

Genetic evidence for protective effects of angiotensin converting enzyme against Alzheimer's disease but not other neurodegenerative diseases in European populations

Supplementary Material

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Supplementary eResults

Colocalisation of cortical *ACE* expression, systolic blood pressure and true case Alzheimer's disease using the Kunkle et al genome-wide association study

De Rojas et al defined Alzheimer's disease based on true cases and cases by proxy (defined as maternal or paternal diagnosis of Alzheimer's disease). To assess whether the use of proxy cases was influencing our analyses, we conducted sensitivity analysis using the largest GWAS of true case Alzheimer's disease (Kunkle et al, 2019). This GWAS comprised of 21,982 Alzheimer's disease cases and 41,944 cognitively normal controls of European ancestry¹. This GWAS was adjusted for adjusting for age (defined as age-at-onset for cases and age-at-last exam for controls), sex, and population substructure. In three-way colocalization by HyPrColoc, the estimated PP of full colocalization = 0.93. The variant rs4291 was the most likely shared causal variant for all traits. This is the same variant that is used in the primary analysis, suggesting that utilising proxy cases did not alter our findings. The same directions of effect were observed, with each A allele of rs4291 being positively associated with AD risk (odds ratio [OR] 1.05, 95% confidence interval [CI] 1.02 to 1.08).

Supplementary eTable 1: Instrumental variables to proxy systolic blood pressure

SNP	Effect allele	Other allele	Beta	Standard error	P value
rs10776752	T	G	0.8211	0.0576	4.61E-46
rs57748895	A	T	-1.0928	0.1159	4.13E-21
rs6699618	C	G	0.9115	0.041	1.68E-109
rs11204684	A	G	-0.1716	0.0305	1.90E-08
rs76719272	T	C	-0.2738	0.0461	2.97E-09
rs7796	C	G	0.3385	0.0314	5.00E-27
rs12731646	T	C	-0.189	0.0307	7.21E-10
rs1043069	T	G	0.234	0.0311	5.26E-14
rs4651224	T	C	0.1986	0.0306	9.00E-11
rs12042924	T	C	-0.1807	0.0303	2.62E-09
rs1474742	A	C	-0.1957	0.0306	1.65E-10
rs68085857	T	C	0.274	0.0357	1.68E-14
rs61825125	A	C	0.4117	0.0513	1.06E-15
rs699	A	G	-0.3748	0.0308	5.59E-34
rs4926499	C	G	0.2965	0.0438	1.33E-11
rs4320727	A	G	0.2338	0.0314	9.89E-14
rs4908349	A	G	0.2326	0.0329	1.57E-12
rs3795261	A	G	0.2914	0.0371	4.15E-15
rs1408945	T	G	-0.3196	0.0304	8.33E-26
rs778124	A	G	0.2965	0.0311	1.45E-21
rs4912303	T	C	0.1839	0.0327	1.79E-08
rs12136922	A	G	0.2027	0.0304	2.69E-11
rs658780	T	G	-0.2028	0.0347	5.29E-09
rs786923	T	C	-0.3082	0.031	2.83E-23
rs7514579	A	C	0.2243	0.0361	5.45E-10
rs1006545	T	G	0.6846	0.048	3.50E-46
rs11191580	T	C	1.0995	0.055	7.74E-89
rs2067831	C	G	-0.2384	0.034	2.30E-12
rs1801253	C	G	0.4626	0.0344	2.84E-41
rs11592107	A	G	0.3024	0.0326	1.55E-20

rs3793742	T	C	0.1934	0.0323	2.11E-09
rs1133400	A	G	-0.2975	0.0376	2.53E-15
rs1779240	A	G	-0.4215	0.0354	1.28E-32
rs12258967	C	G	0.6327	0.0337	1.08E-78
rs7074562	T	C	-0.2394	0.0303	2.61E-15
rs11252324	T	G	-0.4164	0.0573	3.61E-13
rs4948643	T	C	0.2258	0.0338	2.40E-11
rs1709345	T	G	0.1668	0.0303	3.55E-08
rs57946343	T	C	0.716	0.0426	2.10E-63
rs73279609	T	C	0.2058	0.0301	8.32E-12
rs2177843	T	C	0.4394	0.0432	2.80E-24
rs1572816	A	G	0.2098	0.033	2.05E-10
rs142031873	T	G	0.4462	0.0785	1.31E-08
rs2860749	A	G	-0.3898	0.0305	2.63E-37
rs604723	T	C	-0.655	0.0339	2.55E-83
rs7926110	T	G	0.2603	0.0321	5.71E-16
rs236916	A	G	0.3166	0.0446	1.31E-12
rs11222084	A	T	-0.3363	0.0316	1.80E-26
rs7944927	T	C	0.2235	0.0392	1.23E-08
rs2014408	T	C	0.5169	0.0373	1.26E-43
rs378769	A	G	0.2963	0.033	2.99E-19
rs569550	T	G	-0.5765	0.0318	1.33E-73
rs7120567	T	C	0.4276	0.0762	2.01E-08
rs871004	A	G	0.2336	0.0317	1.65E-13
rs713143	A	C	-0.1983	0.0315	3.08E-10
rs11604310	T	C	-0.2778	0.0411	1.46E-11
rs7107356	A	G	-0.4598	0.0301	1.63E-52
rs488769	A	C	0.2472	0.0318	8.21E-15
rs12806665	A	G	0.5728	0.0885	9.45E-11
rs2306363	T	G	-0.4358	0.0376	5.24E-31
rs7927515	A	C	0.2271	0.0319	1.05E-12
rs2289124	A	G	-0.308	0.0415	1.14E-13
rs10840293	A	G	0.3258	0.0307	2.75E-26

rs7310615	C	G	0.585	0.0306	1.32E-81
rs35429	A	G	0.4382	0.0311	3.84E-45
rs7134969	T	C	0.1943	0.0303	1.48E-10
rs35071163	C	G	-0.2226	0.0302	1.64E-13
rs117206641	T	C	0.3154	0.0499	2.66E-10
rs2638432	T	G	-0.3422	0.0386	8.46E-19
rs73075659	A	G	0.3962	0.0321	5.52E-35
rs3819532	T	C	-0.1875	0.0306	9.44E-10
rs2129869	A	T	-0.2643	0.0361	2.44E-13
rs78998485	C	G	-0.2449	0.0346	1.48E-12
rs4760619	A	T	-0.2675	0.0408	5.43E-11
rs12426261	A	G	0.3775	0.0309	2.31E-34
rs67772913	A	G	0.3769	0.033	2.92E-30
rs7306710	T	C	-0.2429	0.0303	1.03E-15
rs7963801	T	C	-0.2362	0.0311	2.87E-14
rs7964067	A	G	0.2673	0.0411	7.90E-11
rs17249754	A	G	-0.8446	0.0403	1.25E-97
rs7331680	T	G	0.4101	0.0423	3.35E-22
rs631660	T	G	-0.2645	0.0308	9.55E-18
rs7338758	T	C	0.3552	0.0352	7.02E-24
rs2065498	T	G	-0.2934	0.0403	3.36E-13
rs55645844	A	G	0.2475	0.0452	4.40E-08
rs9535528	T	C	0.1965	0.0327	1.82E-09
rs75961402	A	G	0.2659	0.0418	1.95E-10
rs78474310	A	G	-0.4699	0.0734	1.51E-10
rs9543423	A	G	-0.1698	0.0301	1.79E-08
rs8003129	A	T	0.2301	0.0409	1.81E-08
rs12885878	A	G	-0.2291	0.0367	4.32E-10
rs365990	A	G	0.225	0.0312	5.95E-13
rs8904	A	G	0.3061	0.0314	1.71E-22
rs142004400	A	C	0.6513	0.083	4.26E-15
rs75720322	A	G	0.309	0.0532	6.53E-09
rs35413927	A	G	-0.3002	0.0328	5.25E-20

rs72731554	A	T	0.2287	0.0381	1.94E-09
rs8003103	A	G	-0.1755	0.0319	3.60E-08
rs11159091	A	G	0.1978	0.0303	6.79E-11
rs7154723	A	G	0.253	0.0309	2.72E-16
rs28866311	T	G	-0.2762	0.0302	5.45E-20
rs1105881	C	G	-0.1943	0.0313	5.27E-10
rs12900430	T	G	0.2005	0.0304	4.15E-11
rs2652812	T	C	-0.2516	0.0353	1.03E-12
rs7183786	A	G	-0.1752	0.0313	2.21E-08
rs11636952	T	C	0.5313	0.0328	4.22E-59
rs11637214	T	C	0.2862	0.0304	5.43E-21
rs4932373	A	C	-0.635	0.0328	2.49E-83
rs11073385	A	G	-0.1941	0.0305	2.03E-10
rs2589218	T	C	-0.2258	0.0339	2.54E-11
rs77924615	A	G	-0.4081	0.039	1.12E-25
rs2286472	A	C	-0.2375	0.033	6.13E-13
rs9926773	A	C	0.2027	0.0322	2.90E-10
rs7204624	A	G	0.2021	0.0354	1.18E-08
rs12446456	T	C	-0.3003	0.0302	2.97E-23
rs34941092	A	G	-0.3225	0.0425	3.23E-14
rs4784541	T	C	-0.2015	0.0307	4.93E-11
rs28485100	T	C	-0.356	0.0594	2.06E-09
rs62058277	T	G	-0.4759	0.0715	2.76E-11
rs4888408	A	G	0.3653	0.0307	1.42E-32
rs28612761	A	T	0.2462	0.0325	3.93E-14
rs908951	T	C	-0.2261	0.0315	7.14E-13
rs4925159	A	G	0.2174	0.0305	9.66E-13
rs11870150	T	C	-0.1785	0.0307	6.06E-09
rs166840	A	G	0.1718	0.0313	4.25E-08
rs1551355	T	C	0.2098	0.0356	3.89E-09
rs9899540	A	T	0.2011	0.0316	1.87E-10
rs12603813	T	C	-0.4327	0.0347	1.02E-35
rs17608766	T	C	-0.6903	0.0433	2.48E-57

rs9221	T	C	0.4362	0.0535	3.70E-16
rs9904730	A	G	-0.2023	0.0342	3.40E-09
rs1000423	T	C	0.4138	0.0346	6.50E-33
rs740698	T	C	-0.2104	0.0308	8.48E-12
rs6504213	T	C	-0.2982	0.0312	1.25E-21
rs113086489	T	C	0.3249	0.0307	3.80E-26
rs4511593	T	C	-0.2881	0.0318	1.28E-19
rs1436138	A	G	0.3119	0.0315	4.73E-23
rs9302885	A	G	0.2242	0.0302	1.03E-13
rs1154214	T	G	-0.2031	0.0306	3.27E-11
rs56407827	T	C	0.3603	0.034	2.78E-26
rs12971067	C	G	0.2833	0.0327	4.97E-18
rs868533	T	G	0.3241	0.039	9.70E-17
rs10048404	T	C	-0.2607	0.0317	1.91E-16
rs10460108	A	G	0.2141	0.0301	1.12E-12
rs34413141	A	T	-0.3531	0.0393	2.47E-19
rs167479	T	G	-0.5642	0.0327	7.21E-67
rs12459625	T	C	-0.2343	0.0353	3.03E-11
rs117717684	A	G	0.848	0.1325	1.54E-10
rs60138042	C	G	0.3395	0.0619	4.14E-08
rs28572357	A	C	-0.2733	0.0308	6.34E-19
rs281379	A	G	0.2284	0.0308	1.16E-13
rs73046792	A	G	-0.3554	0.0426	7.23E-17
rs12985940	T	C	0.4642	0.0434	1.08E-26
rs10207726	T	C	-0.2142	0.033	8.06E-11
rs62158170	A	G	0.2369	0.0368	1.21E-10
rs2580350	A	G	0.1769	0.0307	8.39E-09
rs17257081	A	G	0.2274	0.0392	6.35E-09
rs55944332	A	G	-0.2613	0.0355	1.79E-13
rs62189017	A	G	0.3131	0.0507	6.80E-10
rs73029563	C	G	-0.514	0.0304	4.20E-64
rs72914576	C	G	-0.292	0.0388	5.38E-14
rs34727427	T	C	-0.2353	0.0324	4.02E-13

rs13412750	A	G	-0.2889	0.0341	2.33E-17
rs824516	A	G	0.202	0.0319	2.37E-10
rs12693982	T	C	0.2575	0.0309	7.49E-17
rs3845811	C	G	-0.2942	0.0309	1.88E-21
rs2161967	T	G	0.2836	0.0307	2.87E-20
rs1044822	T	C	-0.248	0.0424	5.16E-09
rs139354822	T	C	0.6115	0.0975	3.51E-10
rs10164842	T	C	-0.2733	0.0319	1.13E-17
rs1275988	T	C	-0.541	0.0308	4.42E-69
rs72792829	T	C	-0.3149	0.0364	4.83E-18
rs115262049	A	T	0.5893	0.0552	1.29E-26
rs17406625	T	C	0.232	0.0335	4.66E-12
rs10427222	T	C	0.2531	0.0357	1.38E-12
rs34688719	A	C	-0.1715	0.0308	2.50E-08
rs2249105	A	G	0.2927	0.0313	7.63E-21
rs2110975	A	G	0.1933	0.033	4.72E-09
rs72847885	A	G	0.2413	0.0318	3.08E-14
rs6108787	T	G	-0.4274	0.03	5.38E-46
rs17812022	T	C	-0.3613	0.0525	5.65E-12
rs4911250	A	T	0.3128	0.0425	1.80E-13
rs6029748	T	C	-0.2689	0.0342	3.91E-15
rs1741344	T	C	0.2043	0.0313	6.94E-11
rs6090907	A	G	-0.3854	0.0425	1.29E-19
rs4810149	T	C	0.1842	0.0316	5.53E-09
rs6026744	A	T	-0.7131	0.0461	7.00E-54
rs6062324	A	G	-0.3294	0.0363	1.18E-19
rs6108168	A	C	-0.2957	0.0344	8.71E-18
rs2736086	T	C	-0.1839	0.0312	3.95E-09
rs1882961	T	C	0.2443	0.0326	6.69E-14
rs2833834	A	C	0.2177	0.0338	1.22E-10
rs12627651	A	G	0.3498	0.0341	1.02E-24
rs34487963	A	C	-0.8819	0.1244	1.35E-12
rs7283362	C	G	0.1758	0.0302	5.75E-09

rs2238787	A	G	0.2552	0.0332	1.45E-14
rs2294239	A	G	0.2051	0.0304	1.53E-11
rs112854918	C	G	-0.5577	0.1004	2.77E-08
rs28578714	T	C	0.2066	0.0327	2.53E-10
rs9848170	C	G	0.3231	0.0307	7.01E-26
rs9842387	A	G	-0.1715	0.0303	1.52E-08
rs1948696	T	C	0.2566	0.031	1.17E-16
rs9880098	A	G	0.3081	0.0308	1.59E-23
rs6789597	A	G	-0.2941	0.0313	5.72E-21
rs1727914	T	C	0.2093	0.0349	1.92E-09
rs79539362	T	C	0.4003	0.0504	2.09E-15
rs17684859	T	C	-0.2241	0.034	4.24E-11
rs11721038	T	C	0.563	0.0564	1.67E-23
rs1290784	T	C	0.4124	0.0303	2.97E-42
rs262986	A	G	-0.2371	0.0305	7.67E-15
rs13091418	C	G	-0.2234	0.0325	6.15E-12
rs9869437	A	C	-0.2001	0.0318	3.22E-10
rs2643826	T	C	0.4473	0.0306	1.74E-48
rs743395	T	C	0.2597	0.0317	2.55E-16
rs1052501	T	C	0.2262	0.0412	4.14E-08
rs6771917	T	C	-0.3793	0.0355	1.39E-26
rs7615099	A	G	0.1891	0.0321	3.90E-09
rs3772219	A	C	0.2733	0.0324	3.10E-17
rs4499560	A	T	-0.2199	0.0326	1.46E-11
rs9874426	T	C	-0.1678	0.0304	3.55E-08
rs1375564	T	C	0.2579	0.0315	2.84E-16
rs1229984	T	C	-0.5989	0.0897	2.42E-11
rs13107325	T	C	-0.9086	0.0592	4.22E-53
rs6842486	A	T	-0.2074	0.0304	8.79E-12
rs4834792	A	T	0.1973	0.0303	7.24E-11
rs7439567	T	C	0.2537	0.0309	2.31E-16
rs72719160	A	T	-0.2243	0.0324	4.34E-12
rs7683728	T	C	-0.3654	0.0304	2.43E-33

rs56329057	T	C	-0.3836	0.0386	2.89E-23
rs4691382	A	G	0.241	0.0353	8.17E-12
rs869396	A	C	-0.2115	0.0305	4.12E-12
rs2610990	A	G	-0.2903	0.0343	2.86E-17
rs61789367	A	G	0.4422	0.0742	2.60E-09
rs1290933	A	C	-0.2847	0.0327	3.17E-18
rs28667801	A	T	-0.2627	0.0314	5.80E-17
rs2073505	A	G	0.3606	0.0598	1.60E-09
rs2291434	T	G	-0.2622	0.0303	5.10E-18
rs62309747	A	G	-0.2244	0.0304	1.59E-13
rs60991988	T	G	0.3789	0.0498	2.82E-14
rs6839100	A	G	0.2139	0.036	2.84E-09
rs12509595	T	C	-0.8367	0.0334	2.55E-138
rs17010957	T	C	-0.534	0.043	1.78E-35
rs10028284	A	T	0.2937	0.0398	1.69E-13
rs4705702	T	G	0.2714	0.0303	2.97E-19
rs6890251	T	C	0.4421	0.0414	1.38E-26
rs6892983	A	C	0.3427	0.0307	7.11E-29
rs10069690	T	C	0.3098	0.0369	4.47E-17
rs702395	T	C	0.2318	0.0305	3.24E-14
rs7732116	A	G	0.2161	0.0342	2.77E-10
rs7725413	T	C	-0.1985	0.0359	3.07E-08
rs7720047	A	G	0.3536	0.0345	1.26E-24
rs11960210	T	C	0.4727	0.0313	1.25E-51
rs13358657	A	G	-0.388	0.0445	2.95E-18
rs3860770	A	G	-0.2663	0.0333	1.20E-15
rs3756712	A	C	0.1944	0.0319	1.17E-09
rs12656497	T	C	-0.6382	0.0307	7.14E-96
rs7721523	A	T	0.2489	0.0331	5.86E-14
rs6449708	T	C	0.1984	0.0302	5.01E-11
rs1694068	A	T	0.2657	0.0311	1.18E-17
rs13163533	C	G	-0.3856	0.0564	8.31E-12
rs246973	T	C	0.2479	0.0335	1.45E-13

rs56719405	A	G	0.3576	0.0651	3.88E-08
rs6452769	A	G	-0.3143	0.0377	7.82E-17
rs76443575	C	G	-0.5233	0.0816	1.40E-10
rs1871190	T	G	0.1954	0.0324	1.66E-09
rs9486916	T	C	0.2657	0.0385	5.42E-12
rs9401025	A	C	0.1735	0.0304	1.15E-08
rs1407590	A	G	-0.1943	0.0303	1.37E-10
rs9401913	A	G	0.5202	0.0305	3.66E-65
rs9349379	A	G	0.2664	0.0312	1.31E-17
rs578340	A	G	0.1804	0.0316	1.15E-08
rs2328813	A	C	-0.1946	0.0305	1.67E-10
rs17080102	C	G	-0.8085	0.0594	3.52E-42
rs6557155	T	G	0.1906	0.0313	1.14E-09
rs509833	A	G	0.329	0.044	7.08E-14
rs2745599	A	G	0.2164	0.0317	8.96E-12
rs9294987	T	C	-0.1934	0.0313	6.25E-10
rs932316	T	C	-0.2228	0.0384	6.45E-09
rs62394270	C	G	-0.4189	0.0454	2.57E-20
rs3132442	T	C	0.3931	0.0304	2.65E-38
rs7763558	A	G	0.3363	0.0321	1.17E-25
rs11967262	C	G	-0.1715	0.0311	3.43E-08
rs78648104	T	C	-0.4287	0.0541	2.37E-15
rs9392172	C	G	-0.1969	0.0302	7.31E-11
rs1984195	A	G	0.2409	0.0303	1.77E-15
rs9361847	T	G	0.2207	0.0362	1.13E-09
rs6921291	T	C	0.3575	0.0385	1.58E-20
rs2392929	T	G	-0.7507	0.0379	1.96E-87
rs35722851	T	C	0.2405	0.0302	1.84E-15
rs35680304	T	C	0.2694	0.031	3.76E-18
rs3918226	T	C	0.664	0.0575	8.46E-31
rs73728279	T	G	0.3808	0.0339	2.71E-29
rs11764203	A	T	0.1975	0.031	2.00E-10
rs3807925	A	G	-0.1859	0.0319	5.39E-09

rs872464	A	G	0.2155	0.0307	2.22E-12
rs12979	C	G	0.2739	0.0449	1.09E-09
rs10282122	T	C	-0.302	0.0327	2.46E-20
rs3735533	T	C	-0.91	0.0577	5.29E-56
rs11977526	A	G	-0.3213	0.0312	6.62E-25
rs4720363	A	C	-0.2105	0.0373	1.67E-08
rs334495	T	C	0.21	0.0345	1.20E-09
rs848445	T	C	-0.2025	0.0339	2.28E-09
rs42377	A	G	-0.3153	0.0331	1.69E-21
rs35783704	A	G	-0.4619	0.0507	8.81E-20
rs1821002	C	G	0.3794	0.0307	5.19E-35
rs7830607	A	G	-0.206	0.0327	3.09E-10
rs2470004	T	C	-0.3454	0.0392	1.28E-18
rs4598218	T	C	0.1911	0.0313	1.00E-09
rs7012866	T	G	-0.2325	0.0301	1.21E-14
rs45613837	A	G	0.2187	0.0304	6.16E-13
rs7463212	A	T	-0.2753	0.0305	1.81E-19
rs7837764	C	G	0.1719	0.0312	3.61E-08
rs7821832	T	G	0.4222	0.0348	6.67E-34
rs1906672	A	G	0.2966	0.0358	1.20E-16
rs4873492	T	C	0.3431	0.0403	1.61E-17
rs2354862	A	C	0.2507	0.0317	2.42E-15
rs2126474	T	G	-0.2601	0.0306	1.87E-17
rs10504641	T	C	0.3538	0.0643	3.82E-08
rs148401029	A	C	-0.4623	0.0848	4.97E-08
rs4551303	T	C	-0.2044	0.0325	3.17E-10
rs2613203	A	T	-0.2681	0.0389	5.81E-12
rs10980408	T	C	-0.7606	0.0827	3.83E-20
rs7033339	A	G	-0.1893	0.0329	8.38E-09
rs4838021	T	C	-0.3009	0.0453	3.13E-11
rs72767003	T	C	0.3343	0.0427	5.25E-15
rs6271	T	C	-0.5547	0.0611	1.18E-19
rs11145807	A	G	0.2135	0.0322	3.54E-11

rs9886665	T	C	0.2048	0.0343	2.47E-09
rs1856201	A	C	0.1702	0.0308	3.28E-08
rs76452347	T	C	-0.2974	0.0397	7.13E-14
rs927315	T	C	0.1689	0.0303	2.44E-08
rs17435526	A	G	0.2428	0.0395	7.73E-10
rs10746963	A	G	-0.2177	0.0388	2.05E-08
rs1332813	T	C	0.2203	0.0314	2.32E-12
rs7045409	A	T	-0.1862	0.0313	2.55E-09

Supplementary eTable 2: Association between cortical ACE expression and neurodegenerative traits

Continuous traits

Exposure	Outcome	Beta estimate	95% lower confidence boundary	95% upper confidence boundary
rs4291	Cognitive function	0.005	-0.001	0.010
rs4291	White matter hyperintensities	-0.019	-0.105	0.067

Categorical traits

Exposure	Outcome	Odds ratio	95% lower confidence boundary	95% upper confidence boundary
rs4291	Alzheimer's disease	1.059	1.039	1.08
rs4291	Lacunar stroke	0.972	0.932	1.014
rs4291	Parkinson's disease	0.992	0.955	1.031

Supplementary eTable 3: Systolic blood pressure and risk of Alzheimer's disease

Method	Odds ratio	95% lower confidence boundary	95% upper confidence boundary	P-value
Simple median	1.006	0.999	1.013	0.084
Weighted median	1.006	1.000	1.013	0.064
MR Egger	1.007	0.995	1.018	0.255
MR Egger intercept	1.000	0.996	1.003	0.830
Inverse variance weighted (multiplicative random effects)	1.005	1.000	1.010	0.059

Bibliography:

1. Kunkle BW, Grenier-Boley B, Sims R, Bis JC, Damotte V, Naj AC, et al. Genetic meta-analysis of diagnosed Alzheimer's disease identifies new risk loci and implicates A β , tau, immunity and lipid processing. *Nat Genet* 2019 513. 2019 Feb 28;51(3):414–30.