JOURNAL OF NEUROGENETICS
2020, VOL. 34, NO. 1, 2–4
https://doi.org/10.1080/01677063.2020.1716749

Taylor & Francis
Taylor & Francis Group

BIOGRAPHICAL SKETCH

A biographical sketch of Troy D. Zars (1967–2018)

Bertram Gerber[a,b,c], Elizabeth G. King[d] and Divya Sitaraman[e]

[a]Department of Genetics of Learning and Memory, Leibniz Institute for Neurobiology, Magdeburg, Germany; [b]Centre for Behavioural Brain Sciences, Magdeburg, Germany; [c]Institute for Biology, Otto von Guericke University Magdeburg, Magdeburg, Germany; [d]Division of Biological Sciences, University of Missouri, Columbia, MO, USA; [e]Department of Psychology, College of Science, California State University-East Bay, Hayward, CA, USA

ABSTRACT

Troy D. Zars (1967–2018) was an American biologist. He studied the relationships between genes, neuronal circuits and behavior in the fruit fly *Drosophila melanogaster*. Zars co-pioneered the use of transgene expression to locally restore gene function in memory-defective fly mutants, an approach that provided breakthrough insights into the localization of memory traces in the fly brain. With ensuing refinements of the methods of transgene expression and the broadening in the range of transgenes to be expressed, this shaped the field of modern behavioral neurogenetics.

ARTICLE HISTORY
Received 8 October 2019
Accepted 22 December 2019

KEYWORDS
Troy D. Zars; *Drosophila melanogaster*; engram; place learning; operant learning; mushroom body; temperature sensation

Troy Daniel Zars (Figure 1) was born on 29 September 1967 in Waterloo, Iowa, USA. He graduated from Cedar Falls High School, Iowa, in 1986. Zars received his Bachelor of Science degree in Biology (1990) from Luther College, Decorah, Iowa, and earned his Master of Science degree, also in Biology (1991), from the University of Northern Iowa, Cedar Falls. From 1991 he studied with David R Hyde at the University of Notre Dame, South Bend, Indiana and in 1996 received his PhD in Biology for his research on the genetics of photoreceptor degeneration in *Drosophila*. During his PhD he was supported through a BBMB and a Navari pre-doctoral fellowship of the University of Notre Dame.

Zars then secured an Alexander von Humboldt Foundation post-doctoral research fellowship (1997–1999) to study the neurogenetics of learning and memory in *Drosophila* with Martin Heisenberg at the Biocentre of the University of Würzburg, Germany. In the context of the German Science Foundation's Collaborative Research Centre 554 *Arthropod Behaviour*, Zars, Heisenberg and colleagues used the Gal4-UAS technique for seminal experiments to localize an associative short-term memory trace in the fly brain. In the memory-defective *rutabaga* mutant they locally restored the function of the mutated gene in select ensembles of neurons. It turned out that for a given memory task, restoring *rutabaga* function in only very small sets of neu-

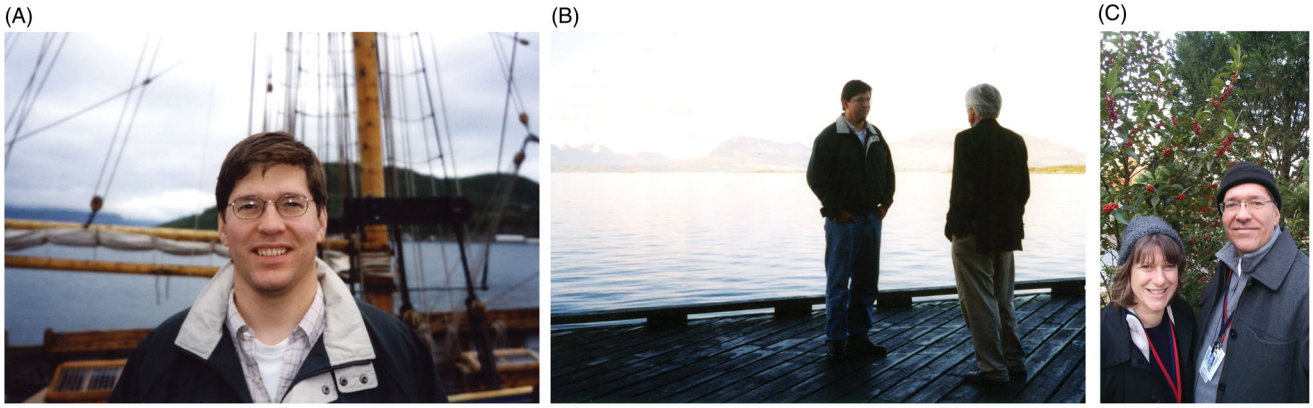

Figure 1. (A) Troy Zars at the ESITO meeting in Harstad, Norway, summer 2003. (B) Troy and Martin Heisenberg, same occasion. Both images © B. Gerber. C: Troy and his wife Melissa Zars, NIH Campus, Washington DC, USA, autumn 2017 (image © M. Zars). Further images of Troy with friends, colleagues, lab members and his family can be found at: https://biology.missouri.edu/news/division-mourns-zars-death/.

CONTACT Bertram Gerber bertram.gerber@lin-magdeburg.de Department of Genetics of Learning and Memory, Leibniz Institute for Neurobiology, Brenneckestraße 6, Magdeburg, 39118, Germany

Supplemental data for this article can be accessed here.

Figure 2. 'Career seal' of Troy Zars. Using https://www.wortwolken.com/ the font-size of the words is proportional to the number of times they occur within the titles of Troy Zars' publications, how often colleagues are listed as co-authors, and how many of his works appeared in the respective journal. Singular/plural use, tempus, and the use of UK/US English was unified. A high-resolution file can be found in Supplemental Material 2.

rons sufficed to restore memory function. Critically, for different tasks, different sets of neurons fulfilled this criterion. For the case of odor-electric shock associative memory their work suggested that the short-term memory trace is local to a subset of neurons in the mushroom body, a third-order central brain structure of insects.

During his post-doctoral period Zars began working on thermosensation and operant learning, topics which then became central to his work after he accepted positions as Assistant Professor (2002), Associate Professor (2009), and Professor (2017) at the University of Missouri, Columbia, Division of Biological Sciences. Landmark discoveries after his return to the Midwest of the United States concerned the way low- versus high-temperature signals are processed for aversive reinforcement in operant learning and place memory, what the roles of biogenic amines are in this context, and the way genetic factors moderate these and other forms of behavioral plasticity. Throughout, his studies were performed within an experimental psychology framework, and with a view towards their biomedical implications e.g., for mood disorders. On these and related topics, Zars contributed commentaries for journals such as *Science*, *Nature*, *Neuron*, and *Current Biology*. Zars initiated collaborations with his colleagues at the University of Missouri, including a project on the quantitative genetics of learning and memory with Elizabeth King and the development of new thermo-genetic tools for investigating neuronal circuits with Mirela and Lorin Milescu. Outside of University of Missouri, Zars collaborated with Ulrike Heberlein (University of California-San Francisco/HHMI) and Paul Shaw (Washington University-St. Louis), Toshi Kitamoto (University of Iowa), Judith L. Fridovich-Keil (Emory University), as well as Björn Brembs (Universität Regensburg), on the relationship of memory with ethanol sensitivity and sleep, transgenic tool development, fly models of galactosemia, as well as on the function of FoxP, respectively (Figure 2).

In addition to his role as a respected researcher, Zars served the University of Missouri as teacher and mentor. He taught undergraduates in *Cell Biology*, co-developed a graduate-level curriculum in *Integrative Neuroscience* and was a mentor to undergraduate students, graduate students, postdoctoral scholars, and junior faculty. Many of Zars's mentees including Sören Diegelmann, Martin Schwärzel, Divya Sitaraman, Holly LaFerriere, Daniela Ostrowski and Lily Kahsai were inspired to continue their science or to pursue a career in science themselves, which testifies to his mentoring abilities and infectious passion for research. He made an impact on the community of neuroscientists at the University of Missouri by leading the development of the

Philip H.-S. Jen Lecture in *Neural Circuits and Behavior*, a regular lecture series that served as a forum for researchers interested in neurobiology and behavior to discuss research and to form collaborations.

He further served the wider scientific community through service as Editor with *PLOS ONE* (2010–2015) and as Reviewer for various scientific journals, institutions and science funders, including the *National Science Foundation* and the *National Institutes of Health*. He co-organized the *Gateway to Behavioral Neuroscience* conference from 2004–2011 to give a platform to graduate students and postdoctoral scholars. In 2014 he co-organized the HHMI Janelia Conference *Learning and Memory: A Synthesis of Bees and Flies*.

As alumnus of the Alexander von Humboldt Foundation Zars was committed to US–Germany exchange and cooperation, including hosting Humboldt Fyodor Lynen Fellows in Columbia (Daniela Ostrowski, Martin Schwärzel), as well as in repeated academic visits to Germany funded through the Alexander von Humboldt Foundation (2008, 2010, 2012, 2016).

Zars died on 27 December 2018, in Columbia, Missouri, surrounded by his family and friends.

A full list of the publications by Troy Zars, and a list with coverage of his work and life are available with Supplemental Material 1.

ORCID

Bertram Gerber http://orcid.org/0000-0003-3003-0051
Elizabeth G. King http://orcid.org/0000-0002-9393-4720
Divya Sitaraman http://orcid.org/0000-0003-1197-0355

A biographical sketch of Troy D. Zars (1967-2018)

Bertram Gerber, Elizabeth G. King, Divya Sitaraman, Journal of Neurogenetics 2020

Supplemental Material 1

Publications by Troy Zars

Coverage of the work and life of Troy Zars

Publications by Troy Zars

Baggett, V., Mishra, A., Kehrer, A. L., Robinson, A. O., Shaw, P. & Zars, T. (2018). Place learning overrides innate behaviors in *Drosophila*. *Learning and Memory*, *25*, 122-128.

Chen, A., Kramer, E. F., Purpura, L., Krill, J. L., Zars, T., Dawson-Scully, K. (2011). The influence of natural variation at the foraging gene on thermotolerance in adult *Drosophila* in a narrow temperature range. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 197*, 1113-1118.

Diegelmann, S., Nieratschker, V., Werner, U., Hoppe, J., Zars, T., Buchner, E. (2006). The conserved protein kinase-A target motif in synapsin of *Drosophila* is effectively modified by pre-mRNA editing. *BMC Neuroscience, 7*, 76.

Diegelmann, S., Zars, M., Zars, T. (2006). Genetic dissociation of acquisition and memory strength in the heat-box spatial learning paradigm in *Drosophila*. *Learning and Memory, 13*, 72-83.

Dissel, S., Morgan, E., Duong, V., Chan, D., van Swinderen, B., Shaw, P., Zars, T. (2020). Sleep restores place learning to the adenylyl cyclase mutant rutabaga. *Journal of Neurogenetics*, in press.

Gioia, A., Zars, T. (2009). Thermotolerance and place memory in adult *Drosophila* are independent of natural variation at the foraging locus. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 195*, 777-782.

Godenschwege, T. A., Reisch, D., Diegelmann, S., Eberle, K., Funk, N., Heisenberg, M., … Buchner, E. (2004). Flies lacking all synapsins are unexpectedly healthy but are impaired in complex behaviour. *European Journal of Neuroscience, 20*, 611-622.

Hoyer, S. C., Eckart, A., Herrel, A., Zars, T., Fischer, S. A., Hardie, S., Heisenberg, M. (2008). Octopamine in male aggression of *Drosophila*. *Current Biology, 18*, 159-167.

Hyde, D. R., Milligan, S., Zars, T. (1997). Rhodopsin-dependent models of *Drosophila* photoreceptor degeneration. In *Degenerative Retinal Diseases*, 145-158. New York: Plenum Press.

Iakhine, R., Chorna-Ornan, I., Zars, T., Elia, N., Cheng, Y., Selinger, Z., Minke, B., Hyde, D. R. (2004). Novel dominant rhodopsin mutation triggers two mechanisms of retinal degeneration and photoreceptor desensitization. *Journal of Neuroscience, 24*, 2516-2526.

Kahsai, L., Zars, T. (2011). Learning and memory in *Drosophila*: Behavior, genetics, and neural systems. *International Review of Neurobiology, 99*, 139-167.

Kahsai, L., Zars, T. (2013). Visual working memory: Now you see it, now you don't. *Current Biology, 23*, R843-R845.

Keller, A., Sweeney, S. T., Zars, T., O'Kane, C. J., Heisenberg, M. (2002). Targeted expression of tetanus neurotoxin interferes with behavioral responses to sensory input in *Drosophila*. *Journal of Neurobiology, 50*, 221-233.

Kosloff, M., Elia, N., Joel-Almagor, T., Timberg, R., Zars, T. D., Hyde, D. R., Minke, B., Selinger, Z. (2003). Regulation of light-dependent Gqα translocation and morphological changes in fly photoreceptors. *EMBO Journal, 22*, 459-468.

LaFerrier, H., Guarnieri, D. J., Sitaraman, D., Diegelmann, S., Heberlein, U., Zars, T. (2008). Genetic dissociation of ethanol sensitivity and memory formation in *Drosophila melanogaster*. *Genetics, 178*, 1895-1902.

LaFerriere, H., Ostrowski, D., Guarnieri, D. J., Zars, T. (2011). The arouser EPS8L3 gene is critical for normal memory in *Drosophila*. *PLoS ONE, 6*, e22867.

LaFerriere, H., Speichinger, K., Stromhaug, A., Zars, T. (2001). The Radish gene reveals a memory component with variable temporal properties. *PLoS ONE, 6*, e24557.

LaFerriere, H., Zars, T. (2017). The *Drosophila melanogaster* tribbles pseudokinase is necessary for proper memory formation. *Neurobiology of Learning and Memory, 144*, 68-76.

Lee, Y. J., Shah, S., Suzuk, E., Zars, T., O'Day, P. M., Hyde, D. R. (1994). The *Drosophila* dgq gene encodes a Gα protein that mediates phototransduction. *Neuron, 13*, 1143-1157.

Liu, G., Seiler, H., Wen, A., Zars, T., Ito, K., Wolf, R., Heisenberg, M., Liu, L. (2006). Distinct memory traces for two visual features in the *Drosophila* brain. *Nature, 439*, 551-556.

Masoner, V., Das, R., Pence, L., Anand, G., LaFerriere, H., Zars, T., Bouyain, S., Dobens, L. L. (2013). The kinase domain of *Drosophila* Tribbles is required for turnover of fly C/EBP during cellmigration. *Developmental Biology, 375*, 33-44.

Mendoza, E., Colomb, J., Rybak, J., Pflüger, H. J., Zars, T., Scharff, C., Brembs, B. (2014). *Drosophila* FoxP mutants are deficient in operant self-learning. *PLoS ONE, 9*, e100648.

Mishra, A., Cronley, P., Ganesan, M., Schulz, D. J., Zars, T. (2020). PAM dopaminergic neurons can influence place learning in the heat box. *Journal of Neurogenetics*, in press.

Mishra, A., Salari, A., Berigan, B. R., Miguel, K. C., Amirshenava, M., Robinson, A., Zars, B. C., Lin, J. L., Milescu, S., Milescu, M. & Zars, T. (2018). The *Drosophila* Gr28bD product is a non-specific cation channel that can be used as a novel thermogenetic tool. *Scientific Reports*, *8*, 19065.

Mishra, A., Zars, T. (2018). Sex: The end is all you need. *Current Biology, 28*, R614-R616.

Ostrowski, D., Kahsai, L., Kramer, E. F., Knutson, P., Zars, T. (2015). Place memory retention in *Drosophila*. *Neurobiology of Learning and Memory, 123*, 217-224.

Ostrowski, D., Salari, A., Zars, M., Zars, T. (2018). A biphasic locomotor response to acute unsignaled high temperature exposure in *Drosophila*. *PLoS ONE, 13*, e0198702.

Ostrowski, D., Zars, T. (2011). Genetics of memory. In *Yearbook of Science and Technology*, 121-124. New York: McGraw-Hill.

Ostrowski, D., Zars, T. (2014). Place memory. In J. Dubnau (Ed.) *Behavioral Genetics of the Fly (Drosophila Melanogaster)*, 125-134. Cambridge: Cambridge University Press.

Putz, G., Bertolucci, F., Raabe, T., Zars, T., Heisenberg, M. (2004). The S6KII(rsk) gene of *Drosophila melanogaster* differentially affects an operant and a classical learning task. *Journal of Neuroscience, 24*, 9745-9751.

Schwaerzel, M., Heisenberg, M., Zars, T. (2002). Extinction antagonizes olfactory memory at the subcellular level. *Neuron, 35*, 951-960.

Sitaraman, D., Kramer, E. F., Kahsai, L., Ostrowski, D., Zars, T. (2017). Discrete serotonin systems mediate memory enhancement and escape latencies after unpredicted aversive experience in *Drosophila* place memory. *Frontiers in Systems Neuroscience, 11*, 92.

Sitaraman, D., LaFerriere, H., Birman, S., Zars, T. (2012). Serotonin is critical for rewarded olfactory short-term memory in *Drosophila*. *Journal of Neurogenetics, 6*, 238-244.

Sitaraman, D., Zars, M., LaFerriere, H., Chen, Y. C., Sable-Smith, A., Kitamoto, T., Rottinghaus, G. E., Zars, T. (2008). Serotonin is necessary for place memory in *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America, 105*, 5579-5584.

Sitaraman, D., Zars, M., Zars, T. (2007). Reinforcement pre-exposure enhances spatial memory formation in *Drosophila*. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 193*, 903-908.

Sitaraman, D., Zars, M., Zars, T. (2010). Place memory formation in *Drosophila* is independent of proper octopamine signaling. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 196*, 299-305.

Sitaraman, D., Zars, T. (2010). Lack of prediction for high-temperature exposures enhances *Drosophila* place learning. *Journal of Experimental Biology, 213*, 4018-4022.

Williams-Simon, P. A., Posey, C., Mitchell, S., Ng'oma, E., Mrkvicka, J. A., Zars, T., & King, E. G. (2019). Multiple genetic loci affect place learning and memory performance in *Drosophila melanogaster*. *Genes, Brain and Behavior*, *18*, e12581.

Zars, M., Zars, T. (2006). High and low temperatures have unequal reinforcing properties in *Drosophila* spatial learning. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology, 192*, 727-735.

Zars, M., Zars, T. (2009). Rapid matching in *Drosophila* place learning. *Naturwissenschaften, 96*, 927-931.

Zars, T. (2000). Behavioral functions of the insect mushroom bodies. *Current Opinion in Neurobiology, 10*, 790-795.

Zars, T. (2001). Two thermosensors in *Drosophila* have different behavioral functions. *Journal of Comparative Physiology - A Sensory, Neural, and Behavioral Physiology, 187*, 235-242.

Zars, T. (2003). Hot and cold in *Drosophila* larvae. *Trends in Neurosciences, 26*, 575-577.

Zars, T. (2009). Spatial orientation in *Drosophila*. *Journal of Neurogenetics, 23*, 104-110.

Zars, T. (2010a). Short-term memories in *Drosophila* are governed by general and specific genetic systems. *Learning and Memory, 17*, 246-251.

Zars, T. (2010b). Visualizing PKA dynamics in a learning center. *Neuron, 65*, 442-444.

Zars, T. (2011). Neuroscience: Flies race to a safe place. *Nature, 474*, 169-170.

Zars, T. (2012). She said no, pass me a beer. *Science, 335*, 1309-1310.

Zars, T. (2017). Working memory: It's a gas, gas, gas. *Current Biology, 27*, R179-R181.

Zars, T., Fischer, M., Schulz, R., Heisenberg, M. (2000). Localization of a short-term memory in *Drosophila*. *Science, 288*, 672-675.

Zars, T., Hyde, D. R. (1996). rdgE: A novel retinal degeneration mutation in *Drosophila melanogaster*. *Genetics, 144*, 127-138.

Zars, T., Wolf, R., Davis, R., Heisenberg, M. (2000). Tissue-specific expression of a type I adenylyl cyclase rescues the rutabaga mutant memory defect: In search of the engram. *Learning and Memory, 7*, 18-31.

Coverage of the work and life of Troy Zars

https://www.sciencedaily.com/releases/2008/03/080324173545.htm
https://www.sciencemag.org/news/2012/03/sexually-rejected-flies-turn-booze
https://www.sciencedaily.com/releases/2012/03/120315145415.htm
https://www.komu.com/news/fruit-flies-help-mu-scientists-study-human-communication/
https://www.sciencedaily.com/releases/2018/03/180321143718.htm
https://biology.missouri.edu/news/division-mourns-zars-death/

A biographical sketch of Troy D. Zars (1967-2018)

Bertram Gerber, Elizabeth G. King, Divya Sitaraman, Journal of Neurogenetics 2020

Supplemental Material 2

A high-resolution file of Troy Zars´ career seal (Figure 1). The font-size of the words is proportional to the number of times they occur within the titles of his publications, how often colleagues are listed as co-authors, and how many of his works appeared in the respective journal.

Drosophila
Memory
Place
Learning
Genetics
SitaramanD
OstrowskiD
HeisenbergM
ZarsM
LaFerriereH
Behavior
CompPhysiolA
JNeurogenet
melanogaster
HydeDR
DiegelmannS
LearnMem
Formation
CurrBiol
PLoSOne
Spatial
Gene
MishraA
KahsaiL
KramerEF
HoppeJ
Mutant
Degeneration
Serotonin
tribbles
Photoreceptor
Octopamine
Neuron
Short-Term
Fly
rutabaga
foraging
Systems
Temperature
Enhance
Adenylyl-Cyclase
Thermotolerance
Olfactory
Operant
Working
Retinal
WolfR
Protein
Necessary
NeurobiolLearnMem
GuarnieriDJ
Heat-Box
ShawP
Expression
Two
Gas
Novel
synapsin
Function
EliaN
Variation
High
Now
Critical
Influence
Independent
Exposure
Nature
JNeurosci
SelingerZ
SalariA
WernerU
BuchnerE
PutzG
Natural
MinkeB
RobinsonA
Mutation
Dissociation
Property
Visual
Adult
Science
Proper