA Medical Center, New York, NY, USA

Carol Harvey,
NorthWestern Mental Health, Melbourne, Victoria, Australia

Christos Pantelis,
NorthWestern Mental Health, Melbourne, Victoria, Australia

Caroline Hayward,
MRC Human Genetics Unit, University of Edinburgh, Institute of Genetics and Cancer, Western General Hospital, Edinburgh, UK

Frans A. Henskens,
School of Medicine and Public Health, University of Newcastle, Newcastle, New South Wales, Australia

Brian J. Kelly,
School of Medicine and Public Health, University of Newcastle, Newcastle, New South Wales, Australia

Stefan Herms,
Division of Medical Genetics, Department of Biomedicine, University of Basel, Basel, Switzerland

Per Hoffmann,
Division of Medical Genetics, Department of Biomedicine, University of Basel, Basel, Switzerland

Daniel P. Howrigan,
Broad Institute of MIT and Harvard, Cambridge, MA, USA

Menachem Fromer,
Broad Institute of MIT and Harvard, Cambridge, MA, USA

Mark J. Daly,
Broad Institute of MIT and Harvard, Cambridge, MA, USA

Masashi Ikeda,
Department of Psychiatry, Fujita Health University School of Medicine, Toyoake Aichi, Japan

Nakao Iwata,
Department of Psychiatry, Fujita Health University School of Medicine, Toyoake Aichi, Japan

Conrad Iyegbe,
Department of Psychosis Studies, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Jim van Os,
Department of Psychosis Studies, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Inge Joa,
Regional Centre for Clinical Research in Psychosis, Department of Psychiatry, Stavanger University Hospital, Stavanger, Norway

Antonio Julià,

Rheumatology Research Group, Vall d'Hebron Research Institute, Barcelona, Spain

Sara Marsal,
Rheumatology Research Group, Vall d'Hebron Research Institute, Barcelona, Spain

Tony Kam-Thong,
Roche Pharma Research and Early Development, Pharmaceutical Sciences, Roche Innovation Center Basel, F. Hoffman-La Roche, Basel, Switzerland

Anna Rautanen,
Roche Pharma Research and Early Development, Pharmaceutical Sciences, Roche Innovation Center Basel, F. Hoffman-La Roche, Basel, Switzerland

Yoichiro Kamatani,
Laboratory of Complex Trait Genomics, Department of Computational Biology and Medical Sciences, Graduate School of Frontier Sciences, The University of Tokyo, Tokyo, Japan

Yoichiro Kamatani,
Laboratory for Statistical Analysis, RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Sena Karachanak-Yankova,
Department of Medical Genetics, Medical University, Sofia, Bulgaria

Draga Toncheva,
Department of Medical Genetics, Medical University, Sofia, Bulgaria

Sena Karachanak-Yankova,
Department of Genetics, Faculty of Biology, Sofia University "St. Kliment Ohridski", Sofia, Bulgaria

Matthew C. Keller,
Institute for Behavioural Genetics, University of Colorado Boulder, Boulder, CO, USA

Andrey Khrunin,
Institute of Molecular Genetics of National Research Centre "Kurchatov Institute", Moscow, Russia

Svetlana Limborska,
Institute of Molecular Genetics of National Research Centre "Kurchatov Institute", Moscow, Russia

Petr Slominsky,
Institute of Molecular Genetics of National Research Centre "Kurchatov Institute", Moscow, Russia

Sung-Wan Kim,
Department of Psychiatry, Chonnam National University Medical School, Gwangju, Korea

Janis Klovins,

Latvian Biomedical Research and Study Centre, Riga, Latvia

Liene Nikitina-Zake,
Latvian Biomedical Research and Study Centre, Riga, Latvia

Nikolay Kondratiev,
Mental Health Research Center, Moscow, Russian Federation

Vera Golimbet,
Mental Health Research Center, Moscow, Russian Federation

Julia Kraft,
Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, Berlin, Germany

Michiaki Kubo,
RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Vaidutis Kučinskas,
Faculty of Medicine, Vilnius University, Vilnius, Lithuania

Zita Ausrele Kučinskiene,
Faculty of Medicine, Vilnius University, Vilnius, Lithuania

Agung Kusumawardhani,
Psychiatry Department, University of Indonesia - Cipto Mangunkusumo National General Hospital, Jakarta, Indonesia

Hana Kuzelova-Ptackova,
Department of Psychiatry, 1st Faculty of Medicine and General University Hospital, Prague, Czech Republic

Stefano Landi,
Dipartimento di Biologia, Universita’ di Pisa, Pisa, Italy

Laura C. Lazzeroni,
Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA, USA

Douglas F. Levinson,
Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA, USA

Laura C. Lazzeroni,
Department of Biomedical Data Science, Stanford University, Stanford, CA, USA

Phil H. Lee,
Psychiatric and Neurodevelopmental Genetics Unit, Department of Psychiatry and Center for Genomic Medicine, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

Tracey L. Petryshen,
Psychiatric and Neurodevelopmental Genetics Unit, Department of Psychiatry and Center for Genomic Medicine, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

Jordan W. Smoller,
Psychiatric and Neurodevelopmental Genetics Unit, Department of Psychiatry and Center for Genomic Medicine, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

Douglas S. Lehrer,
Department of Psychiatry, Wright State University, Dayton, OH, USA

Bernard Lerer,
Department of Psychiatry, Hadassah-Hebrew University Medical Center, Jerusalem, Israel

Miaoxin Li,
Zhongshan School of Medicine and Key Laboratory of Tropical Diseases Control (SYSU), Sun Yat-sen University, Guangzhou, China

Jeffrey Lieberman,
Department of Psychiatry, Columbia University, New York, NY, USA

T. Scott Stroup,
Department of Psychiatry, Columbia University, New York, NY, USA

Gregory A. Light,
VISN 22, Mental Illness Research, Education and Clinical Center (MIRECC), VA San Diego Healthcare System, San Diego, CA, USA

David Braff,
VISN 22, Mental Illness Research, Education and Clinical Center (MIRECC), VA San Diego Healthcare System, San Diego, CA, USA

Chih-Min Liu,
Department of Psychiatry, National Taiwan University Hospital, Taipei, Taiwan

Chih-Min Liu,
Neurobiology and Cognitive Science Center, National Taiwan University, Taipei, Taiwan

Hai-Gwo Hwu,
Neurobiology and Cognitive Science Center, National Taiwan University, Taipei, Taiwan

Jouko Lönnqvist,
Mental Health Unit, Department of Public Health Solutions, National Institute for Health and Welfare, Helsinki, Finland

Jouko Lönnqvist,
Department of Psychiatry, University of Helsinki, Helsinki, Finland

Carmel M. Loughland,
Hunter New England Health and University of Newcastle, Newcastle, New South Wales, Australia

Jan Lubinski,

Department of Genetics and Pathology, International Hereditary Cancer Center, Pomeranian Medical University in Szczecin, Szczecin, Poland

Jurjen J. Luykx,
Department of Psychiatry, UMC Utrecht Brain Center, University Medical Centre Utrecht, Utrecht University, Utrecht, The Netherlands

Steven Bakker,
Department of Psychiatry, UMC Utrecht Brain Center, University Medical Centre Utrecht, Utrecht University, Utrecht, The Netherlands

René Kahn,
Department of Psychiatry, UMC Utrecht Brain Center, University Medical Centre Utrecht, Utrecht University, Utrecht, The Netherlands

Jurjen J. Luykx,
Department of Translational Neuroscience, UMC Utrecht Brain Center, University Medical Center Utrecht, Utrecht University, Utrecht, The Netherlands

Jurjen J. Luykx,
Second Opinion Outpatient Clinic, GGNet Mental Health, Warnsveld, The Netherlands

Milan Macek Jr,
Department of Biology and Medical Genetics, 2nd Faculty of Medicine and University Hospital Motol, Prague, Czech Republic

Andrew Mackinnon,
Black Dog Institute, University of New South Wales, Randwick, New South Wales, Australia

Andrew Mackinnon,
Melbourne School of Population and Global Health, University of Melbourne, Melbourne, Victoria, Australia

Brion S. Maher,
Department of Mental Health, Bloomberg School of Public Health, Johns Hopkins University, Baltimore, MD, USA

Wolfgang Maier,
Department for Neurodegenerative Diseases and Geriatric Psychiatry, University Hospital Bonn, Bonn, Germany

Dolores Malaspina,
Department of Genetics and Genomics, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Eşref Cem Atbaşoğlu,
Department of Genetics and Genomics, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Jacques Mallet,

Asfalia Biologics, iPEPS-ICM, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Stephen R. Marder,
Semel Institute for Neurosciene, University of California Los Angeles, Los Angeles, CA, USA

Alicia R. Martin,
Department of Medicine, Harvard Medical School, Boston, MA, USA

Hailiang Huang,
Department of Medicine, Harvard Medical School, Boston, MA, USA

Lourdes Martorell,
Hospital Universitari Institut Pere Mata, IISPV, Universitat Rovira i Virgili, CIBERSAM, Reus, Spain

Gerard Muntané,
Hospital Universitari Institut Pere Mata, IISPV, Universitat Rovira i Virgili, CIBERSAM, Reus, Spain

Elisabet Vilella,
Hospital Universitari Institut Pere Mata, IISPV, Universitat Rovira i Virgili, CIBERSAM, Reus, Spain

Manuel Mattheisen,
Department of Psychiatry, Dalhousie University, Halifax, Nova Scotia, Canada

Sandra Meier,
Department of Psychiatry, Dalhousie University, Halifax, Nova Scotia, Canada

Manuel Mattheisen,
Department of Community Health and Epidemiology, Dalhousie University, Halifax, Nova Scotia, Canada

Manuel Mattheisen,
Institute of Psychiatric Phenomics and Genomics (IPPG), University Hospital, LMU Munich, Munich, Germany

Thomas G. Schulze,
Institute of Psychiatric Phenomics and Genomics (IPPG), University Hospital, LMU Munich, Munich, Germany

Robert W. McCarley,
VA Boston Health Care System, Brockton, MA, USA

Colm McDonald,
Centre for Neuroimaging, Cognition and Genomics (NICOG), National University of Ireland Galway, Galway, Ireland

Gary Donohoe,
Centre for Neuroimaging, Cognition and Genomics (NICOG), National University of Ireland Galway, Galway, Ireland

Derek W. Morris,
Centre for Neuroimaging, Cognition and Genomics (NICOG), National University of Ireland Galway, Galway, Ireland

John J. McGrath,
Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Sathish Periyasamy,
Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Bryan J. Mowry,
Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Naomi R. Wray,
Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

John J. McGrath,
Queensland Centre for Mental Health Research, The Park Centre for Mental Health, Brisbane, Queensland, Australia

Helena Medeiros,
Department of Psychiatry and the Behavioral Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, USA

Janet L. Sobell,
Department of Psychiatry and the Behavioral Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, USA

Helena Medeiros,
College of Medicine, SUNY Downstate Health Sciences University, New York, NY, USA

Sandra Meier,
Department of Biomedicine, Aarhus University, Aarhus, Denmark

Bela Melegh,
Department of Medical Genetics, University of Pécs, School of Medicine, Pécs, Hungary

Raquelle I. Mesholam-Gately,
Massachusetts Mental Health Center Public Psychiatry Division of the Beth Israel Deaconess Medical Center, Boston, MA, USA

Larry J. Seidman,
Massachusetts Mental Health Center Public Psychiatry Division of the Beth Israel Deaconess Medical Center, Boston, MA, USA

Andres Metspalu,

Estonian Genome Center, Institute of Genomics, University of Tartu, Tartu, Estonia

Lili Milani,
Estonian Genome Center, Institute of Genomics, University of Tartu, Tartu, Estonia

Tõnu Esko,
Estonian Genome Center, Institute of Genomics, University of Tartu, Tartu, Estonia

Patricia T. Michie,
School of Psychology, University of Newcastle, Newcastle, New South Wales, Australia

Vihra Milanova,
Psychiatric Clinic, Alexandrovska University Hospital, Sofia, Bulgaria

Espen Molden,
Department of Pharmacy, University of Oslo, Oslo, Norway

Espen Molden,
Center for Psychopharmacology, Diakonhjemmet Hospital, Oslo, Norway

Esther Molina,
Department of Nursing, Faculty of Health Sciences and Biomedical Research Centre (CIBM), University of Granada, Granada, Spain

María Dolores Molto,
Department of Genetics, Faculty of Biological Sciences, Universidad de Valencia, Valencia, Spain

María Dolores Molto,
Biomedical Research Institute INCLIVA, Valencia, Spain

Julio Sanjuan,
Biomedical Research Institute INCLIVA, Valencia, Spain

Valeria Mondelli,
Department of Psychological Medicine, Institute of Psychiatry, Psychology, and Neuroscience, King’s College London, London, UK

Christopher P. Morley,
Departments of Public Health and Preventive Medicine, Family Medicine, and Psychiatry and Behavioral Sciences, State University of New York, Upstate Medical University, Syracuse, NY, USA

Gerard Muntané,
Institut de Biologia Evolutiva (UPF-CSIC), Departament de Ciències Experimentals i de la Salut, Universitat Pompeu Fabra, PRBB, Barcelona, Spain

Kieran C. Murphy,
Department of Psychiatry, Royal College of Surgeons in Ireland, Dublin, Ireland

Inez Myin-Germeys,
Department for Neurosciences, Center for Contextual Psychiatry, KU Leuven, Leuven, Belgium

Igor Nenadić,
Cognitive Neuropsychiatry Laboratory, Department of Psychiatry and Psychotherapy, Philipps Universität Marburg, Marburg, Germany

Igor Nenadić,
Department of Psychiatry and Psychotherapy, Jena University Hospital, Jena, Germany

Gerald Nestadt,
Department of Psychiatry and Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Ann E. Pulver,
Department of Psychiatry and Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD, USA

F. Anthony O’Neill,
Centre for Public Health, Institute of Clinical Sciences, Queen’s University Belfast, Belfast, UK

Sang-Yun Oh,
Department of Statistics and Applied Probability, University of California at Santa Barbara, Santa Barbara, CA, USA

Sang-Yun Oh,
Computational Research Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA

Ann Olincy,
Department of Psychiatry, University of Colorado Denver, Aurora, CO, USA

Robert Freedman,
Department of Psychiatry, University of Colorado Denver, Aurora, CO, USA

Vanessa Kiyomi Ota,
Department of Morphology and Genetics, Laboratorio de Genetica, Universidade Federal de São Paulo, São Paulo, Brazil

Marcos Leite Santoro,
Department of Morphology and Genetics, Laboratorio de Genetica, Universidade Federal de São Paulo, São Paulo, Brazil

Sintia Iole Belangero,
Department of Morphology and Genetics, Laboratorio de Genetica, Universidade Federal de São Paulo, São Paulo, Brazil

Christos Pantelis,
Melbourne Neuropsychiatry Centre, University of Melbourne and Melbourne Health, Melbourne, Victoria, Australia

Christos Pantelis,

The Florey Institute of Neuroscience and Mental Health, University of Melbourne, Parkville, Victoria, Australia

Bernhard T. Baune,
The Florey Institute of Neuroscience and Mental Health, University of Melbourne, Parkville, Victoria, Australia

Christos Pantelis,
Department of Psychiatry, Melbourne Medical School, University of Melbourne, Parkville, Victoria, Australia

Bernhard T. Baune,
Department of Psychiatry, Melbourne Medical School, University of Melbourne, Parkville, Victoria, Australia

Tiina Paunio,
Department of Public Health Solutions, Genomics and Biomarkers Unit, National Institute for Health and Welfare, Helsinki, Finland

Tiina Paunio,
Department of Psychiatry and SleepWell Research Program, Faculty of Medicine, University of Helsinki and Helsinki University Central Hospital, Helsinki, Finland

Sathish Periyasamy,
Queensland Centre for Mental Health Research, University of Queensland, Brisbane, Queensland, Australia

Bryan J. Mowry,
Queensland Centre for Mental Health Research, University of Queensland, Brisbane, Queensland, Australia

Diana O. Perkins,
Department of Psychiatry, University of North Carolina, Chapel Hill, NC, USA

Patrick F. Sullivan,
Department of Psychiatry, University of North Carolina, Chapel Hill, NC, USA

Bruno Pfuhlmann,
Clinic of Psychiatry and Psychotherapy, Weißer Hirsch, Dresden, Germany

Olli Pietiläinen,
Department of Stem Cell and Regenerative Biology, Harvard University, Cambridge, MA, USA

Steven E. Hyman,
Department of Stem Cell and Regenerative Biology, Harvard University, Cambridge, MA, USA

Olli Pietiläinen,
Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Christian Benner,

Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Matti Pirinen,
Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Aarno Palotie,
Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Mark J. Daly,
Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

David Porteous,
Centre for Genomic and Experimental Medicine, Institute of Genetics and Molecular Medicine, University of Edinburgh, Western General Hospital, Edinburgh, UK

John Powell,
Department of Basic and Clinical Neuroscience, Institute of Psychiatry, Psychology and Neuroscience, King's College London, London, UK

Diego Quattrone,
South London and Maudsley NHS Mental Health Foundation Trust, London, UK

Marta Di Forti,
South London and Maudsley NHS Mental Health Foundation Trust, London, UK

Digby Quested,
Oxford Health NHS Foundation Trust, Warneford Hospital, Oxford, UK

Digby Quested,
Department of Psychiatry, University of Oxford, Oxford, UK

Allen D. Radant,
Department of Psychiatry and Behavioral Sciences, University of Washington, Seattle, WA, USA

Debby W. Tsuang,
Department of Psychiatry and Behavioral Sciences, University of Washington, Seattle, WA, USA

Allen D. Radant,
VA Puget Sound Health Care System, Seattle, WA, USA

Debby W. Tsuang,
VA Puget Sound Health Care System, Seattle, WA, USA

Mark H. Rapaport,
Huntsman Mental Health Institute, Department of Psychiatry, University of Utah School of Medicine, Salt Lake City, UT, USA

Cheryl Roe,

SUNY Upstate Medical University, Syracuse, NY, USA

Chunyu Liu,
SUNY Upstate Medical University, Syracuse, NY, USA

Joshua L. Roffman,
Department of Psychiatry, Massachusetts General Hospital, Boston, MA, USA

Jennifer L. Moran,
Department of Psychiatry, Massachusetts General Hospital, Boston, MA, USA

Julian Roth,
Department of Psychiatry, Psychosomatics and Psychotherapy, Julius-Maximilians-Universität Würzburg, Würzburg, Germany

Micha Gawlik,
Department of Psychiatry, Psychosomatics and Psychotherapy, Julius-Maximilians-Universität Würzburg, Würzburg, Germany

Safaa Saker-Delye,
Généthon, Evry, France

Veikko Salomaa,
THL–Finnish Institute for Health and Welfare, Helsinki, Finland

Jaana Suvisaari,
THL–Finnish Institute for Health and Welfare, Helsinki, Finland

Julio Sanjuan,
Department of Psychiatry, School of Medicine, University of Valencia, Hospital Clínico Universitario de Valencia, Valencia, Spain

Ulrich Schall,
Priority Centre for Brain and Mental Health Research, University of Newcastle, Mater Hospital, McAuley Centre, Newcastle, New South Wales, Australia

Rodney J. Scott,
Division of Molecular Medicine, NSW Health Pathology North, Newcastle, New South Wales, Australia

Jianxin Shi,
Division of Cancer Epidemiology and Genetics, National Cancer Institute, Bethesda, MD, USA

Larry J. Siever,
James J. Peters VA Medical Center, Bronx, NY, USA

Jeremy M. Silverman,
James J. Peters VA Medical Center, Bronx, NY, USA

Engilbert Sigurdsson,
Faculty of Medicine, University of Iceland, Reykjavik, Iceland

Engilbert Sigurdsson,

Department of Psychiatry, Landspitali University Hospital, Reykjavik, Iceland

Kang Sim,
West Region, Institute of Mental Health, Singapore, Singapore

Kang Sim,
Yoo Loo Lin School of Medicine, National University of Singapore, Singapore, Singapore

Kang Sim,
Lee Kong Chian School of Medicine, Nanyang Technological University, Singapore, Singapore

Hon-Cheong So,
School of Biomedical Sciences, The Chinese University of Hong Kong, Hong Kong, China

Hon-Cheong So,
Department of Psychiatry, The Chinese University of Hong Kong, Hong Kong, China

Helen J. Stain,
School of Social and Health Sciences, Leeds Trinity University, Leeds, UK

Helen J. Stain,
TIPS - Network for Clinical Research in Psychosis, Stavanger University Hospital, Stavanger, Norway

Nils Eiel Steen,
NORMENT Centre, Institute of Clinical Medicine, University of Oslo, Oslo, Norway

Erik G. Jönsson,
NORMENT Centre, Institute of Clinical Medicine, University of Oslo, Oslo, Norway

Elisabeth Stögmann,
Department of Neurology, Medical University of Vienna, Vienna, Austria

Fritz Zimprich,
NORMENT Centre, Institute of Clinical Medicine, University of Oslo, Oslo, Norway

Department of Neurology, Medical University of Vienna, Vienna, Austria

William S. Stone,
Harvard Medical School Department of Psychiatry at Beth Israel Deaconess Medical Center, Boston, MA, USA

William S. Stone,
Massachusetts Mental Health Center, Boston, MA, USA

Richard E. Straub,
Lieber Institute for Brain Development, Baltimore, MD, USA

Thomas Hyde,
Lieber Institute for Brain Development, Baltimore, MD, USA

Andrew Jaffe,

Lieber Institute for Brain Development, Baltimore, MD, USA

Daniel R. Weinberger,
Lieber Institute for Brain Development, Baltimore, MD, USA

Eric Strengman,
Department of Medical Genetics, University Medical Centre Utrecht, Utrecht, The Netherlands

Catherine A. Sugar,
Department of Biostatistics, Fielding School of Public Health, University of California Los Angeles, Los Angeles, CA, USA

Dragan M. Svrakic,
Department of Psychiatry, Washington University, St Louis, MO, USA

C. Robert Cloninger,
Department of Psychiatry, Washington University, St Louis, MO, USA

Thi Minh Tam Ta,
Department of Psychiatry, Charité – Universitätsmedizin Berlin, Berlin, Germany

Thi Minh Tam Ta,
Berlin Institute of Health (BIH), Berlin, Germany

Atsushi Takahashi,
Laboratory for Statistical and Translational Genetics, RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Chikashi Terao,
Laboratory for Statistical and Translational Genetics, RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Florence Thibaut,
Université de Paris, Faculté de Médecine, Hôpital Cochin-Tarnier, Paris, France

Florence Thibaut,
INSERM U1266, Institut de Psychiatrie et de Neurosciences, Paris, France

Draga Toncheva,
Bulgarian Academy of Science, Sofia, Bulgaria

Sarah Tosato,
Department of Neuroscience, Biomedicine and Movement Sciences, Section of Psychiatry, University of Verona, Verona, Italy

Gian Battista Tura,
Psychiatry Unit, IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli, Brescia, Italy

Alp Üçok,
Department of Psychiatry, Faculty of Medicine, Istanbul University, Istanbul, Turkey

Arne Vaaler,

Division of Mental Health, St. Olav's Hospital, Trondheim University Hospital, Trondheim, Norway

Arne Vaaler,
Department of Mental Health, Norwegian University of Science and Technology, Trondheim, Norway

Ruud van Winkel,
Department of Neurosciences, Center for Clinical Psychiatry, KU Leuven, Leuven, Belgium

Juha Veijola,
Department of Psychiatry, Research Unit of Clinical Neuroscience, University of Oulu, Oulu, Finland

Ruud van Winkel,
Department of Psychiatry, Research Unit of Clinical Neuroscience, University of Oulu, Oulu, Finland

Juha Veijola,
Medical Research Center Oulu, Oulu University Hospital and University of Oulu, Oulu, Finland

John Waddington,
Molecular and Cellular Therapeutics, Royal College of Surgeons in Ireland, Dublin, Ireland

Anna Waterreus,
Neuropsychiatric Epidemiology Research Unit, School of Population and Global Health, University of Western Australia, Perth, Western Australia, Australia

Vera A. Morgan,
Neuropsychiatric Epidemiology Research Unit, School of Population and Global Health, University of Western Australia, Perth, Western Australia, Australia

Anna Waterreus,
Centre for Clinical Research in Neuropsychiatry, University of Western Australia, Perth, Western Australia, Australia

Assen V. Jablensky,
Centre for Clinical Research in Neuropsychiatry, University of Western Australia, Perth, Western Australia, Australia

Vera A. Morgan,
Centre for Clinical Research in Neuropsychiatry, University of Western Australia, Perth, Western Australia, Australia

Mark Weiser,
Sheba Medical Center, Tel Hashomer, Israel

Jing Qin Wu,
Baker Heart and Diabetes Institute, Melbourne, Victoria, Australia

Zhida Xu,
Department of Psychiatry, GGz Centraal, Utrecht, The Netherlands

Robert Yolken,
Stanley Neurovirology Laboratory, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Clement C. Zai,
Campbell Family Mental Health Research Institute, Centre for Addiction and Mental Health, Toronto, Ontario, Canada

James L. Kennedy,
Campbell Family Mental Health Research Institute, Centre for Addiction and Mental Health, Toronto, Ontario, Canada

Clement C. Zai,
Department of Psychiatry, University of Toronto, Toronto, Ontario, Canada

James L. Kennedy,
Department of Psychiatry, University of Toronto, Toronto, Ontario, Canada

Feng Zhu,
Department of Psychiatry, The First Affiliated Hospital of Xi’an Jiaotong University, Xi’an, China

Feng Zhu,
Center for Translational Medicine, The First Affiliated Hospital of Xi’an Jiaotong University, Xi’an, China

Eşref Cem Atbaşoğlu,
Department of Psychiatry, School of Medicine, Ankara University, Ankara, Turkey

Meram C. Saka,
Department of Psychiatry, School of Medicine, Ankara University, Ankara, Turkey

Muhammad Ayub,
Department of Psychiatry, Queens University Kingston, Kingston, Ontario, Canada

Donald W. Black,
Department of Psychiatry, University of Iowa Carver College of Medicine, Iowa City, IA, USA

Nancy G. Buccola,
School of Nursing, Louisiana State University Health Sciences Center, New Orleans, LA, USA

William F. Byerley,
Department of Psychiatry, University of California San Francisco, San Francisco, CA, USA

Wei J. Chen,
Center for Neuropsychiatric Research, National Health Research Institutes, Zhunan Town, Taiwan

Wei J. Chen,
Institute of Epidemiology and Preventive Medicine, College of Public Health, National Taiwan University, Taipei, Taiwan

Benedicto Crespo-Facorro,
University of Sevilla, CIBERSAM IBiS, Seville, Spain

Benedicto Crespo-Facorro,
Hospital Universitario Virgen del Rocio, Department of Psychiatry, Universidad del Sevilla, Seville, Spain

Cherrie Galletly,
Discipline of Psychiatry, Adelaide Medical School, University of Adelaide, Adelaide, South Australia, Australia

Cherrie Galletly,
Ramsay Health Care (SA) Mental Health, Adelaide, South Australia, Australia

Cherrie Galletly,
Northern Adelaide Local Health Network, Adelaide, South Australia, Australia

Massimo Gennarelli,
Department of Molecular and Translational Medicine, University of Brescia, Brescia, Italy

Massimo Gennarelli,
Genetic Unit, IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli, Brescia, Italy

Hai-Gwo Hwu,
Department of Psychiatry, College of Medicine and National Taiwan University Hospital, National Taiwan University, Taipei, Taiwan

Ole Mors,
Psychosis Research Unit, Aarhus University Hospital, Aarhus, Denmark

Bertram Müller-Myhsok,
Max Planck Institute of Psychiatry, Munich, Germany

Bertram Müller-Myhsok,
Munich Cluster for Systems Neurology, Munich, Germany

Bertram Müller-Myhsok,
Department of Health Data Science, University of Liverpool, Liverpool, UK

Amanda L. Neil,
Menzies Institute for Medical Research, University of Tasmania, Hobart, Tasmania, Australia

Merete Nordentoft,
Mental Health Services in the Capital Region of Denmark, Mental Health Center Copenhagen, University of Copenhagen, Copenhagen, Denmark

Michele T. Pato,

Rutgers University, Robert Wood Johnson Medical School, New Brunswick, NJ, USA

Carlos N. Pato,
Rutgers University, Robert Wood Johnson Medical School, New Brunswick, NJ, USA

Michele T. Pato,
Rutgers University, New Jersey Medical School, Newark, NJ, USA

Carlos N. Pato,
Rutgers University, New Jersey Medical School, Newark, NJ, USA

Matti Pirinen,
Department of Mathematics and Statistics, University of Helsinki, Helsinki, Finland

Matti Pirinen,
Department of Public Health, University of Helsinki, Helsinki, Finland

Thomas G. Schulze,
Department of Psychiatry and Behavioral Sciences, SUNY Upstate Medical University, Syracuse, NY, USA

Thomas G. Schulze,
Department of Psychiatry and Psychotherapy, University Medical Center Göttingen, Göttingen, Germany

Thomas G. Schulze,
Department of Psychiatry and Behavioral Sciences, The Johns Hopkins University, Baltimore, MD, USA

Eli A. Stahl,
Program in Medical and Population Genetics, The Broad Institute of MIT and Harvard, Cambridge, MA, USA

Tõnu Esko,
Program in Medical and Population Genetics, The Broad Institute of MIT and Harvard, Cambridge, MA, USA

Eli A. Stahl,
Regeneron Genetics Center, Orange, CA, USA

Shi-Heng Wang,
College of Public Health, China Medical University, Taichung, Taiwan

Shuhua Xu,
State Key Laboratory of Genetic Engineering and Ministry of Education (MOE) Key Laboratory of Contemporary Anthropology, Collaborative Innovation Center of Genetics and Development, Human Phenome Institute, School of Life Sciences, Fudan University, Shanghai, China

Shuhua Xu,
School of Life Science and Technology, ShanghaiTech University, Shanghai, China

Shuhua Xu,
Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China

Rolf Adolfsson,
Department of Clinical Sciences, Psychiatry, Umeå University, Umeå, Sweden

Elvira Bramon,
Division of Psychiatry, Department of Mental Health Neuroscience, University College London, London, UK

Jorge A. Cervilla,
Department of Psychiatry, San Cecilio University Hospital, University of Granada, Granada, Spain

Sven Cichon,
Institute of Medical Genetics and Pathology, University Hospital Basel, Basel, Switzerland

Sven Cichon,
Department of Biomedicine, University of Basel, Basel, Switzerland

Sven Cichon,
Institute of Neuroscience and Medicine (INM-1), Research Center Juelich, Juelich, Germany

David A. Collier,
Eli Lilly and Company, Windlesham, UK

David A. Collier,
Eli Lilly and Company, Windlesham, UK

Aiden Corvin,
Neuropsychiatric Genetics Research Group, Department of Psychiatry, Trinity College Dublin, Dublin, Ireland

Michael Gill,
Neuropsychiatric Genetics Research Group, Department of Psychiatry, Trinity College Dublin, Dublin, Ireland

David Curtis,
UCL Genetics Institute, University College London, London, UK

David Curtis,
Centre for Psychiatry, Queen Mary University London, London, UK

Enrico Domenici,
Department of Cellular, Computational and Integrative Biology, University of Trento, Trento, Italy

Valentina Escott-Price,
Dementia Research Institute, Cardiff University, Cardiff, UK

Ayman H. Fanous,

Department of Psychiatry, Phoenix VA Healthcare System, Phoenix, AZ, USA

Ayman H. Fanous,
Banner-University Medical Center, Phoenix, AZ, USA

Anna Gareeva,
Department of Human Molecular Genetics of the Institute of Biochemistry and Genetics of the Ufa Federal Research Center of the Russian Academy of Sciences (IBG UFRC RAS), Ufa, Russia

Elza Khusnutdinova,
Department of Human Molecular Genetics of the Institute of Biochemistry and Genetics of the Ufa Federal Research Center of the Russian Academy of Sciences IBG UFRC RAS), Ufa, Russia

Anna Gareeva,
Department of Human Molecular Genetics of the Institute of Biochemistry and Genetics of the Ufa Federal Research Center of the Russian Academy of Sciences (IBG UFRC RAS), Ufa, Russia

Anna Gareeva,
Federal State Educational Institution of Highest Education Bashkir State Medical University of Public Health Ministry of Russian Federation (BSMU), Ufa, Russia

Elza Khusnutdinova,
Federal State Educational Institution of Highest Education Bashkir State Medical University of Public Health Ministry of Russian Federation (BSMU), Ufa, Russia

Anna Gareeva,
Federal State Educational Institution of Highest Education Bashkir State Medical University of Public Health Ministry of Russian Federation (BSMU), Ufa, Russia

Stephen J. Glatt,
Psychiatric Genetic Epidemiology and Neurobiology Laboratory (PsychGENe lab), Department of Psychiatry and Behavioral Sciences, SUNY Upstate Medical University, Syracuse, NY, USA

Kyung Sue Hong,
Department of Psychiatry, Sungkyunkwan University School of Medicine, Samsung Medical Center, Seoul, Korea

James A. Knowles,
Department of Psychiatry and Zilkha Neurogenetics Institute, Keck School of Medicine at University of Southern California, Los Angeles, CA, USA

James A. Knowles,
Department of Cell Biology, State University of New York, Downstate Health Sciences University, New York, NY, USA

Jimmy Lee,
Department of Psychosis, Institute of Mental Health, Singapore, Singapore

Jimmy Lee,
Neuroscience and Mental Health, Lee Kong Chian School of Medicine, Nanyang Technological University, Singapore, Singapore

Todd Lencz,
Institute of Behavioral Science, Feinstein Institutes for Medical Research, Manhasset, NY, USA

Anil K. Malhotra,
Institute of Behavioral Science, Feinstein Institutes for Medical Research, Manhasset, NY, USA

Todd Lencz,
Department of Psychiatry, Zucker School of Medicine at Hofstra/Northwell, Hempstead, NY, USA

Anil K. Malhotra,
Department of Psychiatry, Zucker School of Medicine at Hofstra/Northwell, Hempstead, NY, USA

Jianjun Liu,
Human Genetics, Genome Institute of Singapore, A*STAR, Singapore, Singapore

Jianjun Liu,
Department of Medicine, Yong Loo Lin School of Medicine, National University of Singapore, Singapore, Singapore

Dheeraj Malhotra,
Roche Pharma Research and Early Development, Roche Innovation Center Basel, F. Hoffman-La Roche, Basel, Switzerland

Paulo R. Menezes,
Department of Preventative Medicine, Faculdade de Medicina FMUSP, University of São Paulo, São Paulo, Brazil

Vishwajit Nimgaonkar,
Department of Psychiatry, University of Pittsburgh, Pittsburgh, PA, USA

Roel A. Ophoff,
Center for Neurobehavioral Genetics, Semel Institute for Neuroscience and Human Behavior, University of California Los Angeles, Los Angeles, CA, USA

Roel A. Ophoff,
Department of Psychiatry, Erasmus University Medical Center, Rotterdam, The Netherlands

Sara A. Paciga,
Early Clinical Development, Pfizer Worldwide Research and Development, Groton, CT, USA

Aarno Palotie,

Analytic and Translational Genetics Unit, Department of Medicine, Department of Neurology and Department of Psychiatry, Massachusetts General Hospital, Boston, MA, USA

Aarno Palotie,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stephan Ripke,
Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Shengying Qin,
Shanghai Key Laboratory of Psychotic Disorders, Shanghai Mental Health Center, Shanghai Jiao Tong University School of Medicine, Shanghai, China

Margarita Rivera,
Department of Biochemistry and Molecular Biology II, Faculty of Pharmacy, University of Granada, Granada, Spain

Margarita Rivera,
Institute of Neurosciences, Biomedical Research Center (CIBM), University of Granada, Granada, Spain

Sibylle G. Schwab,
Faculty of Science, Medicine and Health, University of Wollongong, Wollongong, New South Wales, Australia

Sibylle G. Schwab,
Illawarra Health and Medical Research Institute, Wollongong, New South Wales, Australia

Alessandro Serretti,
Department of Biomedical and Neuromotor Sciences, University of Bologna, Bologna, Italy

Pak C. Sham,
Centre for PanorOmic Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Pak C. Sham,
Centre for PanorOmic Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Pak C. Sham,
State Key Laboratory of Brain and Cognitive Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Pak C. Sham,
State Key Laboratory of Brain and Cognitive Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Pak C. Sham,
Department of Psychiatry, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Pak C. Sham,
Department of Psychiatry, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

David St Clair,
Institute of Medical Sciences, University of Aberdeen, Aberdeen, UK

Ming T. Tsuang,
Center for Behavioral Genomics, Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Ming T. Tsuang,
Institute of Genomic Medicine, University of California San Diego, La Jolla, CA, USA

Jim van Os,
University Medical Center Utrecht, Department of Psychiatry, Utrecht, The Netherlands

Marquis P. Vawter,
Department of Psychiatry and Human Behavior, School of Medicine, University of California Irvine, Irvine, CA, USA

Thomas Werge,
Institute of Biological Psychiatry, Mental Health Services, Copenhagen University Hospital, Copenhagen, Denmark

Thomas Werge,
Department of Clinical Medicine, University of Copenhagen, Copenhagen, Denmark

David St Clair,
Department of Clinical Medicine, University of Copenhagen, Copenhagen, Denmark

Thomas Werge,
Center for GeoGenetics, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

Thomas Werge,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research, iPSYCH, Copenhagen, Denmark

Jim van Os,
The Lundbeck Foundation Initiative for Integrative Psychiatric Research, iPSYCH, Copenhagen, Denmark

Dieter B. Wildenauer,
School of Psychiatry and Clinical Neurosciences, University of Western Australia, Perth, Western Australia, Australia

Jim van Os,

School of Psychiatry and Clinical Neurosciences, University of Western Australia, Perth, Western Australia, Australia

Xin Yu,
Peking University Sixth Hospital, Peking University Institute of Mental Health, Beijing, China

Weihua Yue,
Peking University Sixth Hospital, Peking University Institute of Mental Health, Beijing, China

Xin Yu,
National Clinical Research Center for Mental Disorders, NHC Key Laboratory of Mental Health (Peking University) and Chinese Academy of Medical Sciences Research Unit, Beijing, China

Weihua Yue,
National Clinical Research Center for Mental Disorders, NHC Key Laboratory of Mental Health (Peking University) and Chinese Academy of Medical Sciences Research Unit, Beijing, China

Weihua Yue,
PKU–IDG/McGovern Institute for Brain Research, Peking University, Beijing, China

Panos Roussos,
Mental Illness Research, Education, and Clinical Center (VISN 2 South), James J. Peters VA Medical Center, New York, NY, USA

Evangelos Vassos,
Oxford Health NHS Foundation Trust, Oxford, UK

Matthijs Verhage,
Department of Clinical Genetics, Center for Neurogenomics and Cognitive Research, University Medical Center Amsterdam, Amsterdam, The Netherlands

Frank Koopmans,
Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Dnyanada Sahasrabudhe,
Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Ruud F. Toonen,
Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Matthijs Verhage,

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Matthijs Verhage,
Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Danielle Posthuma,
Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Jian Yang,
Westlake Laboratory of Life Sciences and Biomedicine, Hangzhou, China

Nan Dai,
Western Australian Institute for Medical Research and Centre for Medical Research, University of Western Australia, Nedlands, Western Australia, Australia

Qin Wenwen,
Western Australian Institute for Medical Research and Centre for Medical Research, University of Western Australia, Nedlands, Western Australia, Australia

D. B. Wildenauer,
Western Australian Institute for Medical Research and Centre for Medical Research, University of Western Australia, Nedlands, Western Australia, Australia

Nan Dai,
School of Psychiatry and Clinical Neurosciences, University of Western Australia, Crawley, Western Australia, Australia

Qin Wenwen,
School of Psychiatry and Clinical Neurosciences, University of Western Australia, Crawley, Western Australia, Australia

D. B. Wildenauer,
School of Psychiatry and Clinical Neurosciences, University of Western Australia, Crawley, Western Australia, Australia

Feranindhya Agiananda,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Nurmiati Amir,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Ronald Antoni,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Tiana Arsianti,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Asmarahadi Asmarahadi,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

H. Diatri,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Prianto Djatmiko,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Irmansyah Irmansyah,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Siti Khalimah,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Irmia Kusumadewi,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Profitasari Kusumaningrum,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Petrin R. Lukman,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Martina W. Nasrun,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

N. S. Safyuni,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Prasetyawan Prasetyawan,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

G. Semen,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Kristiana Siste,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Heriani Tobing,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Natalia Widiasih,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Tjhin Wiguna,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

D. Wulandari,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

None Evalina,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

A. J. Hananto,

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Joni H. Ismoyo,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

T. M. Marini,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Supiyani Henuhili,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Muhammad Reza,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Suzy Yusnadewi,
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Alexej Abyzov,
Mayo Clinic, Rochester, MN, USA

Schahram Akbarian,
Mount Sinai, New York, NY, USA

Harm van Bakel,
Mount Sinai, New York, NY, USA

Michael Breen,
Mount Sinai, New York, NY, USA

Alex Charney,
Mount Sinai, New York, NY, USA

Stella Dracheva,
Mount Sinai, New York, NY, USA

Kiran Girdhar,
Mount Sinai, New York, NY, USA

Gabriel Hoffman,
Mount Sinai, New York, NY, USA

Yan Jiang,
Mount Sinai, New York, NY, USA

Dalila Pinto,
Mount Sinai, New York, NY, USA

Shaun Purcell,
Mount Sinai, New York, NY, USA

Panagiotis Roussos,
Mount Sinai, New York, NY, USA

Jennifer Wiseman,
Mount Sinai, New York, NY, USA

Allison Ashley-Koch,
Duke University, Durham, NC, USA

Gregory Crawford,
Duke University, Durham, NC, USA

Tim Reddy,
Duke University, Durham, NC, USA

Miguel Brown,
University of Chicago, Chicago, IL, USA

Kay Grennan,
University of Chicago, Chicago, IL, USA

Julien Bryois,
Karolinska Institutet, Stockholm, Sweden

Becky Carlyle,
Yale University, New Haven, CT, USA

Prashant Emani,
Yale University, New Haven, CT, USA

Timur Galeev,
Yale University, New Haven, CT, USA

Mark Gerstein,
Yale University, New Haven, CT, USA

Mengting Gu,
Yale University, New Haven, CT, USA

Brittney Guerra,
Yale University, New Haven, CT, USA

Gamze Gursoy,
Yale University, New Haven, CT, USA

Robert Kitchen,
Yale University, New Haven, CT, USA

Donghoon Lee,
Yale University, New Haven, CT, USA

Mingfeng Li,
Yale University, New Haven, CT, USA

Shuang Liu,
Yale University, New Haven, CT, USA

Fabio Navarro,
Yale University, New Haven, CT, USA

Xinghua Pan,

Yale University, New Haven, CT, USA

Sirisha Pochareddy,
Yale University, New Haven, CT, USA

Joel Rozowsky,
Yale University, New Haven, CT, USA

Nenad Sestan,
Yale University, New Haven, CT, USA

Anurag Sethi,
Yale University, New Haven, CT, USA

Xu Shi,
Yale University, New Haven, CT, USA

Anna Szekely,
Yale University, New Haven, CT, USA

Daifeng Wang,
Yale University, New Haven, CT, USA

Jonathan Warrell,
Yale University, New Haven, CT, USA

Sherman Weissman,
Yale University, New Haven, CT, USA

Feinan Wu,
Yale University, New Haven, CT, USA

Xuming Xu,
Yale University, New Haven, CT, USA

Gerard Coetzee,
University of Southern California, Los Angeles, CA, USA

Peggy Farnham,
University of Southern California, Los Angeles, CA, USA

Fides Lay,
University of Southern California, Los Angeles, CA, USA

Suhn Rhie,
University of Southern California, Los Angeles, CA, USA

Heather Witt,
University of Southern California, Los Angeles, CA, USA

Shannon Wood,
University of Southern California, Los Angeles, CA, USA

Lijing Yao,
University of Southern California, Los Angeles, CA, USA

Mike Gandal,
University of California Los Angeles, Los Angeles, CA, USA

Damon Polioudakis,
University of California Los Angeles, Los Angeles, CA, USA

Vivek Swarup,
University of California Los Angeles, Los Angeles, CA, USA

Hyejung Won,
University of California Los Angeles, Los Angeles, CA, USA

Gina Giase,
University of Illinois at Chicago, Chicago, IL, USA

Shan Jiang,
University of Illinois at Chicago, Chicago, IL, USA

Amira Kefi,
University of Illinois at Chicago, Chicago, IL, USA

Annie Shieh,
University of Illinois at Chicago, Chicago, IL, USA

Fernando Goes,
Johns Hopkins University, Baltimore, MD, USA

Peter Zandi,
Johns Hopkins University, Baltimore, MD, USA

Yunjung Kim,
University of North Carolina - Chapel Hill, Chapel Hill, NC, USA

James A. Knowles,
SUNY Downstate Medical Center, New York, NY, USA

Eugenio Mattei,
University of Massachusetts, Amherst, MA, USA

Michael Purcaro,
University of Massachusetts, Amherst, MA, USA

Henry Pratt,
University of Massachusetts, Amherst, MA, USA

Mette A. Peters,
Sage Bionetworks, Seattle, WA, USA

Stephan Sanders,
University of California San Francisco, San Francisco, CA, USA

Zhiping Weng,
University of Massachusetts Medical School, Worcester, MA, USA

Kevin White,

Yong Loo Lin School of Medicine, National University of Singapore, Singapore, Singapore

Maria J. Arranz,
King's College London, London, UK

Elvira Bramon,
King's College London, London, UK

Conrad Iyegbe,
King's College London, London, UK

Cathryn Lewis,
King's College London, London, UK

Kuang Lin,
King's College London, London, UK

Robin M. Murray,
King's College London, London, UK

John Powell,
King's College London, London, UK

Muriel Walshe,
King's College London, London, UK

Maria J. Arranz,
Fundació de Docència i Recerca Mútua de Terrassa, Universitat de Barcelona, Barcelona, Spain

Stephan Bender,
Child and Adolescent Psychiatry, University of Technology Dresden, Dresden, Germany

Stephan Bender,
Section for Experimental Psychopathology, General Psychiatry, Heidelberg, Germany

Matthias Weisbrod,
Section for Experimental Psychopathology, General Psychiatry, Heidelberg, Germany

Elvira Bramon,
Institute of Cognitive Neuroscience, University College London, London, UK

Benedicto Crepo-Facorro,
University Hospital Marqués de Valdecilla, Instituto de Formación e Investigación Marqués de Valdecilla, University of Cantabria, Santander, Spain

Ignacio Mata,
University Hospital Marqués de Valdecilla, Instituto de Formación e Investigación Marqués de Valdecilla, University of Cantabria, Santander, Spain

Jeremy Hall,
Neuroscience and Mental Health Research Institute, Division of Psychiatry and Clinical Neuroscience, Cardiff University, Cardiff, UK

Stephen Lawrie,
Division of Psychiatry, University of Edinburgh, Edinburgh, UK

Andrew McIntosh,
Division of Psychiatry, University of Edinburgh, Edinburgh, UK

Don H. Linszen,
Department of Psychiatry, Academic Medical Center, University of Amsterdam, Amsterdam, The Netherlands

Roel A. Ophoff,
Department of Human Genetics, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Jim van Os,
Maastricht University Medical Centre, South Limburg Mental Health Research and Teaching Network, EURON, Maastricht, The Netherlands

Jim van Os,
Institute of Psychiatry, King’s College London, London, UK

Dan Rujescu,
Department of Psychiatry, University of Halle, Halle, Germany

Dan Rujescu,
Department of Psychiatry, University of Munich, Munich, Germany

Tilmann Achsel,
Department of Fundamental Neurosciences, University of Lausanne, Lausanne, Switzerland

Claudia Bagni,
Department of Fundamental Neurosciences, University of Lausanne, Lausanne, Switzerland

Maria Andres-Alonso,
RG Neuroplasticity, Leibniz Institute for Neurobiology, Magdeburg, Germany

Michael R. Kreutz,
RG Neuroplasticity, Leibniz Institute for Neurobiology, Magdeburg, Germany

Àlex Bayés,
Molecular Physiology of the Synapse Laboratory, Biomedical Research Institute Sant Pau, Barcelona, Spain

Thomas Biederer,
Department of Neurology, Yale School of Medicine, New Haven, CT, USA

Nils Brose,

Department of Molecular Neurobiology, Max Planck Institute of Experimental Medicine, Göttingen, Germany

John Jia En Chua,
LSI Neurobiology Programme, National University of, Singapore, Singapore

Marcelo P. Coba,
Zilkha Neurogenetic Institute and Department of Psychiatry and Behavioral Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, USA

L. Niels Cornelisse,
Functional Genomics section, Department of Human Genetics, Center for Neurogenomics and Cognitive Research, Amsterdam University Medical Center, Amsterdam, The Netherlands

Jan R. T. van Weering,
Functional Genomics section, Department of Human Genetics, Center for Neurogenomics and Cognitive Research, Amsterdam University Medical Center, Amsterdam, The Netherlands

Arthur P. H. de Jong,
Cell Biology, Neurobiology and Biophysics, Department of Biology, Faculty of Science, Utrecht University, Utrecht, The Netherlands

Harold D. MacGillavry,
Cell Biology, Neurobiology and Biophysics, Department of Biology, Faculty of Science, Utrecht University, Utrecht, The Netherlands

Jaime de Juan-Sanz,
Sorbonne Université, Institut du Cerveau - Paris Brain Institute - ICM, Inserm, CNRS, APHP, Hôpital de la Pitié Salpêtrière, Paris, France

Daniela C. Dieterich,
Institute for Pharmacology and Toxicology, Medical Faculty Otto-von-Guericke University Magdeburg, Magdeburg, Germany

Rainer Pielot,
Institute for Pharmacology and Toxicology, Medical Faculty Otto-von-Guericke University Magdeburg, Magdeburg, Germany

Karl-Heinz Smalla,
Institute for Pharmacology and Toxicology, Medical Faculty Otto-von-Guericke University Magdeburg, Magdeburg, Germany

Daniela C. Dieterich,
Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Eckart D. Gundelfinger,
Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Rainer Pielot,

Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Karl-Heinz Smalla,
Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Guoping Feng,
McGovern Institute for Brain Research, Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology (MIT), Cambridge, MA, USA

Hana L. Goldschmidt,
Solomon H. Snyder Department of Neuroscience, Kavli Neuroscience Discovery Institute, The Johns Hopkins University School of Medicine, Baltimore, MD, USA

Richard L. Huganir,
Solomon H. Snyder Department of Neuroscience, Kavli Neuroscience Discovery Institute, The Johns Hopkins University School of Medicine, Baltimore, MD, USA

Casper Hoogenraad,
Department of Neuroscience, Genentech, South San Francisco, CA, USA

Steven E. Hyman,
Department of Stem Cell and Regenerative Biology, Harvard University, Cambridge, MA, USA

Cordelia Imig,
Department of Neuroscience, University of Copenhagen, Copenhagen, Denmark

Reinhard Jahn,
Laboratory of Neurobiology, Max-Planck Institute for Biophysical Chemistry, Göttingen, Germany

Hwajin Jung,
Center for Synaptic Brain Dysfunctions, Institute for Basic Science (IBS), Department of Biological Sciences, Korea Advanced Institute of Science and Technology (KAIST), Daejeon, South Korea

Eunjoon Kim,
Center for Synaptic Brain Dysfunctions, Institute for Basic Science (IBS), Department of Biological Sciences, Korea Advanced Institute of Science and Technology (KAIST), Daejeon, South Korea

Pascal S. Kaeser,
Department of Neurobiology, Harvard Medical School, Boston, MA, USA

Noa Lipstein,
Department of Molecular Physiology and Cell Biology, Leibniz-Forschungsinstitut für Molekulare Pharmakologie, Berlin, Germany

Robert Malenka,
Nancy Pritzker Laboratory, Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA, USA

Peter S. McPherson,

Department of Neurology and Neurosurgery, Montreal Neurological Institute, McGill University, Montreal, Québec, Canada

Vincent O’Connor,
Biological Sciences, University of Southampton, Southampton, UK

Timothy A. Ryan,
Department of Biochemistry, Weill Cornell Medicine, New York, NY, USA

Carlo Sala,
CNR Neuroscience Institute, Milan, Italy

Chiara Verpelli,
CNR Neuroscience Institute, Milan, Italy

August B. Smit,
Department of Molecular and Cellular Neurobiology, Center for Neurogenomics and Cognitive Research, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

Thomas C. Südhof,
Department of Molecular and Cellular Physiology, Howard Hughes Medical Institute, Stanford University, Stanford, CA, USA

Paul D. Thomas
Division of Bioinformatics, Department of Preventive Medicine, Keck School of Medicine of USC, University of Southern California, Los Angeles, CA, USA

Affiliations

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

Department of Psychiatry and Psychotherapy, Charité - Universitätsmedizin, Berlin, Germany

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

MRC Centre for Neuropsychiatric Genetics and Genomics, Division of Psychological Medicine and Clinical Neurosciences, Cardiff University, Cardiff, UK

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

Institute for Molecular Bioscience, University of Queensland, Brisbane, Queensland, Australia

School of Life Sciences, Westlake University, Hangzhou, China

School of Life Sciences, Westlake University, Hangzhou, China

Department of Psychiatry and the Behavioral Sciences, SUNY Downstate Medical Center, New York, NY, USA

Department of Psychiatry, Veterans Affairs New York Harbor Healthcare System, New York, NY, USA

Institute for Genomic Health, SUNY Downstate Medical Center, New York, NY, USA

Department of Psychiatry, Veterans Affairs New York Harbor Healthcare System, New York, NY, USA

Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Department of Medical Epidemiology and Biostatistics, Karolinska Institutet, Stockholm, Sweden

Biogen, Cambridge, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Psychiatric and Neurodevelopmental Genetics Unit, Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Analytic and Translational Genetics Unit, Massachusetts General Hospital, Boston, MA, USA

Psychiatric and Neurodevelopmental Genetics Unit, Center for Genomic Medicine, Massachusetts General Hospital, Boston, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Research Division, Institute of Mental Health, Singapore, Republic of Singapore

Research Division, Institute of Mental Health, Singapore, Republic of Singapore

Research Division, Institute of Mental Health, Singapore, Republic of Singapore

Division of Psychiatry Research, Zucker Hillside Hospital, Glen Oaks, NY, USA

Division of Psychiatry Research, Zucker Hillside Hospital, Glen Oaks, NY, USA

Division of Psychiatry Research, Zucker Hillside Hospital, Glen Oaks, NY, USA

Department of Complex Trait Genetics, Center for Neurogenomics and Cognitive Research, Amsterdam Neuroscience, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

NORMENT Centre, Division of Mental Health and Addiction, University of Oslo, Oslo, Norway

Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Division of Mental Health and Addiction, Oslo University Hospital, Oslo, Norway

Center for Bioinformatics, Department of Informatics, University of Oslo, Oslo, Norway

Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Department of Psychiatry, Harvard Medical School, Boston, MA, USA

Department of Molecular and Cellular Neurobiology, Center for Neurogenomics and Cognitive Research, Faculty of Science, Amsterdam Neuroscience, Vrije Universiteit, Amsterdam, The Netherlands

deCODE Genetics, Amgen, Reykjavik, Iceland

deCODE Genetics, Amgen, Reykjavik, Iceland

deCODE Genetics, Amgen, Reykjavik, Iceland

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

National Centre for Register-based Research, Aarhus University, Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

National Centre for Register-based Research, Aarhus University, Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research (iPSYCH), Aarhus, Denmark

Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Department of Biomedicine and Centre for Integrative Sequencing (iSEQ), Aarhus University, Aarhus, Denmark

Center for Genomics and Personalized Medicine, Aarhus, Denmark

Center for Genomics and Personalized Medicine, Aarhus, Denmark

Center for Genomics and Personalized Medicine, Aarhus, Denmark

Center for Genomics and Personalized Medicine, Aarhus, Denmark

Department of Psychiatry, Semel Institute, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Department of Psychiatry, Semel Institute, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Affiliated Hospital of Qingdao University and Biomedical Sciences Institute of Qingdao University (Qingdao Branch of SJTU Bio-X Institutes), Qingdao University, Qingdao, China

Affiliated Hospital of Qingdao University and Biomedical Sciences Institute of Qingdao University (Qingdao Branch of SJTU Bio-X Institutes), Qingdao University, Qingdao, China

Affiliated Hospital of Qingdao University and Biomedical Sciences Institute of Qingdao University (Qingdao Branch of SJTU Bio-X Institutes), Qingdao University, Qingdao, China

Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Bio-X Institutes, Key Laboratory for the Genetics of Developmental and Neuropsychiatric Disorders (Ministry of Education), Collaborative Innovation Center for Brain Science, Shanghai Jiao Tong University, Shanghai, China

Department of Psychiatry, Pamela Sklar Division of Psychiatric Genomics, Friedman Brain Institute, Department of Genetics and Genomic Science and Institute for Data Science and Genomic Technology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Pamela Sklar Division of Psychiatric Genomics, Friedman Brain Institute, Department of Genetics and Genomic Science and Institute for Data Science and Genomic Technology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Pamela Sklar Division of Psychiatric Genomics, Friedman Brain Institute, Department of Genetics and Genomic Science and Institute for Data Science and Genomic Technology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Genetics and Genomic Sciences and Institute for Genomics and Multiscale Biology, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Division of Psychiatry, Centre for Clinical Brain Sciences, University of Edinburgh, Royal Edinburgh Hospital, Edinburgh, UK

Division of Psychiatry, Centre for Clinical Brain Sciences, University of Edinburgh, Royal Edinburgh Hospital, Edinburgh, UK

Department of Psychiatric Research, Diakonhjemmet Hospital, Oslo, Norway

Centre for Psychiatry Research, Department of Clinical Neuroscience, Karolinska Institutet and Stockholm Health Care Services, Stockholm Region, Stockholm, Sweden

Centre for Psychiatry Research, Department of Clinical Neuroscience, Karolinska Institutet and Stockholm Health Care Services, Stockholm Region, Stockholm, Sweden

Centre for Psychiatry Research, Department of Clinical Neuroscience, Karolinska Institutet and Stockholm Health Care Services, Stockholm Region, Stockholm, Sweden

National Centre for Register-based Research, Aarhus University, Aarhus, Denmark

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Molecular Psychiatry Laboratory, Division of Psychiatry, University College London, London, UK

Comedicum Lindwurmhof, Munich, Germany

Center for Depression, Anxiety and Stress Research, McLean Hospital, Belmont, MA, USA

University Medical Center Groningen, University Center for Psychiatry, Rob Giel Research Center, University of Groningen, Groningen, The Netherlands

University Medical Center Groningen, University Center for Psychiatry, Rob Giel Research Center, University of Groningen, Groningen, The Netherlands

Department of Epidemiology, University Medical Center Groningen, University of Groningen, Groningen, The Netherlands

Department of Psychiatry, Dokuz Eylül University School of Medicine, Izmir, Turkey

Department of Neuroscience, Dokuz Eylül University Graduate School of Health Sciences, Izmir, Turkey

Department of Psychiatry and Behavioral Sciences, Emory University, Atlanta, GA, USA

Department of Psychiatry, University of Münster, Münster, Germany

Department of Psychiatry, University of Münster, Münster, Germany

Department of Psychiatry, University of Münster, Münster, Germany

Department of Psychiatry, University of Münster, Münster, Germany

Servizo de Psiquiatría, Complexo Hospitalario Universitario de Santiago de Compostela, Servizo Galego de Saúde (SERGAS), Santiago de Compostela, Spain

Institute of Medical Psychology, Faculty of Medicine, University of Coimbra, Coimbra, Portugal

Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Virginia Institute for Psychiatric and Behavioral Genetics, Department of Psychiatry, Virginia Commonwealth University, Richmond, VA, USA

Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Clinical Neuroscience, Max Planck Institute of Experimental Medicine, Göttingen, Germany

Department of Medical Genetics, Medical School, University of Pécs, Pécs, Hungary

Australian Centre for Precision Health, University of South Australia Cancer Research Institute, University of South Australia, Adelaide, South Australia, Australia

UniSA Allied Health and Human Performance, University of South Australia, Adelaide, South Australia, Australia

South Australian Health and Medical Research Institute, Adelaide, South Australia, Australia

Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Department of Basic Medical Science, Neuroscience and Sense Organs, University of Bari ‘Aldo Moro’, Bari, Italy

Área de Psiquiatría-Universidad de Oviedo, Hospital Universitario Central de Asturias (HUCA), Asturias, Spain

Instituto de Investigación Sanitaria del Principado de Asturias (ISPA), Oviedo, Asturias, Spain

Centro de Investigación Biomédica en Red de Salud Mental, Oviedo, Asturias, Spain

Unit of Clinical and Molecular Epidemiology, IRCCS San Raffaele Roma and San Raffaele University, Rome, Italy

Department of Psychiatry, Universidade Federal de São Paulo, São Paulo, Brazil

Department of Psychiatry, Universidade Federal de São Paulo, São Paulo, Brazil

Department of Psychiatry, Universidade Federal de São Paulo, São Paulo, Brazil

Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Laboratory of Integrative Neuroscience, Universidade Federal de São Paulo, São Paulo, Brazil

Department of Psychiatry and Behavioural Health, Stony Brook University, Stony Brook, NY, USA

Department of Clinical and Developmental Neuropsychology, University of Groningen, Groningen, The Netherlands

Health Science Center, University of Tennessee, Memphis, TN, USA

Department of Psychology, Harvard University, Cambridge, MA, USA

Center for Neonatal Screening, Department for Congenital Disorders, Statens Serum Institut, Copenhagen, Denmark

Center for Neonatal Screening, Department for Congenital Disorders, Statens Serum Institut, Copenhagen, Denmark

University Medical Center Utrecht, Department of Psychiatry, Rudolf Magnus Institute of Neuroscience, Utrecht, The Netherlands

University Medical Center Utrecht, Department of Psychiatry, Rudolf Magnus Institute of Neuroscience, Utrecht, The Netherlands

Altrecht, General Menthal Health Care, Utrecht, The Netherlands

School of Biomedical Sciences and Pharmacy, University of Newcastle, Newcastle, New South Wales, Australia

School of Biomedical Sciences and Pharmacy, University of Newcastle, Newcastle, New South Wales, Australia

School of Biomedical Sciences and Pharmacy, University of Newcastle, Newcastle, New South Wales, Australia

Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Hunter Medical Research Institute, Newcastle, New South Wales, Australia

Centre for Brain and Mental Health Research, University of Newcastle, Newcastle, New South Wales, Australia

Centre for Brain and Mental Health Research, University of Newcastle, Newcastle, New South Wales, Australia

Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

Department of Psychiatry, University of Pennsylvania, Philadelphia, PA, USA

School of Psychiatry, University of New South Wales, Sydney, New South Wales, Australia

Department of Psychiatry, Monash University, Melbourne, Victoria, Australia

Neuroscience Research Australia, Sydney, New South Wales, Australia

Department of Psychiatry, University of Melbourne, Parkville, Victoria, Australia

Department of Psychiatry, University of Melbourne, Parkville, Victoria, Australia

St Vincent’s Hospital, Melbourne, Victoria, Australia

Brain and Mind Centre, The University of Sydney, Sydney, New South Wales, Australia

School of Medicine, University of Queensland, Herston, Queensland, Australia

Institute of Psychology, Chinese Academy of Science, Beijing, China

Department of Psychology, University of Chinese Academy of Sciences, Beijing, China

INSERM U1266, Institute of Psychiatry and Neuroscience of Paris, Université de Paris, GHU Paris Psychiatrie & Neurosciences, Paris, France

INSERM U1266, Institute of Psychiatry and Neuroscience of Paris, Université de Paris, GHU Paris Psychiatrie & Neurosciences, Paris, France

INSERM U1266, Institute of Psychiatry and Neuroscience of Paris, Université de Paris, GHU Paris Psychiatrie & Neurosciences, Paris, France

Department of Psychiatry, McGill University, Montreal, Québec, Canada

Department of Computer Science, University of North Carolina, Chapel Hill, NC, USA

Castle Peak Hospital, Hong Kong, China

Saw Swee Hock School of Public Health, National University of Singapore, Singapore, Republic of Singapore

Saw Swee Hock School of Public Health, National University of Singapore, Singapore, Republic of Singapore

Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Faculté de Médecine Sorbonne Université, Groupe de Recherche Clinique no. 15 - Troubles Psychiatriques et Développement (PSYDEV), Department of Child and Adolescent Psychiatry, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Centre de Référence des Maladies Rares à Expression Psychiatrique, Department of Child and Adolescent Psychiatry, AP-HP Sorbonne Université, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Institut des Systèmes Intelligents et de Robotique (ISIR), CNRS UMR7222, Faculté des Sciences et Ingénierie, Sorbonne Université, Paris, France

Department of Psychiatry, Irmandade da Santa Casa de Misericórdia de São Paulo, São Paulo, Brazil

Instituto de Investigación Sanitaria (IDIS) de Santiago de Compostela, Complexo Hospitalario Universitario de Santiago de Compostela (CHUS), Servizo Galego de Saúde (SERGAS), Santiago de Compostela, Spain

Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Social, Genetic and Developmental Psychiatry Centre, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King’s College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King's College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King's College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King's College London, London, UK

National Institute for Health Research (NIHR) Maudsley Biomedical Research Centre at South London and Maudsley NHS Foundation Trust and King's College London, London, UK

University of Nicosia Medical School, Nicosia, Cyprus

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Psychiatry, Academic Medical Centre, University of Amsterdam, Amsterdam, The Netherlands

Department of Psychiatry, Academic Medical Centre, University of Amsterdam, Amsterdam, The Netherlands

Arkin, Institute for Mental Health, Amsterdam, The Netherlands

Arkin, Institute for Mental Health, Amsterdam, The Netherlands

Institute of Human Genetics, University of Bonn, Bonn, Germany

Institute of Human Genetics, University of Bonn, Bonn, Germany

Institute of Human Genetics, University of Bonn, Bonn, Germany

Cambridge Health Alliance, Cambridge, MA, USA

Sheppard Pratt Health System, Baltimore, MD, USA

First Department of Psychiatry, Medical School, National and Kapodistrian University of Athens, Eginition Hospital, Athens, Greece

First Department of Psychiatry, Medical School, National and Kapodistrian University of Athens, Eginition Hospital, Athens, Greece

Department of Psychiatry and Neurobehavioural Sciences, University College Cork, Cork, Ireland

APC Microbiome Ireland, University College Cork, Cork, Ireland

NORMENT Centre, Department of Clinical Science, University of Bergen, Bergen, Norway

Department of Medical Genetics, Oslo University Hospital, Oslo, Norway

Center for Psychiatric Genetics, NorthShore University HealthSystem, Evanston, IL, USA

Center for Psychiatric Genetics, NorthShore University HealthSystem, Evanston, IL, USA

Center for Psychiatric Genetics, NorthShore University HealthSystem, Evanston, IL, USA

Department of Psychiatry and Behavioral Neurosciences, The University of Chicago, Chicago, IL, USA

Department of Psychiatry and Behavioral Neurosciences, The University of Chicago, Chicago, IL, USA

Department of Psychiatry and Behavioral Neurosciences, The University of Chicago, Chicago, IL, USA

Department of Mental Health, ASL Rome 1, Rome, Italy

Department of Health Sciences, University of Leicester, Leicester, UK

Department of General Practice and Primary Health Care, University of Helsinki and Helsinki University Hospital, Helsinki, Finland

Folkhälsan Research Center, Helsinki, Finland

Department of Obstetrics and Gynecology, Yong Loo Lin School of Medicine, National University of Singapore, Singapore, Republic of Singapore

Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Centro de Investigación Biomédica en Red en Salud Mental (CIBERSAM), Madrid, Spain

Departments of Psychiatry and Neuroscience and Physiology, SUNY Upstate Medical University, Syracuse, NY, USA

Centre for Human Genetics, University of Marburg, Marburg, Germany

Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Department of Genetic Epidemiology in Psychiatry, Central Institute of Mental Health, Medical Faculty Mannheim, University of Heidelberg, Mannheim, Germany

Department of Human Genetics, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Department of Human Genetics, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Department of Psychiatry and Biobehavioral Sciences, University of California Los Angeles, Los Angeles, CA, USA

Division of Psychiatric Genomics, Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Division of Psychiatric Genomics, Department of Psychiatry, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Barnet, Enfield and Haringey Mental Health NHS Trust, St Ann’s Hospital, London, UK

Departments of Psychiatry and Human Genetics, University of Chicago, Chicago, IL, USA

Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Department of Psychiatry and Psychotherapy, Medical University of Vienna, Vienna, Austria

Department of Genetics, University of North Carolina, Chapel Hill, NC, USA

Department of Genetics, University of North Carolina, Chapel Hill, NC, USA

Department of Genetics, University of North Carolina, Chapel Hill, NC, USA

Departments of Psychiatry and Human and Molecular Genetics, INSERM, Institut de Myologie, Hôpital de la Pitiè-Salpêtrière, Paris, France

Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

Department of Child and Adolescent Psychiatry, Institute of Psychiatry and Mental Health, General Universitario Gregorio Marañón, School of Medicine, Universidad Complutense, IiSGM, Madrid, Spain

BIOARABA Health Research Institute, OSI Araba, University Hospital, University of the Basque Country, Vitoria, Spain

Neuroscience Therapeutic Area, Janssen Research and Development, Titusville, NJ, USA

Neuroscience Therapeutic Area, Janssen Research and Development, Titusville, NJ, USA

Neuroscience Therapeutic Area, Janssen Research and Development, Titusville, NJ, USA

Mater Research Institute, University of Queensland, Brisbane, Queensland, Australia

Department of Psychiatry and Biobehavioral Sciences, Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Department of Psychiatry and Biobehavioral Sciences, Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Department of Psychiatry and Biobehavioral Sciences, Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

VA Greater Los Angeles Healthcare System, Los Angeles, CA, USA

Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

INSERM, Rouen, France

INSERM, Rouen, France

Centre Hospitalier du Rouvray, Rouen, France

Centre Hospitalier du Rouvray, Rouen, France

UFR Santé, Université de Rouen Normandie, Rouen, France

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry and Neuropsychology, School for Mental Health and Neuroscience, Maastricht University Medical Centre, Maastricht, The Netherlands

Department of Psychiatry, Yale School of Medicine, New Haven, CT, USA

Department of Psychiatry, Faculty of Medicine and Biomedical Research Centre (CIBM), University of Granada, Granada, Spain

Department of Psychiatry, Charité - Universitätsmedizin, Berlin, Germany

Children’s Hospital of Philadelphia, Leonard Madlyn Abramson Research Center, Philadelphia, PA, USA

Children’s Hospital of Philadelphia, Leonard Madlyn Abramson Research Center, Philadelphia, PA, USA

Department of Neuroscience, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Mental Illness Research Clinical and Education Center (MIRECC), JJ Peters VA Medical Center, New York, NY, USA

NorthWestern Mental Health, Melbourne, Victoria, Australia

NorthWestern Mental Health, Melbourne, Victoria, Australia

MRC Human Genetics Unit, University of Edinburgh, Institute of Genetics and Cancer, Western General Hospital, Edinburgh, UK

School of Medicine and Public Health, University of Newcastle, Newcastle, New South Wales, Australia

School of Medicine and Public Health, University of Newcastle, Newcastle, New South Wales, Australia

Division of Medical Genetics, Department of Biomedicine, University of Basel, Basel, Switzerland

Division of Medical Genetics, Department of Biomedicine, University of Basel, Basel, Switzerland

Broad Institute of MIT and Harvard, Cambridge, MA, USA

Broad Institute of MIT and Harvard, Cambridge, MA, USA

Broad Institute of MIT and Harvard, Cambridge, MA, USA

Department of Psychiatry, Fujita Health University School of Medicine, Toyoake Aichi, Japan

Department of Psychiatry, Fujita Health University School of Medicine, Toyoake Aichi, Japan

Department of Psychosis Studies, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Department of Psychosis Studies, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

Regional Centre for Clinical Research in Psychosis, Department of Psychiatry, Stavanger University Hospital, Stavanger, Norway

Rheumatology Research Group, Vall d’Hebron Research Institute, Barcelona, Spain

Rheumatology Research Group, Vall d’Hebron Research Institute, Barcelona, Spain

Roche Pharma Research and Early Development, Pharmaceutical Sciences, Roche Innovation Center Basel, F. Hoffman-La Roche, Basel, Switzerland

Roche Pharma Research and Early Development, Pharmaceutical Sciences, Roche Innovation Center Basel, F. Hoffman-La Roche, Basel, Switzerland

Laboratory of Complex Trait Genomics, Department of Computational Biology and Medical Sciences, Graduate School of Frontier Sciences, The University of Tokyo, Tokyo, Japan

Laboratory for Statistical Analysis, RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Department of Medical Genetics, Medical University, Sofia, Bulgaria

Department of Medical Genetics, Medical University, Sofia, Bulgaria

Department of Genetics, Faculty of Biology, Sofia University “St. Kliment Ohridski”, Sofia, Bulgaria

Institute for Behavioural Genetics, University of Colorado Boulder, Boulder, CO, USA

Institute of Molecular Genetics of National Research Centre “Kurchatov Institute”, Moscow, Russia

Institute of Molecular Genetics of National Research Centre “Kurchatov Institute”, Moscow, Russia

Institute of Molecular Genetics of National Research Centre “Kurchatov Institute”, Moscow, Russia

Department of Psychiatry, Chonnam National University Medical School, Gwangju, Korea

Latvian Biomedical Research and Study Centre, Riga, Latvia

Latvian Biomedical Research and Study Centre, Riga, Latvia

Mental Health Research Center, Moscow, Russian Federation

Mental Health Research Center, Moscow, Russian Federation

Berlin School of Mind and Brain, Humboldt-Universität zu Berlin, Berlin, Germany

RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Faculty of Medicine, Vilnius University, Vilnius, Lithuania

Faculty of Medicine, Vilnius University, Vilnius, Lithuania

Psychiatry Department, University of Indonesia - Cipto Mangunkusumo National General Hospital, Jakarta, Indonesia

Department of Psychiatry, 1st Faculty of Medicine and General University Hospital, Prague, Czech Republic

Dipartimento di Biologia, Universita' di Pisa, Pisa, Italy

Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA, USA

Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA, USA

Department of Biomedical Data Science, Stanford University, Stanford, CA, USA

Psychiatric and Neurodevelopmental Genetics Unit, Department of Psychiatry and Center for Genomic Medicine, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

Psychiatric and Neurodevelopmental Genetics Unit, Department of Psychiatry and Center for Genomic Medicine, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

Psychiatric and Neurodevelopmental Genetics Unit, Department of Psychiatry and Center for Genomic Medicine, Massachusetts General Hospital, Harvard Medical School, Boston, MA, USA

Department of Psychiatry, Wright State University, Dayton, OH, USA

Department of Psychiatry, Hadassah-Hebrew University Medical Center, Jerusalem, Israel

Zhongshan School of Medicine and Key Laboratory of Tropical Diseases Control (SYSU), Sun Yat-sen University, Guangzhou, China

Department of Psychiatry, Columbia University, New York, NY, USA

Department of Psychiatry, Columbia University, New York, NY, USA

VISN 22, Mental Illness Research, Education and Clinical Center (MIRECC), VA San Diego Healthcare System, San Diego, CA, USA

VISN 22, Mental Illness Research, Education and Clinical Center (MIRECC), VA San Diego Healthcare System, San Diego, CA, USA

Department of Psychiatry, National Taiwan University Hospital, Taipei, Taiwan

Neurobiology and Cognitive Science Center, National Taiwan University, Taipei, Taiwan

Neurobiology and Cognitive Science Center, National Taiwan University, Taipei, Taiwan

Mental Health Unit, Department of Public Health Solutions, National Institute for Health and Welfare, Helsinki, Finland

Department of Psychiatry, University of Helsinki, Helsinki, Finland

Hunter New England Health and University of Newcastle, Newcastle, New South Wales, Australia

Department of Genetics and Pathology, International Hereditary Cancer Center, Pomeranian Medical University in Szczecin, Szczecin, Poland

Department of Psychiatry, UMC Utrecht Brain Center, University Medical Centre Utrecht, Utrecht University, Utrecht, The Netherlands

Department of Psychiatry, UMC Utrecht Brain Center, University Medical Centre Utrecht, Utrecht University, Utrecht, The Netherlands

Department of Psychiatry, UMC Utrecht Brain Center, University Medical Centre Utrecht, Utrecht University, Utrecht, The Netherlands

Department of Translational Neuroscience, UMC Utrecht Brain Center, University Medical Center Utrecht, Utrecht University, Utrecht, The Netherlands

Second Opinion Outpatient Clinic, GGNet Mental Health, Warnsveld, The Netherlands

Department of Biology and Medical Genetics, 2nd Faculty of Medicine and University Hospital Motol, Prague, Czech Republic

Black Dog Institute, University of New South Wales, Randwick, New South Wales, Australia

Melbourne School of Population and Global Health, University of Melbourne, Melbourne, Victoria, Australia

Department of Mental Health, Bloomberg School of Public Health, Johns Hopkins University, Baltimore, MD, USA

Department for Neurodegenerative Diseases and Geriatric Psychiatry, University Hospital Bonn, Bonn, Germany

Department of Genetics and Genomics, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Department of Genetics and Genomics, Icahn School of Medicine at Mount Sinai, New York, NY, USA

Asfalia Biologics, iPEPS-ICM, Hôpital Universitaire de la Pitié-Salpêtrière, Paris, France

Semel Institute for Neurosciene, University of California Los Angeles, Los Angeles, CA, USA

Department of Medicine, Harvard Medical School, Boston, MA, USA

Department of Medicine, Harvard Medical School, Boston, MA, USA

Hospital Universitari Institut Pere Mata, IISPV, Universitat Rovira i Virgili, CIBERSAM, Reus, Spain

Hospital Universitari Institut Pere Mata, IISPV, Universitat Rovira i Virgili, CIBERSAM, Reus, Spain

Hospital Universitari Institut Pere Mata, IISPV, Universitat Rovira i Virgili, CIBERSAM, Reus, Spain

Department of Psychiatry, Dalhousie University, Halifax, Nova Scotia, Canada

Department of Psychiatry, Dalhousie University, Halifax, Nova Scotia, Canada

Department of Community Health and Epidemiology, Dalhousie University, Halifax, Nova Scotia, Canada

Institute of Psychiatric Phenomics and Genomics (IPPG), University Hospital, LMU Munich, Munich, Germany

Institute of Psychiatric Phenomics and Genomics (IPPG), University Hospital, LMU Munich, Munich, Germany

VA Boston Health Care System, Brockton, MA, USA

Centre for Neuroimaging, Cognition and Genomics (NICOG), National University of Ireland Galway, Galway, Ireland

Centre for Neuroimaging, Cognition and Genomics (NICOG), National University of Ireland Galway, Galway, Ireland

Centre for Neuroimaging, Cognition and Genomics (NICOG), National University of Ireland Galway, Galway, Ireland

Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Queensland Brain Institute, University of Queensland, Brisbane, Queensland, Australia

Queensland Centre for Mental Health Research, The Park Centre for Mental Health, Brisbane, Queensland, Australia

Department of Psychiatry and the Behavioral Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, USA

Department of Psychiatry and the Behavioral Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, USA

College of Medicine, SUNY Downstate Health Sciences University, New York, NY, USA

Department of Biomedicine, Aarhus University, Aarhus, Denmark

Department of Medical Genetics, University of Pécs, School of Medicine, Pécs, Hungary

Massachusetts Mental Health Center Public Psychiatry Division of the Beth Israel Deaconess Medical Center, Boston, MA, USA

Massachusetts Mental Health Center Public Psychiatry Division of the Beth Israel Deaconess Medical Center, Boston, MA, USA

Estonian Genome Center, Institute of Genomics, University of Tartu, Tartu, Estonia

Estonian Genome Center, Institute of Genomics, University of Tartu, Tartu, Estonia

Estonian Genome Center, Institute of Genomics, University of Tartu, Tartu, Estonia

School of Psychology, University of Newcastle, Newcastle, New South Wales, Australia

Psychiatric Clinic, Alexandrovska University Hospital, Sofia, Bulgaria

Department of Pharmacy, University of Oslo, Oslo, Norway

Center for Psychopharmacology, Diakonhjemmet Hospital, Oslo, Norway

Department of Nursing, Faculty of Health Sciences and Biomedical Research Centre (CIBM), University of Granada, Granada, Spain

Department of Genetics, Faculty of Biological Sciences, Universidad de Valencia, Valencia, Spain

Biomedical Research Institute INCLIVA, Valencia, Spain

Biomedical Research Institute INCLIVA, Valencia, Spain

Department of Psychological Medicine, Institute of Psychiatry, Psychology, and Neuroscience, King’s College London, London, UK

Departments of Public Health and Preventive Medicine, Family Medicine, and Psychiatry and Behavioral Sciences, State University of New York, Upstate Medical University, Syracuse, NY, USA

Institut de Biologia Evolutiva (UPF-CSIC), Departament de Ciències Experimentals i de la Salut, Universitat Pompeu Fabra, PRBB, Barcelona, Spain

Department of Psychiatry, Royal College of Surgeons in Ireland, Dublin, Ireland

Department for Neurosciences, Center for Contextual Psychiatry, KU Leuven, Leuven, Belgium

Cognitive Neuropsychiatry Laboratory, Department of Psychiatry and Psychotherapy, Philipps Universität Marburg, Marburg, Germany

Department of Psychiatry and Psychotherapy, Jena University Hospital, Jena, Germany

Department of Psychiatry and Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Department of Psychiatry and Behavioral Sciences, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Centre for Public Health, Institute of Clinical Sciences, Queen’s University Belfast, Belfast, UK

Department of Statistics and Applied Probability, University of California at Santa Barbara, Santa Barbara, CA, USA

Computational Research Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA

Department of Psychiatry, University of Colorado Denver, Aurora, CO, USA

Department of Psychiatry, University of Colorado Denver, Aurora, CO, USA

Department of Morphology and Genetics, Laboratorio de Genetica, Universidade Federal de São Paulo, São Paulo, Brazil

Department of Morphology and Genetics, Laboratorio de Genetica, Universidade Federal de São Paulo, São Paulo, Brazil

Department of Morphology and Genetics, Laboratorio de Genetica, Universidade Federal de São Paulo, São Paulo, Brazil

Melbourne Neuropsychiatry Centre, University of Melbourne and Melbourne Health, Melbourne, Victoria, Australia

The Florey Institute of Neuroscience and Mental Health, University of Melbourne, Parkville, Victoria, Australia

The Florey Institute of Neuroscience and Mental Health, University of Melbourne, Parkville, Victoria, Australia

Department of Psychiatry, Melbourne Medical School, University of Melbourne, Parkville, Victoria, Australia

Department of Psychiatry, Melbourne Medical School, University of Melbourne, Parkville, Victoria, Australia

Department of Public Health Solutions, Genomics and Biomarkers Unit, National Institute for Health and Welfare, Helsinki, Finland

Department of Psychiatry and SleepWell Research Program, Faculty of Medicine, University of Helsinki and Helsinki University Central Hospital, Helsinki, Finland

Queensland Centre for Mental Health Research, University of Queensland, Brisbane, Queensland, Australia

Queensland Centre for Mental Health Research, University of Queensland, Brisbane, Queensland, Australia

Department of Psychiatry, University of North Carolina, Chapel Hill, NC, USA

Department of Psychiatry, University of North Carolina, Chapel Hill, NC, USA

Clinic of Psychiatry and Psychotherapy, Weißer Hirsch, Dresden, Germany

Department of Stem Cell and Regenerative Biology, Harvard University, Cambridge, MA, USA

Department of Stem Cell and Regenerative Biology, Harvard University, Cambridge, MA, USA

Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Institute for Molecular Medicine Finland (FIMM), University of Helsinki, Helsinki, Finland

Centre for Genomic and Experimental Medicine, Institute of Genetics and Molecular Medicine, University of Edinburgh, Western General Hospital, Edinburgh, UK

Department of Basic and Clinical Neuroscience, Institute of Psychiatry, Psychology and Neuroscience, King’s College London, London, UK

South London and Maudsley NHS Mental Health Foundation Trust, London, UK

South London and Maudsley NHS Mental Health Foundation Trust, London, UK

Oxford Health NHS Foundation Trust, Warneford Hospital, Oxford, UK

Department of Psychiatry, University of Oxford, Oxford, UK

Department of Psychiatry and Behavioral Sciences, University of Washington, Seattle, WA, USA

Department of Psychiatry and Behavioral Sciences, University of Washington, Seattle, WA, USA

VA Puget Sound Health Care System, Seattle, WA, USA

VA Puget Sound Health Care System, Seattle, WA, USA

Huntsman Mental Health Institute, Department of Psychiatry, University of Utah School of Medicine, Salt Lake City, UT, USA

SUNY Upstate Medical University, Syracuse, NY, USA

SUNY Upstate Medical University, Syracuse, NY, USA

Department of Psychiatry, Massachusetts General Hospital, Boston, MA, USA

Department of Psychiatry, Massachusetts General Hospital, Boston, MA, USA

Department of Psychiatry, Psychosomatics and Psychotherapy, Julius-Maximilians-Universität Würzburg, Würzburg, Germany

Department of Psychiatry, Psychosomatics and Psychotherapy, Julius-Maximilians-Universität Würzburg, Würzburg, Germany

Généthon, Evry, France

THL–Finnish Institute for Health and Welfare, Helsinki, Finland

THL–Finnish Institute for Health and Welfare, Helsinki, Finland

Department of Psychiatry, School of Medicine, University of Valencia, Hospital Clínico Universitario de Valencia, Valencia, Spain

Priority Centre for Brain and Mental Health Research, University of Newcastle, Mater Hospital, McAuley Centre, Newcastle, New South Wales, Australia

Division of Molecular Medicine, NSW Health Pathology North, Newcastle, New South Wales, Australia

Division of Cancer Epidemiology and Genetics, National Cancer Institute, Bethesda, MD, USA

James J. Peters VA Medical Center, Bronx, NY, USA

James J. Peters VA Medical Center, Bronx, NY, USA

Faculty of Medicine, University of Iceland, Reykjavik, Iceland

Department of Psychiatry, Landspitali University Hospital, Reykjavik, Iceland

West Region, Institute of Mental Health, Singapore, Singapore

Yoo Loo Lin School of Medicine, National University of Singapore, Singapore, Singapore

Lee Kong Chian School of Medicine, Nanyang Technological University, Singapore, Singapore

School of Biomedical Sciences, The Chinese University of Hong Kong, Hong Kong, China

Department of Psychiatry, The Chinese University of Hong Kong, Hong Kong, China

School of Social and Health Sciences, Leeds Trinity University, Leeds, UK

TIPS - Network for Clinical Research in Psychosis, Stavanger University Hospital, Stavanger, Norway

NORMENT Centre, Institute of Clinical Medicine, University of Oslo, Oslo, Norway

NORMENT Centre, Institute of Clinical Medicine, University of Oslo, Oslo, Norway

Department of Neurology, Medical University of Vienna, Vienna, Austria

NORMENT Centre, Institute of Clinical Medicine, University of Oslo, Oslo, Norway

Department of Neurology, Medical University of Vienna, Vienna, Austria

Harvard Medical School Department of Psychiatry at Beth Israel Deaconess Medical Center, Boston, MA, USA

Massachusetts Mental Health Center, Boston, MA, USA

Lieber Institute for Brain Development, Baltimore, MD, USA

Lieber Institute for Brain Development, Baltimore, MD, USA

Lieber Institute for Brain Development, Baltimore, MD, USA

Lieber Institute for Brain Development, Baltimore, MD, USA

Department of Medical Genetics, University Medical Centre Utrecht, Utrecht, The Netherlands

Department of Biostatistics, Fielding School of Public Health, University of California Los Angeles, Los Angeles, CA, USA

Department of Psychiatry, Washington University, St Louis, MO, USA

Department of Psychiatry, Washington University, St Louis, MO, USA

Department of Psychiatry, Charité – Universitätsmedizin Berlin, Berlin, Germany

Berlin Institute of Health (BIH), Berlin, Germany

Laboratory for Statistical and Translational Genetics, RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Laboratory for Statistical and Translational Genetics, RIKEN Center for Integrative Medical Sciences, Yokohama, Japan

Université de Paris, Faculté de Médecine, Hôpital Cochin-Tarnier, Paris, France

INSERM U1266, Institut de Psychiatrie et de Neurosciences, Paris, France

Bulgarian Academy of Science, Sofia, Bulgaria

Department of Neuroscience, Biomedicine and Movement Sciences, Section of Psychiatry, University of Verona, Verona, Italy

Psychiatry Unit, IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli, Brescia, Italy

Department of Psychiatry, Faculty of Medicine, Istanbul University, Istanbul, Turkey

Division of Mental Health, St. Olav’s Hospital, Trondheim University Hospital, Trondheim, Norway

Department of Mental Health, Norwegian University of Science and Technology, Trondheim, Norway

Department of Neurosciences, Center for Clinical Psychiatry, KU Leuven, Leuven, Belgium

Department of Psychiatry, Research Unit of Clinical Neuroscience, University of Oulu, Oulu, Finland

Department of Psychiatry, Research Unit of Clinical Neuroscience, University of Oulu, Oulu, Finland

Medical Research Center Oulu, Oulu University Hospital and University of Oulu, Oulu, Finland

Molecular and Cellular Therapeutics, Royal College of Surgeons in Ireland, Dublin, Ireland

Neuropsychiatric Epidemiology Research Unit, School of Population and Global Health, University of Western Australia, Perth, Western Australia, Australia

Neuropsychiatric Epidemiology Research Unit, School of Population and Global Health, University of Western Australia, Perth, Western Australia, Australia

Centre for Clinical Research in Neuropsychiatry, University of Western Australia, Perth, Western Australia, Australia

Centre for Clinical Research in Neuropsychiatry, University of Western Australia, Perth, Western Australia, Australia

Centre for Clinical Research in Neuropsychiatry, University of Western Australia, Perth, Western Australia, Australia

Sheba Medical Center, Tel Hashomer, Israel

Baker Heart and Diabetes Institute, Melbourne, Victoria, Australia

Department of Psychiatry, GGz Centraal, Utrecht, The Netherlands

Stanley Neurovirology Laboratory, Johns Hopkins University School of Medicine, Baltimore, MD, USA

Campbell Family Mental Health Research Institute, Centre for Addiction and Mental Health, Toronto, Ontario, Canada

Campbell Family Mental Health Research Institute, Centre for Addiction and Mental Health, Toronto, Ontario, Canada

Department of Psychiatry, University of Toronto, Toronto, Ontario, Canada

Department of Psychiatry, University of Toronto, Toronto, Ontario, Canada

Department of Psychiatry, The First Affiliated Hospital of Xi’an Jiaotong University, Xi’an, China

Center for Translational Medicine, The First Affiliated Hospital of Xi’an Jiaotong University, Xi’an, China

Department of Psychiatry, School of Medicine, Ankara University, Ankara, Turkey

Department of Psychiatry, School of Medicine, Ankara University, Ankara, Turkey

Department of Psychiatry, Queens University Kingston, Kingston, Ontario, Canada

Department of Psychiatry, University of Iowa Carver College of Medicine, Iowa City, IA, USA

School of Nursing, Louisiana State University Health Sciences Center, New Orleans, LA, USA

Department of Psychiatry, University of California San Francisco, San Francisco, CA, USA

Center for Neuropsychiatric Research, National Health Research Institutes, Zhunan Town, Taiwan

Institute of Epidemiology and Preventive Medicine, College of Public Health, National Taiwan University, Taipei, Taiwan

University of Sevilla, CIBERSAM IBiS, Seville, Spain

Hospital Universitario Virgen del Rocio, Department of Psychiatry, Universidad del Sevilla, Seville, Spain

Discipline of Psychiatry, Adelaide Medical School, University of Adelaide, Adelaide, South Australia, Australia

Ramsay Health Care (SA) Mental Health, Adelaide, South Australia, Australia

Northern Adelaide Local Health Network, Adelaide, South Australia, Australia

Department of Molecular and Translational Medicine, University of Brescia, Brescia, Italy

Genetic Unit, IRCCS Istituto Centro San Giovanni di Dio Fatebenefratelli, Brescia, Italy

Department of Psychiatry, College of Medicine and National Taiwan University Hospital, National Taiwan University, Taipei, Taiwan

Psychosis Research Unit, Aarhus University Hospital, Aarhus, Denmark

Max Planck Institute of Psychiatry, Munich, Germany

Munich Cluster for Systems Neurology, Munich, Germany

Department of Health Data Science, University of Liverpool, Liverpool, UK

Menzies Institute for Medical Research, University of Tasmania, Hobart, Tasmania, Australia

Mental Health Services in the Capital Region of Denmark, Mental Health Center Copenhagen, University of Copenhagen, Copenhagen, Denmark

Rutgers University, Robert Wood Johnson Medical School, New Brunswick, NJ, USA

Rutgers University, Robert Wood Johnson Medical School, New Brunswick, NJ, USA

Rutgers University, New Jersey Medical School, Newark, NJ, USA

Rutgers University, New Jersey Medical School, Newark, NJ, USA

Department of Mathematics and Statistics, University of Helsinki, Helsinki, Finland

Department of Public Health, University of Helsinki, Helsinki, Finland

Department of Psychiatry and Behavioral Sciences, SUNY Upstate Medical University, Syracuse, NY, USA

Department of Psychiatry and Psychotherapy, University Medical Center Göttingen, Göttingen, Germany

Department of Psychiatry and Behavioral Sciences, The Johns Hopkins University, Baltimore, MD, USA

Program in Medical and Population Genetics, The Broad Institute of MIT and Harvard, Cambridge, MA, USA

Program in Medical and Population Genetics, The Broad Institute of MIT and Harvard, Cambridge, MA, USA

Regeneron Genetics Center, Orange, CA, USA

College of Public Health, China Medical University, Taichung, Taiwan

State Key Laboratory of Genetic Engineering and Ministry of Education (MOE) Key Laboratory of Contemporary Anthropology, Collaborative Innovation Center of Genetics and Development, Human Phenome Institute, School of Life Sciences, Fudan University, Shanghai, China

School of Life Science and Technology, ShanghaiTech University, Shanghai, China

Center for Excellence in Animal Evolution and Genetics, Chinese Academy of Sciences, Kunming, China

Department of Clinical Sciences, Psychiatry, Umeå University, Umeå, Sweden

Division of Psychiatry, Department of Mental Health Neuroscience, University College London, London, UK

Department of Psychiatry, San Cecilio University Hospital, University of Granada, Granada, Spain

Institute of Medical Genetics and Pathology, University Hospital Basel, Basel, Switzerland

Department of Biomedicine, University of Basel, Basel, Switzerland

Institute of Neuroscience and Medicine (INM-1), Research Center Juelich, Juelich, Germany

Eli Lilly and Company, Windlesham, UK

Eli Lilly and Company, Windlesham, UK

Neuropsychiatric Genetics Research Group, Department of Psychiatry, Trinity College Dublin, Dublin, Ireland

Neuropsychiatric Genetics Research Group, Department of Psychiatry, Trinity College Dublin, Dublin, Ireland

UCL Genetics Institute, University College London, London, UK

Centre for Psychiatry, Queen Mary University London, London, UK

Department of Cellular, Computational and Integrative Biology, University of Trento, Trento, Italy

Dementia Research Institute, Cardiff University, Cardiff, UK

Department of Psychiatry, Phoenix VA Healthcare System, Phoenix, AZ, USA

Banner-University Medical Center, Phoenix, AZ, USA

Department of Human Molecular Genetics of the Institute of Biochemistry and Genetics of the Ufa Federal Research Center of the Russian Academy of Sciences (IBG UFRC RAS), Ufa, Russia

Department of Human Molecular Genetics of the Institute of Biochemistry and Genetics of the Ufa Federal Research Center of the Russian Academy of Sciences IBG UFRC RAS), Ufa, Russia

Department of Human Molecular Genetics of the Institute of Biochemistry and Genetics of the Ufa Federal Research Center of the Russian Academy of Sciences (IBG UFRC RAS), Ufa, Russia

Federal State Educational Institution of Highest Education Bashkir State Medical University of Public Health Ministry of Russian Federation (BSMU), Ufa, Russia

Federal State Educational Institution of Highest Education Bashkir State Medical University of Public Health Ministry of Russian Federation (BSMU), Ufa, Russia

Federal State Educational Institution of Highest Education Bashkir State Medical University of Public Health Ministry of Russian Federation (BSMU), Ufa, Russia

Psychiatric Genetic Epidemiology and Neurobiology Laboratory (PsychGENe lab), Department of Psychiatry and Behavioral Sciences, SUNY Upstate Medical University, Syracuse, NY, USA

Department of Psychiatry, Sungkyunkwan University School of Medicine, Samsung Medical Center, Seoul, Korea

Department of Psychiatry and Zilkha Neurogenetics Institute, Keck School of Medicine at University of Southern California, Los Angeles, CA, USA

Department of Cell Biology, State University of New York, Downstate Health Sciences University, New York, NY, USA

Department of Psychosis, Institute of Mental Health, Singapore, Singapore

Neuroscience and Mental Health, Lee Kong Chian School of Medicine, Nanyang Technological University, Singapore, Singapore

Institute of Behavioral Science, Feinstein Institutes for Medical Research, Manhasset, NY, USA

Institute of Behavioral Science, Feinstein Institutes for Medical Research, Manhasset, NY, USA

Department of Psychiatry, Zucker School of Medicine at Hofstra/Northwell, Hempstead, NY, USA

Department of Psychiatry, Zucker School of Medicine at Hofstra/Northwell, Hempstead, NY, USA

Human Genetics, Genome Institute of Singapore, A*STAR, Singapore, Singapore

Department of Medicine, Yong Loo Lin School of Medicine, National University of Singapore, Singapore, Singapore

Roche Pharma Research and Early Development, Roche Innovation Center Basel, F. Hoffman-La Roche, Basel, Switzerland

Department of Preventative Medicine, Faculdade de Medicina FMUSP, University of São Paulo, São Paulo, Brazil

Department of Psychiatry, University of Pittsburgh, Pittsburgh, PA, USA

Center for Neurobehavioral Genetics, Semel Institute for Neuroscience and Human Behavior, University of California Los Angeles, Los Angeles, CA, USA

Department of Psychiatry, Erasmus University Medical Center, Rotterdam, The Netherlands

Early Clinical Development, Pfizer Worldwide Research and Development, Groton, CT, USA

Analytic and Translational Genetics Unit, Department of Medicine, Department of Neurology and Department of Psychiatry, Massachusetts General Hospital, Boston, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Stanley Center for Psychiatric Research, Broad Institute of MIT and Harvard, Cambridge, MA, USA

Shanghai Key Laboratory of Psychotic Disorders, Shanghai Mental Health Center, Shanghai Jiao Tong University School of Medicine, Shanghai, China

Department of Biochemistry and Molecular Biology II, Faculty of Pharmacy, University of Granada, Granada, Spain

Institute of Neurosciences, Biomedical Research Center (CIBM), University of Granada, Granada, Spain

Faculty of Science, Medicine and Health, University of Wollongong, Wollongong, New South Wales, Australia

Illawarra Health and Medical Research Institute, Wollongong, New South Wales, Australia

Department of Biomedical and Neuromotor Sciences, University of Bologna, Bologna, Italy

Centre for PanorOmic Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Centre for PanorOmic Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

State Key Laboratory of Brain and Cognitive Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

State Key Laboratory of Brain and Cognitive Sciences, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Department of Psychiatry, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Department of Psychiatry, LKS Faculty of Medicine, The University of Hong Kong, Hong Kong, China

Institute of Medical Sciences, University of Aberdeen, Aberdeen, UK

Center for Behavioral Genomics, Department of Psychiatry, University of California San Diego, La Jolla, CA, USA

Institute of Genomic Medicine, University of California San Diego, La Jolla, CA, USA

University Medical Center Utrecht, Department of Psychiatry, Utrecht, The Netherlands

Department of Psychiatry and Human Behavior, School of Medicine, University of California Irvine, Irvine, CA, USA

Institute of Biological Psychiatry, Mental Health Services, Copenhagen University Hospital, Copenhagen, Denmark

Department of Clinical Medicine, University of Copenhagen, Copenhagen, Denmark

Department of Clinical Medicine, University of Copenhagen, Copenhagen, Denmark

Center for GeoGenetics, GLOBE Institute, University of Copenhagen, Copenhagen, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research, iPSYCH, Copenhagen, Denmark

The Lundbeck Foundation Initiative for Integrative Psychiatric Research, iPSYCH, Copenhagen, Denmark

School of Psychiatry and Clinical Neurosciences, University of Western Australia, Perth, Western Australia, Australia

School of Psychiatry and Clinical Neurosciences, University of Western Australia, Perth, Western Australia, Australia

Peking University Sixth Hospital, Peking University Institute of Mental Health, Beijing, China

Peking University Sixth Hospital, Peking University Institute of Mental Health, Beijing, China

National Clinical Research Center for Mental Disorders, NHC Key Laboratory of Mental Health (Peking University) and Chinese Academy of Medical Sciences Research Unit, Beijing, China

National Clinical Research Center for Mental Disorders, NHC Key Laboratory of Mental Health (Peking University) and Chinese Academy of Medical Sciences Research Unit, Beijing, China

PKU–IDG/McGovern Institute for Brain Research, Peking University, Beijing, China

Mental Illness Research, Education, and Clinical Center (VISN 2 South), James J. Peters VA Medical Center, New York, NY, USA

Oxford Health NHS Foundation Trust, Oxford, UK

Department of Clinical Genetics, Center for Neurogenomics and Cognitive Research, University Medical Center Amsterdam, Amsterdam, The Netherlands

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Department of Functional Genomics, Faculty of Exact Science, Center for Neurogenomics and Cognitive Research, VU University Amsterdam and VU Medical Center, Amsterdam, The Netherlands

Westlake Laboratory of Life Sciences and Biomedicine, Hangzhou, China

Western Australian Institute for Medical Research and Centre for Medical Research, University of Western Australia, Nedlands, Western Australia, Australia

Western Australian Institute for Medical Research and Centre for Medical Research, University of Western Australia, Nedlands, Western Australia, Australia

Western Australian Institute for Medical Research and Centre for Medical Research, University of Western Australia, Nedlands, Western Australia, Australia

School of Psychiatry and Clinical Neurosciences, University of Western Australia, Crawley, Western Australia, Australia

School of Psychiatry and Clinical Neurosciences, University of Western Australia, Crawley, Western Australia, Australia

School of Psychiatry and Clinical Neurosciences, University of Western Australia, Crawley, Western Australia, Australia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

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Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

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Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

Department of Psychiatry, University of Indonesia, Jakarta, Indonesia

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Department of Psychiatry, University of Indonesia, Jakarta, Indonesia
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia
Department of Psychiatry, University of Indonesia, Jakarta, Indonesia
Mayo Clinic, Rochester, MN, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Mount Sinai, New York, NY, USA
Duke University, Durham, NC, USA
Duke University, Durham, NC, USA
Duke University, Durham, NC, USA
University of Chicago, Chicago, IL, USA
University of Chicago, Chicago, IL, USA
Karolinska Institutet, Stockholm, Sweden
Yale University, New Haven, CT, USA
Yale University, New Haven, CT, USA
Yale University, New Haven, CT, USA
Yale University, New Haven, CT, USA
Yale University, New Haven, CT, USA
Yale University, New Haven, CT, USA
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Yale University, New Haven, CT, USA

Yale University, New Haven, CT, USA

Yale University, New Haven, CT, USA

Yale University, New Haven, CT, USA

Yale University, New Haven, CT, USA

University of Southern California, Los Angeles, CA, USA

University of Southern California, Los Angeles, CA, USA

University of Southern California, Los Angeles, CA, USA

University of Southern California, Los Angeles, CA, USA

University of Southern California, Los Angeles, CA, USA

University of Southern California, Los Angeles, CA, USA

University of Southern California, Los Angeles, CA, USA

University of California Los Angeles, Los Angeles, CA, USA

University of California Los Angeles, Los Angeles, CA, USA

University of California Los Angeles, Los Angeles, CA, USA

University of California Los Angeles, Los Angeles, CA, USA

University of Illinois at Chicago, Chicago, IL, USA

University of Illinois at Chicago, Chicago, IL, USA

University of Illinois at Chicago, Chicago, IL, USA

University of Illinois at Chicago, Chicago, IL, USA

Johns Hopkins University, Baltimore, MD, USA

Johns Hopkins University, Baltimore, MD, USA

University of North Carolina - Chapel Hill, Chapel Hill, NC, USA

SUNY Downstate Medical Center, New York, NY, USA

University of Massachusetts, Amherst, MA, USA

University of Massachusetts, Amherst, MA, USA

University of Massachusetts, Amherst, MA, USA

Sage Bionetworks, Seattle, WA, USA

University of California San Francisco, San Francisco, CA, USA

University of Massachusetts Medical School, Worcester, MA, USA

Yong Loo Lin School of Medicine, National University of Singapore, Singapore, Singapore

King’s College London, London, UK

King’s College London, London, UK

King’s College London, London, UK

King’s College London, London, UK

King’s College London, London, UK

King’s College London, London, UK

King’s College London, London, UK

King’s College London, London, UK

Fundació de Docència i Recerca Mútua de Terrassa, Universitat de Barcelona, Barcelona, Spain

Child and Adolescent Psychiatry, University of Technology Dresden, Dresden, Germany

Section for Experimental Psychopathology, General Psychiatry, Heidelberg, Germany

Section for Experimental Psychopathology, General Psychiatry, Heidelberg, Germany

Institute of Cognitive Neuroscience, University College London, London, UK

University Hospital Marqués de Valdecilla, Instituto de Formación e Investigación Marqués de Valdecilla, University of Cantabria, Santander, Spain

University Hospital Marqués de Valdecilla, Instituto de Formación e Investigación Marqués de Valdecilla, University of Cantabria, Santander, Spain

Neuroscience and Mental Health Research Institute, Division of Psychiatry and Clinical Neuroscience, Cardiff University, Cardiff, UK

Division of Psychiatry, University of Edinburgh, Edinburgh, UK

Division of Psychiatry, University of Edinburgh, Edinburgh, UK

Department of Psychiatry, Academic Medical Center, University of Amsterdam, Amsterdam, The Netherlands

Department of Human Genetics, David Geffen School of Medicine, University of California Los Angeles, Los Angeles, CA, USA

Maastricht University Medical Centre, South Limburg Mental Health Research and Teaching Network, EURON, Maastricht, The Netherlands

Institute of Psychiatry, King’s College London, London, UK

Department of Psychiatry, University of Halle, Halle, Germany

Department of Psychiatry, University of Munich, Munich, Germany

Department of Fundamental Neurosciences, University of Lausanne, Lausanne, Switzerland

Department of Fundamental Neurosciences, University of Lausanne, Lausanne, Switzerland

RG Neuroplasticity, Leibniz Institute for Neurobiology, Magdeburg, Germany

RG Neuroplasticity, Leibniz Institute for Neurobiology, Magdeburg, Germany

Molecular Physiology of the Synapse Laboratory, Biomedical Research Institute Sant Pau, Barcelona, Spain

Department of Neurology, Yale School of Medicine, New Haven, CT, USA

Department of Molecular Neurobiology, Max Planck Institute of Experimental Medicine, Göttingen, Germany

LSI Neurobiology Programme, National University of, Singapore, Singapore

Zilkha Neurogenetic Institute and Department of Psychiatry and Behavioral Sciences, Keck School of Medicine, University of Southern California, Los Angeles, CA, USA

Functional Genomics section, Department of Human Genetics, Center for Neurogenomics and Cognitive Research, Amsterdam University Medical Center, Amsterdam, The Netherlands

Functional Genomics section, Department of Human Genetics, Center for Neurogenomics and Cognitive Research, Amsterdam University Medical Center, Amsterdam, The Netherlands

Cell Biology, Neurobiology and Biophysics, Department of Biology, Faculty of Science, Utrecht University, Utrecht, The Netherlands

Cell Biology, Neurobiology and Biophysics, Department of Biology, Faculty of Science, Utrecht University, Utrecht, The Netherlands

Sorbonne Université, Institut du Cerveau - Paris Brain Institute - ICM, Inserm, CNRS, APHP, Hôpital de la Pitié Salpêtrière, Paris, France

Institute for Pharmacology and Toxicology, Medical Faculty Otto-von-Guericke University Magdeburg, Magdeburg, Germany

Institute for Pharmacology and Toxicology, Medical Faculty Otto-von-Guericke University Magdeburg, Magdeburg, Germany

Institute for Pharmacology and Toxicology, Medical Faculty Otto-von-Guericke University Magdeburg, Magdeburg, Germany

Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

Leibniz Institute for Neurobiology (LIN), Magdeburg, Germany

McGovern Institute for Brain Research, Department of Brain and Cognitive Sciences, Massachusetts Institute of Technology (MIT), Cambridge, MA, USA

Solomon H. Snyder Department of Neuroscience, Kavli Neuroscience Discovery Institute, The Johns Hopkins University School of Medicine, Baltimore, MD, USA

Solomon H. Snyder Department of Neuroscience, Kavli Neuroscience Discovery Institute, The Johns Hopkins University School of Medicine, Baltimore, MD, USA

Department of Neuroscience, Genentech, South San Francisco, CA, USA

Department of Stem Cell and Regenerative Biology, Harvard University, Cambridge, MA, USA

Department of Neuroscience, University of Copenhagen, Copenhagen, Denmark

Laboratory of Neurobiology, Max-Planck Institute for Biophysical Chemistry, Göttingen, Germany

Center for Synaptic Brain Dysfunctions, Institute for Basic Science (IBS), Department of Biological Sciences, Korea Advanced Institute of Science and Technology (KAIST), Daejeon, South Korea

Center for Synaptic Brain Dysfunctions, Institute for Basic Science (IBS), Department of Biological Sciences, Korea Advanced Institute of Science and Technology (KAIST), Daejeon, South Korea

Department of Neurobiology, Harvard Medical School, Boston, MA, USA

Department of Molecular Physiology and Cell Biology, Leibniz-Forschungsinstitut für Molekulare Pharmakologie, Berlin, Germany

Nancy Pritzker Laboratory, Department of Psychiatry and Behavioral Sciences, Stanford University, Stanford, CA, USA

Department of Neurology and Neurosurgery, Montreal Neurological Institute, McGill University, Montreal, Québec, Canada

Biological Sciences, University of Southampton, Southampton, UK

Department of Biochemistry, Weill Cornell Medicine, New York, NY, USA

CNR Neuroscience Institute, Milan, Italy

CNR Neuroscience Institute, Milan, Italy

Department of Molecular and Cellular Neurobiology, Center for Neurogenomics and Cognitive Research, Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

Department of Molecular and Cellular Physiology, Howard Hughes Medical Institute, Stanford University, Stanford, CA, USA

Division of Bioinformatics, Department of Preventive Medicine, Keck School of Medicine of USC, University of Southern California, Los Angeles, CA, USA

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CONFLICTS OF INTEREST

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Consortia

Indonesia Schizophrenia Consortium

- Nan Dai
- Qin Wenwen
- D. B. Wildenauer
- Feranindhya Agiananda
- Nurmiati Amir
- Ronald Antoni

- Tiana Arsianti
- Asmarahadi Asmarahadi
- H. Diatri
- Prianto Djatmiko
- Irmansyah Irmansyah
- Siti Khalimah
- Irmia Kusumadewi
- Profitasari Kusumaningrum
- Petrin R. Lukman
- Martina W. Nasrun
- N. S. Safyuni
- Prasetyawan Prasetyawan
- G. Semen
- Kristiana Siste
- Heriani Tobing
- Natalia Widiasih
- Tjhin Wiguna
- D. Wulandari
- None Evalina
- A. J. Hananto
- Joni H. Ismoyo
- T. M. Marini
- Supiyani Henuhili
- Muhammad Reza
- & Suzy Yusnadewi

PsychENCODE

- Alexej Abyzov
- Schahram Akbarian
- Allison Ashley-Koch
- Harm van Bakel
- Michael Breen
- Miguel Brown
- Julien Bryois
- Becky Carlyle
- Alex Charney
- Gerard Coetzee
- Gregory Crawford
- Stella Dracheva
- Prashant Emani
- Peggy Farnham
- Menachem Fromer
- Timur Galeev
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- Michael C. O’Donovan

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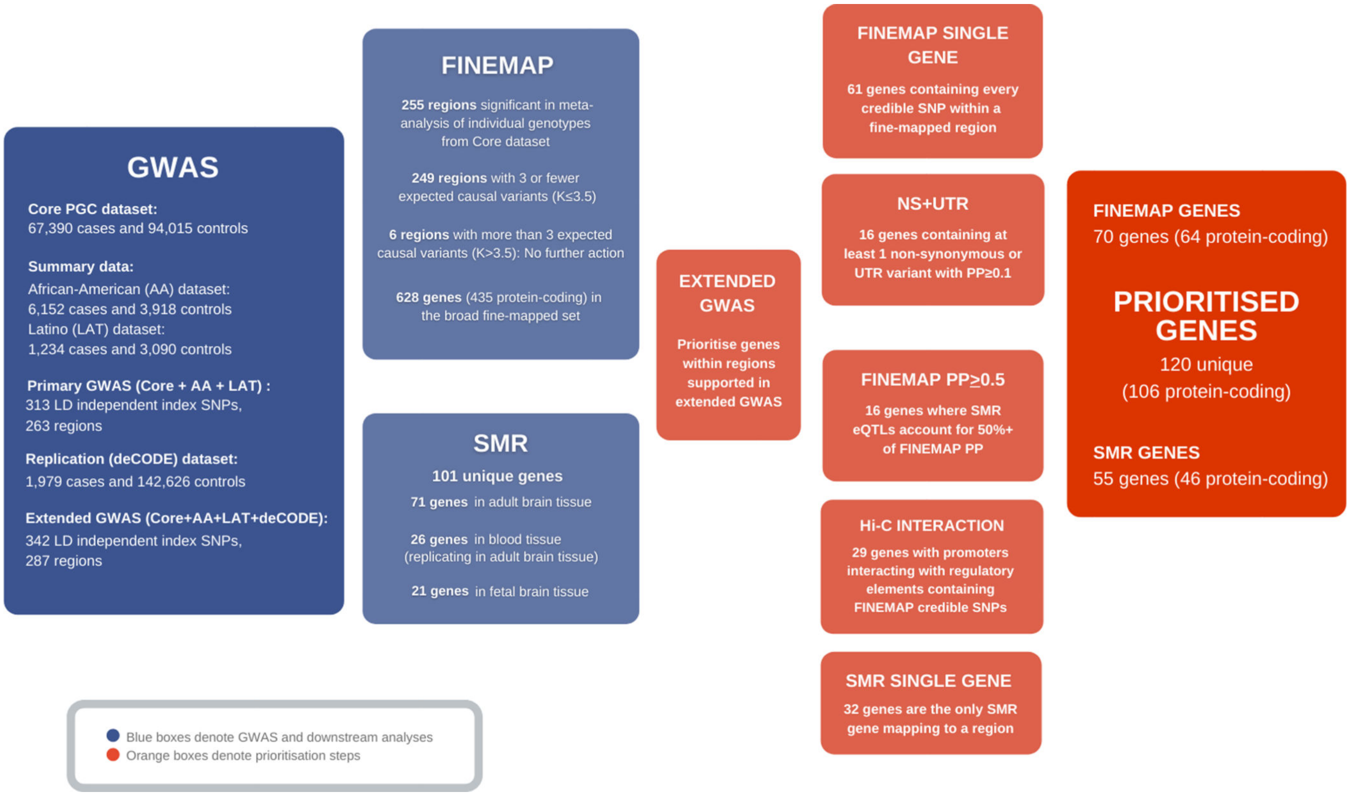

Figure 1: Overview of GWAS and gene prioritisation.

Flow diagram summarising GWAS, fine-mapping and SMR analyses and how these informed gene prioritisation.

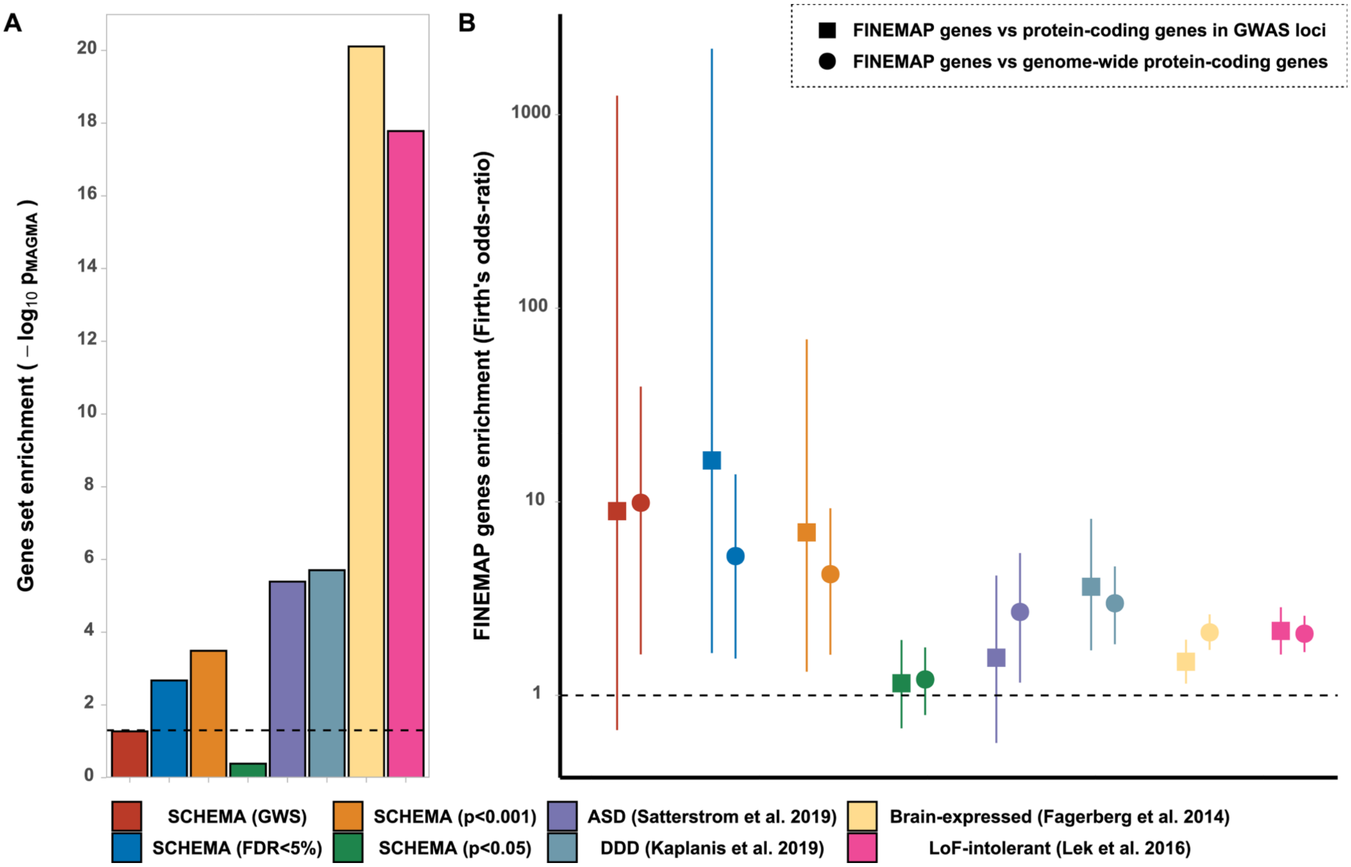

Figure 2: Gene set enrichment tests at genome-wide level and for protein coding genes containing FINEMAP credible SNPs.

Gene sets tested were retrieved from sequencing studies of schizophrenia (SCHEMA; companion paper), autism-spectrum disorder[33] and developmental disorders[32]. Sets representing genes that are intolerant to loss-of function mutations[40] (LoF-intolerant) and brain-expressed genes[41]are also shown. A) MAGMA gene set enrichment analysis, dotted line indicates nominal significance (p=0.05). B) Logistic regression (with Firth's bias reduction method) showing the odds-ratio (and 95% CI) for association between protein-coding genes containing at least 1 credible FINEMAP SNP (N=418 after excluding genes with no LoF-intolerance data) and genes from the sets indicated. Odds-ratios are relative to protein-coding genes within GWAS K≤3.5 loci (1,283 genes, squares) or across the genome excluding the xMHC (19,547 genes; circles). Dotted line indicates no enrichment.

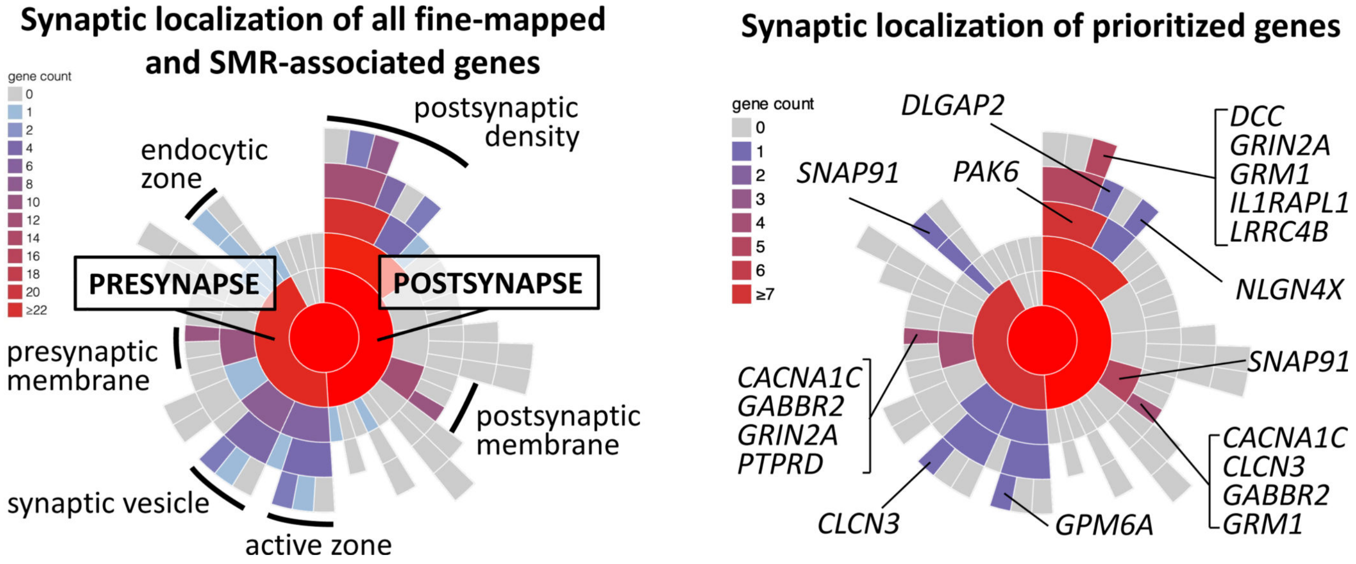

Figure 3: Mapping of all FINEMAP/SMR genes (A) and prioritised genes (B) to synaptic locations using SYNGO.

Sunburst plots depict synaptic locations with child terms in concentric rings, starting with the synapse (center), pre- and postsynaptic locations in the first ring and child terms in subsequent ring. The number of genes in each term is indicated by the colour scheme in the legend. **A)** FINEMAP/SMR genes are protein coding genes tagged by at least one credible SNP identified by FINEMAP and/or associated using SMR (N=470) of which N=58 are SynGO annotated, 51 to cellular components. **B)** Prioritised (Extended Data Table 1; N=106) of which 15 are SynGO annotated, 14 to cellular components.

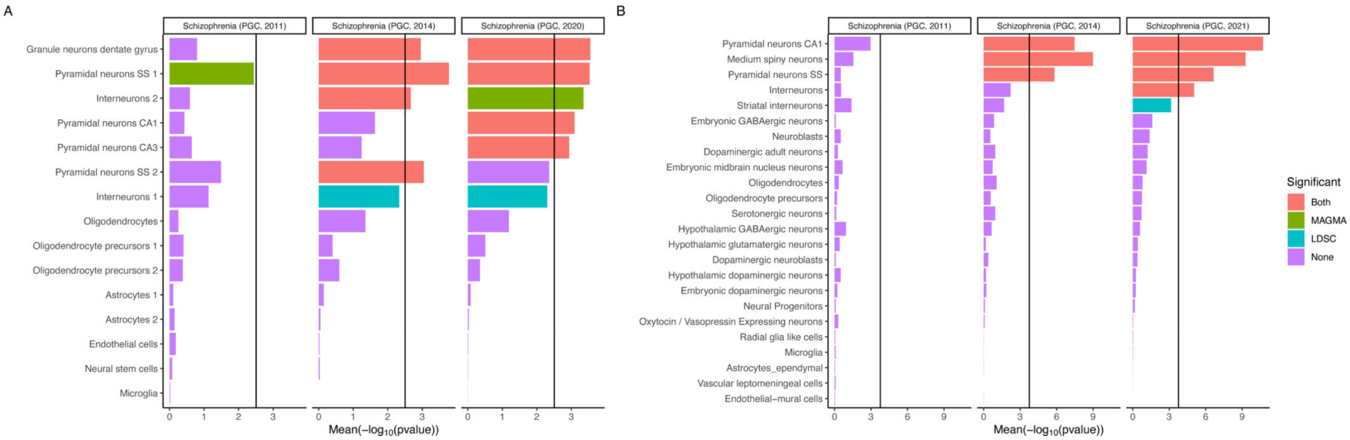

Figure 4: Associations between schizophrenia and cell types from multiple brain regions in human and mouse.

a, b, The mean of the evidence ($-\log_{10} P$ value) obtained from two methods (MAGMA and LDSC) for testing GWAS data for enrichment of associations in genes with high expression in cell types. 15 human cell types (derived from single nuclei) from the cortex and hippocampus (**a**) and 24 cell types (derived from single-cell RNA-seq) from 5 different brain regions in mouse (cortex, hippocampus, striatum, midbrain and hypothalamus) and from specific enrichments of oligodendrocytes, serotonergic neurons, dopaminergic neurons and cortical parvalbuminergic interneurons (**b**). Bar colour indicates whether the cell type is significantly associated with both methods, one method or none. The black vertical line represents the significance threshold corrected for the total number of cell types tested in each analysis. Results obtained for previous iterations of schizophrenia GWAS12,18 are shown for comparison. Pyramidal SS, pyramidal neurons from the somatosensory cortex; pyramidal CA1/CA3, pyramidal neurons from the CA1/CA3 region of the hippocampus. Where types of cell (such as interneurons) formed sub-clusters in the source data, these are designated by the suffix 1 or 2.