# GREGORY WILLIAM CARTER

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## POSITIONS

Associate Professor, The Jackson Laboratory, 2016-Present

Assistant Professor, The Jackson Laboratory, 2010-2016

Affiliate Professor, Sackler School of Medicine, Tufts University, 2011-Present

Graduate Faculty, Graduate School of Biological Sciences, University of Maine, 2010-Present

Affiliate Professor, Computer Science and Engineering Dept, University of Connecticut, 2020-Present

Senior Research Scientist, Institute for Systems Biology, 2007-2010

Postdoctoral Research Fellow, Galitski Lab, Institute for Systems Biology, 2003-2007

Postdoctoral Research Fellow, Physics, University of Washington (Seattle), 2001-2003

Postdoctoral Research Associate, Physics, Stony Brook University (New York), 1999-2001

Postdoctoral Research Fellow and Leon Rosenfeld Fellow, Physics, The Niels Bohr Institute (Copenhagen, Denmark), 1997-1999

## EDUCATION

Ph. D. in Physics, University of Minnesota (Minneapolis, MN), 1997.
 Thesis: *A Chiral Effective Lagrangian Approach to Nuclear Physics.* Advisor: Paul J. Ellis.

B. S. in Physics, Case Western Reserve University (Cleveland, OH), 1993

## ACTIVE FUNDING

NIH/NIGMS **R01** GM115518  Carter (PI)
*Methods and Tools to Analyze Genetic Complexity*

NIH/NIGMS **R01** GM115518-S4  Carter (PI)
Supplement for Alzheimer's-related QTL analysis

NIH/NIA **U54** AG054345  Carter, Howell, Lamb, Territo (multiPI)
*Alzheimer's Disease Translational Center for Disease Model Resources, aka MODEL-AD*
Role: Head of Bioinformatics and Data Management

NIH/NEI **R01** EY027860  Carter, Nishina (multiPI)
*Identifying Shared Pathogenic Networks and Molecular Targets Underlying Retinal Pigmented Epithelial Associated Disease*

NIH/NIA **R01** AG055104  Carter, Howell, Sasner (multiPI)
*Determining Genetic Interactors of Apolipoprotein E in Alzheimer's disease*

NIH/NLM **R21** LM012615  Tyler, Mahoney (multiPI), Carter (Co-I)
*Inferring Molecular Mechanisms of Complex Disease by Integrating Patterns of*

*Epistasis with Functional Genomic Networks.*

NIH/NEI **R01** EY011996          Nishina (PI), Carter (Co-I)
*Retinal Disease: Molecular Basis and Pathophysiology*

NIH/NIA **RF1** AG051496          Howell, Stevens (multiPI), Carter (Co-I)   9/2015-8/2020
*Investigating the Role of Complement-expressing Myeloid Cells in Synapse Loss and Vascular Compromise in Alzheimer's Disease*

NIH **U54** OD020351          Burgess (PI), Carter (Co-I)
*The Jackson Laboratory Center for Precision Genetics: From New Models to Novel Therapeutics*

NIH **U54** AG065187          Levey, et al (PI), Carter (Co-I)
*The Open Drug Discovery Center for Alzheimer's Disease*
Role: Co-Head of Bioinformatics Core

NIH/NIA **R01** AG054180          Kaczorowski (PI), Carter (Co-I)
*Systems Control of Normal Aging and Alzheimer's Disease*

NIH/NIA **R01** AG057914          Kaczorowski (PI), Carter (Co-I)
*Systems Genetics of Resilience to Alzheimer's Disease*

**COMPLETED FUNDING**

NIH/NIGMS **P01** GM099640      Paigen (PI)
*Molecular Regulation of Mammalian Meiosis*
Role: Project Leader and Head of Computational Core

NIA/NIGMS **P50** GM076468      Churchill (PI)
*Center for Genome Dynamics   Project G: Using Multiple Phenotypes to Model Genetic Epistasis*
Role: Project Leader

NIH/NIGMS **K25** GM079404      Carter (PI)
*Inference and Testing of Quantitative Models of Genetic Interaction*

Alliance for Lupus Research      Roopenian (PI), Carter (Co-I)
*Novel Approach to Modeling the Functional Genomics of Human SLE in Mice*

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**PUBLICATIONS**

**Biology – Peer Reviewed (\*equal contribution, †corresponding author)**

1. Milind N, Preuss C, Haber A, Ananda G, Mukherjee S, John C, Shapley S, Tyler AL, Logsdon BA, Crane PA, **Carter GW†**. 2020. *Transcriptomic Stratification of Late-Onset Alzheimer's Cases Reveals Novel Genetic Modifiers of Disease Pathology*, PLoS Genetics (in press), bioRxiv doi.org/10.1101/763516.

2. Spruce C, Dlamini S, Ananda G, Bronkema N, Tian H, Paigen K, **Carter GW**, Baker CL†. 2020. *HELLS and PRDM9 form a Pioneer Complex to Open Chromatin at Meiotic Recombination Hotspots*, Genes and Development 34(5-6):398-412.

3. Pandey RS, Graham L, Uyar A, Preuss C, Howell GR†, **Carter GW†**. 2019. *Genetic perturbations of disease risk genes in mice capture transcriptomic signatures of late-onset Alzheimer's disease*, Molecular Neurodegeneration 14(1):50.

4. Chintapaludi SR, Uyar A, Jackson HM, Acklin CJ, Wang X, Sasner M, **Carter GW†**, Howell GR†. 2019. *Staging Alzheimer's disease in the brain and retina of B6.APP/PS1 mice by transcriptional profiling,* J Alzheimers Dis 73(4):1421-1434.

5. Tyler AL, Mahoney JM, **Carter GW†**. 2019. *Genetic interactions affect lung function in patients with systemic sclerosis*, G3 **10**(1):151-163.

6. Onos K, Uyar A, Keezer KJ, Jackson HM, Preuss C, Acklin CJ, O"Rourke R, Buchanan RA, Cossette TL, Rizzo SJS, Soto I, **Carter GW**, Howell GR†. 2019. *Enhancing face validity of mouse models of Alzheimer's disease with natural genetic variation*. PLoS Genetics **15**(5):e1008155.

7. Mukherjee S, Logsdon B, Perumal T, Daily K, Sieberts S, Omberg L, Preuss C, **Carter GW**, Mangravite L. 2019. *Identifying and ranking potential driver genes of Alzheimer's Disease using multi-view evidence aggregation*, Bioinformatics **35**(14):i568-i576, bioRxiv doi.org/10.1101/534305.

8. Fine AD, Ball RL, Fujiwara Y, Handel MA**, Carter GW†**. 2019. *Uncoupling of transcription and cytodifferentiation in mouse spermatocytes with impaired meiosis*, Mol Biol Cell, mbcE18100681.

9. Baker C†, Walker M, Arat S, Ananda G, Petkova P, Powers N, Tian H, Spruce C, Ji B, Rausch D, Choi KB, Petkov P, **Carter GW**, Paigen K†. 2018. *Tissue-specific trans regulation of the mouse epigenome,* Genetics **211**(3):831-845.

10. Menghi F, Barthel FP, Yadav V, Tang M, Ji B, Tang Z, **Carter GW**, Ruan Y, Scully R, Verhaak RGW, Jonkers J, Liu ET†. 2018. *The tandem duplicator phenotype is prevalent in genome-wide cancer configuration driven by distinct genetic mutations*, Cancer Cell **34**:1-14.

11. Wang X, Philip V, Ananda G, White CC, Malhotra A, Michalski P, Karuturi RMK, Chintalapudi SR, Acklin C, Sasner M, Bennett DA, De Jager PL, Howell GR, Carter GW†. 2018. *A Bayesian generalized linear mixed model identifies novel loci for late-onset Alzheimer's disease*, Genetics **209**(1), 51-64.

12. Marnik EA, Wang X, Sproule TJ, Park G, Christianson GJ, Lane-Retiker SK, **Carter GW**, Morse III HC†, Roopenian DC†. 2017. *Precocious Interleukin 21 Expression by CD4 T cells of Naïve Mice Identifies a Novel Stage of T follicular Helper Cell Development in Autoimmune Disease*, Cell Reports, **21**(1):208-221.

13. Wu JW, Preuss C, Wang SP, Yang H, Ji B, **Carter GW**, Gladdy R, Andelfinger G, Mitchell GA†. 2017. *Epistatic interaction between the lipase-encoding genes Pnpla2 and Lipe causes liposarcoma in mice*, PLoS Genetics, **13**(5):1007716.

14. Tyler AL, Ji B, Gatti DM, Munger SC, Churchill GA, Svenson KL, **Carter GW†**. 2017. *Epistatic networks jointly influence phenotypes related to metabolic disease and gene expression in Diversity Outbred mice*, Genetics **206**, 621-639.

15. Ball RL, Fujiwara Y, Sun F, Hu J, Hibbs, M, Handel MA†, **Carter GW†**. 2016. *Regulatory complexity revealed by integrated cytological and RNA-seq analyses of meiotic substages in mouse spermatocytes*, BMC Genomics, **17**:628.

16. Tyler AL, Donahue LR, Churchill GA, **Carter GW†**. 2016. *Weak Epistasis Generally Stabilizes Phenotypes in a Mouse Intercross*, PLoS Genetics, **12**(2): e1005805.

17. Walker M, Billings T, Baker CL, Powers N, Tian H, Saxl RL, Choi K, Hibbs MA, **Carter GW**, Handel MA, Paigen K, Petkov PM†. 2015. *Affinity-seq detects genome-wide PRDM9 binding sites and reveals the impact of prior chromatin modifications on mammalian recombination hotspot usage*, Epigenetics and Chromatin, **8**(1):1-13.

18. Tyler AL, McGarr TC, Beyer BJ, Frankel WN, **Carter GW†**. 2014. *A Genetic Interaction Network Model of a Complex Neurological Disorder*, Genes Brain & Behavior, **13**(8):831-840.

19. Philip VM, Tyler AL, **Carter GW†**. 2014. *Dissection of Complex Gene Expression Using the Combined Analysis of Pleiotropy and Epistasis*, Pac Symp Biocomput., **19**:200-211.

20. Jackson HM, Soto I, Graham LC, **Carter GW**, Howell GR†. 2013. *Clustering of transcriptional profiles identifies changes to insulin signaling as an early event in a mouse model of Alzheimer's disease,* BMC Genomics, **14**(1):831.

21. Tyler AL, Lu W, Hendrick J, Philip V, **Carter GW†**. 2013. *CAPE: An R Package for Combined Analysis of Pleiotropy and Epistasis*, PLoS Computational Biology, **9**(10): e1003270.

22. **Carter GW†**. 2013. *Inferring Gene Function and Network Organization in Drosophila Signaling by Combined Analysis of Pleiotropy and Epistasis*, G3 **3**(5):807-14.

23. Mirzaei H, Knijnenburg T, Kim B, Robinson M, Picotti P, **Carter GW**, Li S, Dilworth D, Eng J, Aitchison J, Shmulevich I, Galitski T, Aebersold R†, and Ranish J†. 2013. *Systematic measurement of transcription factor-DNA interactions by SRM mass spectrometry identifies candidate gene regulatory proteins*, PNAS **110**(9):3645-3650.

24. **Carter GW†**, Hays M, Sherman A, Galitski T. 2012. *Use of Pleiotropy to Model Genetic Interactions in a Population*, PLoS Genetics **8**(10): e1003010.

25. **Carter GW†**, Hays M, Li S, and Galitski T. 2012. *Predicting the Effects of Copy-Number Variation in Double and Triple Mutant Combinations*, Pac Symp Biocomput. **17**:19-30.

26. **Carter GW**, Rush CG, Uygun F, Sakhanenko NA, Galas DJ, and Galitski T. 2010. *A Systems Biology Approach to Modular Genetic Complexity*, Chaos **20**:026102.

27. Galas DJ†, Nykter M, **Carter GW**, Price N, and Shmulevich I. 2010. *Biological Information as Set-Based Complexity,* IEEE Transactions on Information Theory **56**(2):667-677, preprint arXiv:0801.4024.

28. **Carter GW†**, Galas DJ, and Galitski, T. 2009. *Maximal Extraction of Biological Information from Genetic Interaction Data*, PLoS Computational Biology **5**(4):e1000347.

29. **Carter GW†**, Prinz S, Neou C, Shelby JP, Marzolf B, Thorsson V, and Galitski T. 2007 *Prediction of phenotype and genomic expression for combinations of mutations*, Molecular Systems Biology **3**:96.

30. Selinummi J, Niemistö A, Saleem R, **Carter GW**, Aitchison J, Yli-Harja O, Shmulevich I, and Boyle J†. 2007. *A case study on 3-D reconstruction and shape description of perioxisomes in yeast*, Proceedings of the 2007 IEEE International Conference on Signal Processing and Communication (ICSPC 2007) 672-675.

31. **Carter GW**, Rupp S, Fink GR, and Galitski T†. 2006. *Disentangling information flow in the Ras-cAMP signaling network*, Genome Research **16**: 520-526.

32. *Drees BL, *Thorsson V, ***Carter GW**, Rives AW, Raymond M, Avila-Campillo I, Shannon P, and Galitski T†. 2005. *Derivation of genetic interaction networks from quantitative phenotype data* , Genome Biology **6**: R38.

**Biology – Preprints**

1. Logsdon B, et al. 2019. *Meta-analysis of human brain transcriptome identifies heterogeneity across human AD coexpression modules robust to sample collection and methodological approach*, bioRxiv doi.org/10.1101/510420.

2. Mukherjee S, Preuss C, Jayadev S, Garden G, Greenwood AK, Sieberts SK, De Jager PL, Eretkin-Taner N, **Carter GW**, Mangravite LM†, Logsdon BA†. 2019. *Molecular estimation of neurodegeneration pseudotime in older brains*, bioRxiv doi.org/10.1101/686824.

3. Preuss C, Pandey RS, Piazza E, Fine A, Uyar A, Perumal T, Garceau D, Kotredes KP, Williams H, Mangravite LM, Lamb BT, Oblak AL, Howell GR, Sasner M, Logsdon BA, **Carter GW†**. 2019*. A novel systems biology approach to evaluate mouse models of late-onset Alzheimer's disease*, bioRxiv doi.org/10.1101/682856.

4. Li Y, Haber A, Preuss C, John C, Uyar A, Yang H, Logsdon BA, Philip V, Karuturi K, ADNI Consortium, **Carter GW†.** 2019. *Transfer Learning-Derived Image Phenotypes Power Up Genome-wide Association Analysis for Late Onset Alzheimer's Disease,* submitted, bioRxiv TBD.

**Biology – Reviews and Book Chapters**

5. Tyler AL and **Carter GW**. 2017. Genetic Interactions Improve Models of Quantitative Traits, Nature Genetics, **49**(4): 486-488. News and Views.

1. **Carter GW** and Dudley, AM. 2009. *Systems genetics of complex traits*, in Robert, ed., "Encyclopedia of Complexity and Systems Science", Springer, New York, 9105-9124.

2. Killcoyne S, **Carter GW**, Smith J, and Boyle J. 2009. *Cytoscape: A Community-Based Framework for Network Modeling*, Methods Mol Biology **563**: 219-239.

3. **Carter GW**, Thorsson V, and Galitski T. 2007. *Network Modeling of Molecular and Genetic Interactions*, in Conn PM, ed., "Source Book of Models for Biomedical Research", Chapter 9, Humana Press.

4. **Carter GW**. 2005. *Inferring Network Interactions within a Cell*, Briefings in Bioinformatics **6**(4): 380-389.

**Physics**

1. Carter GW and Henley EM, *Corrections to the Nuclear Axial Coupling in a Nuclear Medium*, nucl-th/0404037, Int. J. Mod. Phys. E **14** (2005) 1017.

2. Henley EM and Carter GW, *$g_A$ in Nuclei*, in "Proceedings of the 10th International Conference on Nuclear Reaction Mechanisms", Eur. Phys. J. A **24S2** (2005) 103.

3. Carter GW, *Axial Vector Current and Coupling of the Quark in the Instanton Model* , hep-ph/0208250, Phys. Rev. D **67** (2003) 014008.

4. Ostrovsky DM, Carter GW, and Shuryak EV, *Forced Tunneling and Turning State Explosion in Pure Yang-Mills Theory*, hep-ph/0204224, Phys. Rev. D **66** (2002) 036004.

5. Carter GW, Ostrovsky DM, and Shuryak EV, *Instanton-Induced Semi-Hard Parton Interactions and Phenomenology of High Energy Hadron Collisions*, hep-ph/0112036, Phys. Rev. D **65** (2002) 074034.

6. Carter GW, *Color Superconductivity and Blinking Proto-Neutron Stars*, in proceedings of "Compact Stars in the QCD Phase Diagram", hep-ph/0111353, eConf C010815 (2002) 149-154.

7. Carter GW and Prakash M, *The Quenching of the Axial Coupling in Nuclear and Neutron-Star Matter*, nucl-th/0106029, Phys. Lett. **B525** (2002) 249.

8. Carter GW, *Classical Gluon Production in Hadronic Collisions*, in proceedings of the "RIKEN/BNL Workshop on High Energy QCD: Beyond the Pomeron", Guryn W and Kovchegov Yu, Eds., (2001).

9. Carter GW and Shuryak EV, *Do Instantons and Strings Cluster when the Number of Colors is Large?*, hep-ph/0101061, Phys. Lett. **B524** (2002) 297.

10. Carter GW and Reddy S, *Neutrino Propagation in Color Superconducting Quark Matter*, hep-ph/0005228, Phys. Rev. D **62** (2000) 103002.

11. Carter GW and Diakonov D, *The Nonperturbative Color Meissner Effect in a Two-Flavor Color Superconductor*, hep-ph/0001318, Nucl. Phys. **B582** (2000) 571.

12. Carter GW and Diakonov D, *Instanton-Induced Interactions in Finite Density QCD*, hep-ph/9908314, in "Panic 99: Proceedings of the XVth Particles and Nuclei International Conference", Nucl. Phys. **A663** (2000) 741.

13. Carter GW and Diakonov D, *Instanton-Induced Interactions in Finite Density QCD: from Chiral Symmetry Breaking to Colour Superconductivity*, hep-ph/9908314, in "Proceedings of the XIV International Conference on Ultra-Relativistic Nucleus-Nucleus Collisions (Quark Matter 99)", Nucl. Phys. **A661** (1999) 625.

14. Carter GW and Diakonov D, *Chiral Symmetry Breaking and Color Superconductivity in the Instanton Picture*, hep-ph/9905465, in "ECT* International Workshop on Understanding Deconfinement in QCD", Blaschke D, Karsch F, and Roberts CD, Eds. (Singapore, World Scientific, 2000).

15. Carter GW and Jackson AD, *Finding the Pion in the Chiral Random Matrix Vacuum*, hep-ph/9905231, Phys. Rev. D **61** (2000) 077902.

16. Carter GW and Diakonov D, *Light Quarks in the Instanton Vacuum at Finite Baryon Density*, hep-ph/9812445, Phys. Rev. D **60** (1999) 016004.

17. Carter GW, Scavenius O, Mishustin IN, and Ellis PJ, *An Effective Model for Hot Gluodynamics*, nucl-th/9812014, Phys. Rev. C **61** (2000) 045206.

18. Carter GW and Diakonov D, *Symmetry Breaking by Instantons at Finite Density*, in proceedings of the "RIKEN/BNL Workshop on QCD Phase Transitions", Schäfer T and Shuryak EV, Eds. (1998).

19. Carter GW and Diakonov D, *Towards a Theory of Instantons at Nonzero Fermion Density*, hep-ph/9807219, Nucl. Phys. **A642** (1998) 78.

20. Carter GW and Ellis PJ, *An Effective Lagrangian with Broken Scale and Chiral Symmetry IV: Nucleons and Mesons at Finite Temperature*, nucl-th/9707051, Nucl. Phys. **A628** (1998) 325.

21. Carter GW, Ellis PJ, and Rudaz S, *An Effective Lagrangian with Broken Scale and Chiral Symmetry III: Mesons at Finite Temperature*, nucl-th/9612043, Nucl. Phys. **A618** (1997) 317.

22. Carter GW, Ellis PJ, and Rudaz S, *An Effective Lagrangian with Broken Scale and Chiral Symmetry II: Pion Phenomenology*, nucl-th/9512033, Nucl. Phys. **A603** (1996) 367; erratum **A608** (1996) 514.

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**INTELLECTUAL PROPERTY**

*A genetically modified mouse expressing human APOE4 and Mouse Trem2 pR47H,* 2019.

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**EDUCATION AND MENTORING**

**Postdoctoral Mentoring**
Dr. Rawan Olayan, 2018-present.
Dr. Ann Wells, 2018-present.
Dr. Ravi Pandey, 2017-present.
Dr. Seda Arat, 2015-2019. Senior Computational Toxicologist at Pfizer.
Dr. Xulong Wang, 2013-2016. Senior Scientist at Merck.
Dr. Bo Ji, 2013-2017. Scientist at Washington University in St. Louis.
Dr. Anna L. Tyler, 2012-2016. Promoted to Associate Research Scientist (2016) and Research Scientist (2019).
Dr. Robert Valenzuela, 2012. Biostatistician at Marshfield Clinic.

**Graduate Student Advising**
Lauren Kuffler, Tufts University, 2018-present.
Alexander Fine, Tufts University, 2014-2019. Scientist I, Foundation Medicine.

**Other Student Mentoring**
Peter Benson, Mount Desert High School (internship), 2019-2020.
Nikhil Milind, North Carolina State University (internship), 2018, 2019.
Joshua Mincer, Rensselaer Polytechnic Institute, NY (internship), 2019.
Meredith Mayer, Delaware Valley University, PA (internship), 2019.
Madelyn Adams, Falmouth High School, Falmouth, ME (internship), 2017.
Catrina Spruce, University of Maine (MSc), 2015-2016.
Arya Royal, Lafayette High School, Wildwood, MO, (internship), 2016.
Julia Huesa, North Carolina School of Science and Math (internship), 2016.

Wendy Pitman, Johns Hopkins University (MSc), 2015.
Reanna Dona, The Ohio State University (internship), 2015.
Cai John, University of Edinburgh (internship), 2015.
Kristoph Naggert, Mount Desert High School (internship), 2015-2016.
Eraj Khokhar, University of Maine (rotation), 2015.
Tian-shun Allan Jiang, North Carolina School of Science and Math (internship), 2014.
Xiaojie Ji, University of Maine (rotation), 2014.
Justin Hendrick, Cornell University (internship), 2013.
Patrick Kane, North Carolina School of Science and Math (internship), 2013.
Wei Lu, Duke University (internship), 2012.
Justin Hendrick, North Carolina School of Science and Math (internship), 2012.
Mehmet Umut Caglar, Texas Tech University (visiting graduate student), 2012.
Leonard Tan, Tufts University (rotation), 2011.
Yang Zhang, New Mexico State University (visiting graduate student), 2011.
Kavya Sekar, University of North Carolina (internship), 2011.
Sangeetha Kumar, North Carolina School of Science and Math (internship), 2011.
Gokcen Cilingir and Dake Sun (software engineers), 2009-2010.
Cynthia Rush, UNC (internship), 2009.
Adam Waite, University of Washington (rotation student), 2008.
Gina Fridley, MIT (internship), 2008.
Aaron Brooks, University of Washington (rotation student), 2008.

## Teaching

Short Course on Principles and Techniques for Improving Preclinical Translation in Alzheimer's Disease, The Jackson Laboratory, 2017-present.
Short Course on 21$^{st}$ Century Mouse Genetics, The Jackson Laboratory, 2016-present.
Short Course on Big Data for Professors, The Jackson Laboratory, 2016-present.
Graduate Course on Mammalian Genetics, Tufts University, 2012-present.
Short Course on Experimental Models of Human Cancer, The Jackson Laboratory, 2018.
Short Course on Neurogenetic Tools, The Jackson Laboratory, 2017- 2018.
Graduate course on Computational Biology, University of Maine and Tufts University, 2016-2019.
Short Course on Systems Genetics, The Jackson Laboratory, 2010-2016.
Graduate Course on Biological Pathways, University of Maine, 2012-2014.
Introduction to Systems Biology Course, Institute for Systems Biology, 2007-2009.
Computational Biology for summer students, Institute for Systems Biology, 2007-2009.
Electrodynamics, U of Washington, 2002-2003.
Introductory Physics, Stony Brook U and U of Minnesota, 1993-2001.

## Educational Software Engineer

Case Western Reserve University, 1991-1993.

## Society Memberships

Genetics Society of America, International Society of Computational Biology, International Mammalian Genome Society, Human Genome Organization, International Society to Advance Alzheimer's Research and Treatment, International Behavioral and Neural Genetics Society, Society for Neuroscience.