

CURRICULUM VITAE

Robert L. Spencer

Place of Birth: Denver, Colorado

Address: Department of Psychology and Neuroscience, 2860 Wilderness Pl, Boulder, CO 80301; phone (303) 492-0854; email Robert.spencer@colorado.edu

Education:

Ph.D., 1986	University of Arizona, Tucson, Arizona (Biopsychology and Neuropharmacology)
M.A., 1983	University of Arizona, Tucson, Arizona (Biopsychology)
B.A., 1978 Summa Cum Laude	Oral Roberts University, Tulsa, Oklahoma (Psychology and Social Work)
1974	Golden Senior High School, Golden, Colorado

Professional Appointments:

Jan. 2017 – Dec 2022	Associate Chair and Director of Neuroscience Major, University of Colorado, Boulder, CO
July 2012 – Dec 2015	Associate Chair and Director of Undergraduate Education, Department of Psychology, University of Colorado, Boulder, CO
2009 – <i>present</i>	Professor: Department of Psychology, University of Colorado, Boulder, CO
Aug. 1999 – Jul. 2008	Associate Professor: Department of Psychology, University of Colorado, Boulder, CO
Jan. 1994 - Jul. 1999	Assistant Professor: Department of Psychology, University of Colorado, Boulder, CO
Sept. 1991 - Dec. 1993	Assistant Professor: Laboratory of Neuroendocrinology, Rockefeller University, New York, NY
Sept. 1986 - Aug. 1991	Postdoctoral Fellow and Research Associate with: Bruce S. McEwen, Ph.D., Professor and Head of Lab of Neuroendocrinology, Rockefeller University, New York, NY
Sept. 1983 - Aug. 1986	Graduate Research Assistant with: Thomas F. Burks, Ph.D., Chair and Professor, Dept. of Pharmacology, University of Arizona, Tucson, AZ
Sept. 1979 - Aug. 1982	Graduate Research Assistant with: Sigmund Hsiao, Ph.D., Professor, Dept. of Psychology, University of Arizona, Tucson, AZ

Awards:

- 2014 College Scholars Award, College Arts and Sciences, Univ Colorado
- 2008 Outstanding Teaching Award, Department of Psychology, University of Colorado
- 2004 Outstanding Service Award, Department of Psychology, University of Colorado
- 2001 Briggs Memorial Award, for support of undergraduate research, University of Colorado
- 1998 U.S. West Dex/C.U. Athletic Department Excellence in Education Outstanding Professor
- 1996 Outstanding Neuroscience Professor Award, The C.U. Neuroscience Club
- 1994 Junior Faculty Development Award, University of Colorado
- 1986 Individual National Research Service Award, 3 yr. Postdoctoral Fellowship, National Institute on Alcohol Abuse and Alcoholism, (PHS# AA05256)
- 1983 Summer Research Support Award, Graduate College, University of Arizona, Tucson, AZ
- 1982 Meritorious Performance in Teaching, The Univ. of Arizona Foundation, Tucson, AZ
- 1981 Graduate College Scholarship, University of Arizona, Tucson, AZ

Membership in Professional Organizations:

- American Association for the Advancement of Science, 1986 to present
- Society for Neuroscience, Student member 1983-1986, Member 1986 to present
- Psychoneuroimmunology Research Society, 1993-1999
- International Society of Psychoneuroendocrinology, 1995-2000
- Endocrine Society, 1996 to present
- American Neuroendocrinology Society, 2004 to 2010
- Rocky Mountain Region Neuroscience Group, 1994 to present
- Front Range Neuroscience Group, 2001 to present
- American Physiological Society, 2013 to present
- Society for Research on Biological Rhythms, 2017 to present
- American Association of Laboratory Animal Science, 2019 to present

Research Support:

- Principal Investigator, NIH grant R01 MH115947: “Circadian Regulation of Prefrontal Cortex-Dependent Emotional Memories”, 1/1/19 to 11/30/2024.
Total Direct Costs: \$1,550,685
- Principal Investigator, Subcontract for NIH Grant R44 MH119734 (Sloan PI, Vulintus): “HabiTrak: low-cost, wireless home cage health and activity monitoring”, 6/24/2020 to 5/31/2022.
Total Direct Costs: \$102,271.

- Principal Investigator, American Association for Laboratory Animal Science:
“Evaluation of the response of the rat circadian system to vivarium nighttime “safe”
red light”, 7/1/19 to 12/15/21.
Total Direct Costs: \$36,067
- Principal Investigator, NSF grant IOS1456706: “Glucocorticoid Hormone Entrainment of
Prefrontal Cortex Circadian Function”, 7/1/15 to 6/30/20.
Total Direct Costs: \$355,358
- Principal Investigator, Univ. of Colorado Innovative Seed Grant: “Circadian salivary
cortisol hormone profile as an innovative biomarker and treatment target for
improving recovery from mild traumatic brain injury”, 7/1/17 to 12/31/19.
Total Direct Costs: \$50,000
- Principal Investigator, Subcontract for NIH Grant R01 AG043467 (Deak PI, Univ
Binghamton): “Neuroinflammation and Social Behavior Across the Lifespan”,
5/15/14 to 5/14/20.
Total Direct Costs: \$196,180
- Principal Investigator, NIH grant R01 MH75968: “Glucocorticoid Negative Feedback:
Intrinsic and Extrinsic Mechanisms”, 7/20/06 to 6/30/14.
Total Direct Costs: \$1,475,000
- Independent Scientist Award, NIH award K02 MH065977: “Glucocorticoid Negative
Feedback: Intrinsic and Extrinsic Mechanisms”, 4/16/09 to 3/31/12.
Total Direct Costs: \$343,360
- Multiple Principal Investigators (Spencer, Herman, Koenig), NIH grant R13 MH090623:
“Neurobiology of Stress Workshop 2010”, 6/1/10 to 5/31/11.
Total Direct Costs: \$19,353
- Principal Investigator, Univ. of Colorado Innovative Seed Grant: “Evaluation of the Role
of the Medial Prefrontal Cortex in Psychological Stress Adaptation”, 7/1/08 to
6/30/10.
Total Direct Costs: \$43,500
- Independent Scientist Award, NIH award K02 MH065977: "Corticosteroid Dependent
Mechanisms of Stress Adaptation", 9/1/02 to 8/31/07.
Total Direct Costs: \$466,696
- Principal Investigator, NIH grant R01 MH/DK62456: "Corticosteroid Dependent
Mechanisms of Stress Adaptation", 7/1/01 to 6/30/06.
Total Direct Costs: \$858,547
- Sponsor, NIH Individual National Research Service Award predoctoral fellowship for
Thaddeus Pace: "Mineralocorticoid Receptor Control of HPA Stress Response",
9/1/01 to 8/30/04.
- Principal Investigator, Subcontract for NIH Grant R01 AG12962 (Herman PI, Univ
Cincinnati): "Glucocorticoid Receptor Mechanisms, Stress and Aging", 5/6/96 to
4/30/00; 6/1/02 to 5/31/07
Total Direct Costs for Subcontract: \$55,920; \$98,518
- Principal Investigator, FIRST award NIH Grant NIDDK R29 DK49143: "Corticosteroid
Receptors and HPA Axis Adaptation", 8/1/95 to 7/31/00.
Total Direct Costs: \$350,000
- Principal Investigator, B-Start Small Research Grant NIMH R03 MH54742: "Stress-
induced Changes in Corticosteroid Receptors", 4/1/95 to 7/31/95.

Direct Costs: \$25,000

Collaborator, MacArthur Foundation Grant: "Brain, Behavior and Immunity", 8/1/91 to 12/31/94.

Direct Costs for Research at University of Colorado: \$2,000

Principal Investigator of Subcontract, for NIMH Grant R01 MH47674 (Miller PI, Mt. Sinai Sch Med): "Adrenal Steroid Receptors in Immune Cells and Tissues", 3/1/91 to 12/31/93.

Direct Costs for Subcontract: \$177,365

Research Record

Thesis and Dissertation:

The effects of cholecystokinin on milk and water intake and licking behavior of rats. M.A. Thesis, Univ. of Arizona, 1983.

Tolerance development to the effects of ethanol: role of behavioral thermoregulatory responses. Ph.D. Dissertation, Univ. of Arizona, 1986.

Journal Articles (in reverse chronological order)

1. Ravenel, JR, Perkins, AE, Tomczik, A, Defendini, A, Strnad, HK, Varlinskaya, E, Deak, T, RL Spencer. Age-related decline in social interaction is associated with decreased c-Fos induction in select brain regions independent of oxytocin receptor expression profiles. *Aging Brain*, 2024, **in press**.
2. Hartsock, MJ, Brennan, N, and RL Spencer. Circadian rhythms in fear extinction recall depend on the time of day of extinction recall, not the time of day of extinction learning. *Journal of Biological Rhythms*, **38**:109-115, 2023.
3. Wong, SD, Wright, KP, Spencer, RL, Vetter, C, Hicks, LM, Jenni, OG, and LeBourgeois, M. Development of the Circadian System in Early Life: Maternal and Environmental Factors. *Journal of Physiological Anthropology*, **41**:22, 2022.
4. Villegas, E, Hartsock, MJ, Aben, BLLG, Lenahan, KN, Hernandez, T and RL Spencer. Association between altered cortisol profiles and neurobehavioral impairment after mild traumatic brain injury in college students. *Journal of Neurotrauma*, **39**:809-820, 2022.
5. Hartsock, MJ, Strnad, HK, and RL Spencer. Iterative metaplasticity across timescales: how circadian, ultradian, and infradian rhythms modulate memory mechanisms. *Journal of Biological Rhythms*, **37**:29-42, 2022. [PMCID:9236757]
6. Carol, EE, Spencer, RL, VA Mittal. Acute physiological and psychological stress response in youth at clinical high-risk for psychosis. *Frontiers in Psychiatry* **12**:article 641762, 2021.
7. Dhabhar, FS, Meaney, MJ, Sapolsky, RM, and RL Spencer. Reflections on Bruce S. McEwen's contributions to stress neurobiology and so much more. *Stress* **23**:499-508, 2020.
8. Hartsock MJ, Spencer RL. Memory and the circadian system: identifying candidate mechanisms by which local clocks in the brain may regulate synaptic plasticity. *Neuroscience and Biobehavioral Reviews*. **118**:134-162, 2020.
9. Daut RA, Hartsock MJ, Tomczik AC, Watkins LR, Spencer RL, Maier SF and LK Fonken. Circadian misalignment has differential effects on affective behavior following exposure to controllable or uncontrollable stress. *Behavioural brain research*. **359**:440-445, 2019 doi:10.1016/j.bbr.2018.10.013.

10. Woodruff ER, Chun LE, Hinds LR, Varra NM, Tirado D, Morton SJ, McClung CA and RL Spencer. Coordination between prefrontal cortex clock gene expression and corticosterone contributes to enhanced conditioned fear extinction recall. *eNeuro*, 2018. <https://doi.org/10.1523/ENEURO.0455-18.2018>
11. Spencer RL, Chun LE, Hartsock MJ, Woodruff ER. Glucocorticoid hormones are both a major circadian signal and major stress signal: How this shared signal contributes to a dynamic relationship between the circadian and stress systems. *Frontiers in Neuroendocrinology*, **49**, 52-71, 2018.
12. Chun LE, Christensen J, Woodruff ER, Morton SJ, Hinds LR, Spencer RL. Adrenal-dependent and -independent stress-induced Per1 mRNA in hypothalamic paraventricular nucleus and prefrontal cortex of male and female rats. *Stress (Amsterdam, Netherlands)*. **28**: 69-83, 2018 doi:10.1080/10253890.2017.1404571.
13. Hinds LR, Chun LE, Woodruff ER, Christensen JA, Hartsock MJ, Spencer RL. Dynamic glucocorticoid-dependent regulation of Sgk1 expression in oligodendrocytes of adult male rat brain by acute stress and time of day. Kavushansky A, ed. *PLoS ONE* 2017;12(4):e0175075.
14. Perkins AE, Woodruff ER, Chun LE, Spencer RL, Varlinskaya E, Deak T. Analysis of c-Fos induction in response to social interaction in male and female Fisher 344 rats. *Brain Res*. **1672**:113-121, 2017.
15. Carol EE, Spencer RL, Mittal VA. The relationship between cannabis use and cortisol levels in youth at ultra high-risk for psychosis. *Psychoneuroendocrinology*. 2017;83:58-64.
16. Spencer RL, Deak T. A users guide to HPA axis research. *Physiol Behav*, **178**, 43-65, 2017.
17. Carol, EE, Spencer, RL and VA Mittal. Sex differences in morning cortisol in youth at ultra high-risk for psychosis. *Psychoneuroendocrinology*, **72**, 87-93, 2016.
18. Osterlund, CD, Rodriguez-Santiago, M, Woodruff, ER, Newsom, RJ, Chadayammurri, AP and RL Spencer. Glucocorticoid fast feedback inhibition of stress-induced ACTH secretion in the male rat: rate-independence and stress-state resistance. *Endocrinology*, **157**, 2785-2798, 2016.
19. Woodruff, ER, Chun, LE, Hinds, LR and RL Spencer. Diurnal corticosterone presence and phase modulate clock gene expression in the male rat prefrontal cortex. *Endocrinology*, **157**, 1522-1534, 2016.
20. O'Neill, CE, Newsom, RJ, Stafford, J, Scott, T, Archuleta, S, Levis, SC, Spencer, RL, Campeau, S, and R Bachtell. Adolescent caffeine consumption increases adulthood anxiety-related behavior and modifies neuroendocrine signaling. *Psychoneuroendocrinology*, **67**, 40-50, 2016.
21. Perkins, AE, Doremus-Fitzwater, TL, Spencer, RL, Varlinskaya, EI, Conti, MM, Bishop, C and T Deak. A working model for the assessment of disruptions in social behavior among aged rats: the role of sex differences, social recognition, and sensorimotor processes. *Experimental Gerontology*, **76**: 46-57, 2016.
22. Chun, LE, Woodruff, ER, Morton, S, Hinds, LR and RL Spencer. Variations in phase and amplitude of rhythmic clock gene expression across prefrontal cortex, hippocampus, amygdala, and hypothalamic paraventricular and suprachiasmatic nuclei of male and female rats. *J Biol Rhythms*, **30**: 417-436, 2015.
23. Woodruff ER, Greenwood BN, Chun LE, Fardi S, Hinds LR, & Spencer RL. Adrenal-dependent diurnal modulation of conditioned fear extinction learning. *Behavioural Brain Research*, **286**: 249-255, 2015.

24. Barrientos, RM, Thompson, VM, Kitt, MM, Amat, J, Hale, MW, Frank, MG, Crysdale, NY, Stamper, CE, Hennessey, PA, Watkins, LR, Spencer, RL, Lowry, CA and SF Maier. Greater glucocorticoid receptor activation in hippocampus of aged rats sensitizes microglia. *Neurobiology of Aging*, **36**:1483-1495, 2015.
25. Stamper, C.E, Hennessey, PA, Hale, MW, Lukkes, JL, Donner, NC, Lowe, KR, Paul, ED, Spencer, RL, Renner, KJ, Orchinik, M and CA Lowry. Role of the dorsomedial hypothalamus in glucocorticoid-mediated feedback inhibition of the hypothalamic-pituitary-adrenal axis. *Stress (Amsterdam, Netherlands)*, **18**:76-87, 2015.
26. Sollars, PJ, Weiser, MJ, Kudwa, AE, Bramley, JR, Ogilvie, MD, Spencer, RL, Handa, RJ and GE Pickard. (2014). Altered entrainment to the day/night cycle attenuates the daily rise in circulating corticosterone in the mouse. *PLOS One*, **9(11)**, e111944, 2014.
27. Highland, JA, Weiser, MJ, Hinds, L and RL Spencer. CRTRC2 activation in the suprachiasmatic nucleus, but not paraventricular nucleus, varies in a diurnal fashion and increases with nighttime light exposure. *Am J Physiol Cell Physiol*, **307**:C611-C621, 2014.
28. Osterlund, CD, Thompson, V, Hinds, L and RL Spencer. Absence of glucocorticoids augments stress-induced Mkp-1 mRNA expression within the HPA axis. *J Endocrinol*, **220**:1-11, 2014.
29. Kearns, RR and RL Spencer. An unexpected increase in restraint duration alters the expression of stress response habituation. *Physiology and Behavior*, **122**:193-200, 2013.
30. Newsom, RJ, Osterlund, C, Masini, CV, Day, HE, Spencer, RL and S Campeau. Cannabinoid receptor type 1 antagonism significantly modulates basal and loud noise induced neural and hypothalamic-pituitary-adrenal axis responses in male Sprague-Dawley rats. *Neuroscience*, **204**, 64-73, 2012.
31. Osterlund, CD, Jarvis, E, Chadayammuri, A, Unnithan, R, Weiser, MJ, and RL Spencer. Tonic, but not phasic corticosterone constrains stress activated extracellular-regulated-kinase 1/2 immunoreactivity within the hypothalamic paraventricular nucleus. *J Neuroendo*, **23**: 1241-1251, 2011.
32. Weiser, MJ, Osterlund, C, RL Spencer. Inhibitory effects of corticosterone in the hypothalamic paraventricular nucleus (PVN) on stress-induced ACTH secretion and gene expression in the PVN and anterior pituitary. *J Neuroendo*, **23**: 1231-1240, 2011.
33. VanElzakker, MB, Zoladz, PR, Thompson, VM, Park, CR, Halonen, JD, Spencer, RL and DM Diamond. Influence of pre-training predator stress on the expression of c-fos mRNA in the hippocampus, amygdala, and striatum following long-term spatial memory retrieval. *Frontiers in Behavioral Neuroscience* **5**:article 30, 1-13, 2011.
34. Osterlund, C and RL Spencer. Corticosterone pretreatment suppresses stress-induced hypothalamic-pituitary-adrenal axis activity via multiple actions that vary with time, site of action and de novo protein synthesis. *J Endocrinol* **208**:1-12, 2011.
35. Weinberg, MS, Grissom, N., Paul E., Bhatnagar, S, Maier, SF and RL Spencer. Inescapable but not escapable stress leads to increased struggling behavior and basolateral amygdala c-fos gene expression in response to subsequent novel stress challenge. *Neuroscience* **170**: 138-148, 2010.
36. Weinberg, MS, Johnson, DC, Bhatt, AP and RL Spencer. Medial prefrontal cortex activity can disrupt the expression of stress response habituation. *Neuroscience* **168**:744-756, 2010.
37. Spencer, R.L. and Weiser, M.J. TORC: A new twist on corticotropin-releasing hormone gene expression. (News and Views invited editorial) *Endocrinology* **151**, 855-858, 2010.

38. Girotti, M, Weinberg, MS and RL Spencer. Diurnal expression of functional and clock-related genes in the rat hypothalamic-pituitary-adrenal axis. System-wide shifts in response to a restricted feeding schedule. *American Journal of Physiology: Endocrinology and Metabolism*, **296**:888-897, 2009.
39. Pace, TWW, Gaylord, RI, Jarvis, E, Girotti, M and RL Spencer. Differential glucocorticoid effects on stress-induced gene expression in the paraventricular nucleus of the hypothalamus and ACTH secretion. *Stress*, **12**:400-411, 2009.
40. Weinberg, MS, Bhatt, AP, Girotti, M, Masini, CV, Day, HEW, Campeau, S and RL Spencer. Repeated ferret odor exposure induces different temporal patterns of same-stressor habituation and novel-stressor sensitization in both HPA-axis activity and forebrain c-fos expression in the rat. *Endocrinology*, **150**: 749-761, 2009.
41. VanElzaker, M, Fevurly, RD, Breindel, T and RL Spencer. Environmental novelty is associated with a selective increase in Fos expression in the output elements of the hippocampal formation and the perirhinal cortex. *Learning and Memory*, **15**:899-908, 2008.
42. Parker, CC, Ponicsan, H, Spencer, RL, Holmes A and TE Johnson. Restraint stress and exogenous corticosterone differentially alter sensitivity to the sedative-hypnotic effects of ethanol in ILS and ISS mice. *Alcohol*, **42**:477-485, 2008.
43. Weinberg, MS, Girotti, M and RL Spencer. Restraint-induced fra-2 and c-fos expression in the rat forebrain: relationship to stress duration. *Neuroscience*, **150**: 478-486, 2007.
44. Brown, DA, Johnson, MS, Armstrong, CJ, Lynch, JM, Caruso, NM, Ehlers, LB, Fleshner, M, Spencer, RL and RL Moore. Short-term treadmill running in the rat: what kind of stressor is it? *J Applied Physiology*, **103**:1979-1985, 2007.
45. Girotti, M, Weinberg, MS and RL Spencer. Differential responses of HPA axis immediate early genes to corticosterone and circadian drive. *Endocrinology*, **148**: 2542-2552, 2007.
46. Francis, AB, Pace, TWW, Ginsberg, AB, Rubin, BA and RL Spencer. Limited brain diffusion of the glucocorticoid receptor agonist RU28362 following i.c.v. administration: implications for i.c.v. drug delivery and glucocorticoid negative feedback in the hypothalamic-pituitary-adrenal axis. *Neuroscience*, **141**: 1503-1515, 2006.
47. Der-Avakian A, Bland ST, Schmid MJ, Watkins LR, Spencer RL, Maier SF. The role of glucocorticoids in the uncontrollable stress-induced potentiation of nucleus accumbens shell dopamine and conditioned place preference responses to morphine. *Psychoneuroendocrinology*, **31**: 653-663, 2006.
48. Girotti, M, Pace, TWW, Gaylord, RI, Rubin, BA, Herman, JP and RL Spencer. Habituation to repeated restraint stress is associated with lack of stress-induced c-fos expression in primary sensory processing areas of the rat brain. *Neuroscience*, **138**: 1067-1081, 2006.
49. Ginsberg, AB, Frank, MG, Francis, AB, Rubin, BA, O'Connor, KA and RL Spencer. Specific and time-dependent effects of glucocorticoid receptor agonist RU28362 on stress-induced POMC hnRNA, c-fos mRNA and zif268 mRNA in the pituitary. *Journal of Neuroendocrinology*, **18**:129-138, 2006.
50. *Pace, TWW, *Gaylord, R, Topczewski, F, Girotti, M, Rubin, B and RL Spencer. Immediate early gene induction in hippocampus and cortex as a result of novel experience is not directly related to the stressfulness of that experience. *European Journal of Neuroscience*, **22**:1679-1690, 2005. *T.W.W.P and R.G contributed equally to this work.
51. Pace, TWW and RL Spencer. Disruption of mineralocorticoid receptor function increases corticosterone responding to a mild, but not moderate, psychological stressor. *American Journal of Physiology: Endocrinology and Metabolism*, **288**: 1082-1088, 2005.

52. Bland, S.T., Schmid, M.J., Der-Avakian, A., Watkins, L.R., Spencer, R.L. and S.F. Maier. Expression of c-fos and BDNF mRNA in subregions of the prefrontal cortex of male and female rats after acute uncontrollable stress. *Brain Research*, **1051**:90-99, 2005
53. Der-Avakian, A., Will, M.J., Bland, S. T., Deak, T., Nguyen, K. T., Schmid, M. J., Spencer, R. L., Watkins, L. R., & Maier, S. F. Surgical and pharmacological suppression of glucocorticoids prevents the enhancement of morphine conditioned place preference by uncontrollable stress in rats. *Psychopharmacology*, **179**:409-417, 2005.
54. RD Fevurly and RL Spencer. Fos expression is selectively and differentially regulated by endogenous glucocorticoids in the paraventricular nucleus of the hypothalamus and dentate gyrus. *Journal of Neuroendocrinology*, **16**:970-979,2004.
55. O'Connor, K. A., Ginsberg, A. B., Maksimova, E., Wiesler-Frank, J. L., Johnson, J. D., Spencer, R. L., Campeau, S., Watkins, R. L., & Maier, S. F. Stress-induced sensitization of the hypothalamic-pituitary-adrenal axis is associated with alterations of hypothalamic and pituitary gene expression. *Neuroendocrinology*, **80**:252-263, 2004.
56. A.B. Ginsberg, S. Campeau, H.A. Day, R.L. Spencer. Acute glucocorticoid pretreatment suppresses stress-induced HPA axis hormone secretion and expression of CRH hnRNA, but not c-fos mRNA or Fos protein in the paraventricular nucleus of the hypothalamus. *Journal of Neuroendocrinology*, **15**:1075-1083, 2003.
57. K.A. O'Connor, J.D. Johnson, S.E. Hammack, L.M. Brooks, R.L. Spencer, L.R. Watkins and S.F. Maier. Inescapable shock induces resistance to the effects of dexamethasone. *Psychoneuroendocrinology*, **28**: 481–500, 2003.
58. Kalman, B.A. and Spencer, R. L. Rapid corticosteroid dependent regulation of mineralocorticoid receptor protein expression in rat brain. *Endocrinology*, **143**: 4184-4195, 2002.
59. Murphy, E.K., Spencer, R.L., Sipe, K.J. and Herman, J.P.. Nuclear glucocorticoid receptor deficiency in aged rat hippocampus. *Endocrinology*, **143**: 1362-1370, 2002.
60. Beane, M.L., Cole, M.A., Spencer, R.L. and Rudy, J.W. Neonatal handling enhances contextual fear conditioning and alters corticosterone stress responses in young rats. *Hormones and Behavior*, **41**: 33-40, 2002.
61. Johnson, J.D., O'Connor, K.A., Deak, T., Spencer, R.L., Watkins, L.R. and Maier, S.F. Prior stressor exposure primes the HPA axis. *Psychoneuroendocrinology*, **27**: 353-365, 2002.
62. Pace, T.W., Cole, M.A., Ward, G., Kalman, B.A. and Spencer, R.L. Acute exposure to a novel stressor enhances the corticosterone response habituation to restraint in rats. *Stress*, **4**: 319-331, 2001.
63. Cole M.A., Kalman, B.A., Pace, T.W.W., Topczewski, R., Lowrey, M.J., and Spencer, R.L. Selective blockade of the mineralocorticoid receptor impairs hypothalamic-pituitary-adrenal axis expression of habituation. *J Neuroendocrinology*, **12**, 1034-1042, 2000.
64. Moraska, A., Deak, T., Spencer, R.L., Roth, D. and Fleshner, M. Treadmill running produces both positive and negative physiological adaptations in Sprague-Dawley rats. *Am J Physiol Regulatory Integrative Comp Physiol*, **279**, R1321-R1329, 2000.
65. Spencer, R.L., Kalman, B.A., Cotter, C.S. and Deak, T. Discrimination between changes in glucocorticoid receptor expression and activation in rat brain using western blot analysis. *Brain Research*, **868**, 275-286, 2000.
66. Cole, M.A., Kim, P.J., Kalman, B.A., and Spencer, R.L. Dexamethasone suppression of corticosteroid secretion: evaluation of the site of action by receptor measures and function studies. *Psychoneuroendocrinology*, **25**, 151-167, 2000.

67. Spencer, R.L. and Hutchison, K.E. Alcohol, aging and the stress response. *Alcohol Research & Health*, **23**, 272-283, 2000.
68. Herman, J.P., Watson, S.J., and Spencer, R.L. Defense of adrenocorticosteroid receptor expression in rat hippocampus: effects of stress and strain. *Endocrinology*, **140**, 3981-3991, 1999.
69. Deak, T., Nguyen, K.T., Cotter, C.S., Fleshner, M., Watkins, L.R., Maier, S.F., and Spencer R.L. Long term changes in mineralocorticoid and glucocorticoid receptor occupancy following exposure to an acute stressor. *Brain Research*, **847**, 211-220, 1999.
70. Deak, T., Nguyen, K.T., Ehrlich, A.L., Watkins, L.R., Spencer, R.L., Maier, S.F., Licinio, J., Wong, M-L., Chrousos, G.P., Webster, E. and Gold, P.W. The impact of the nonpeptide CRH antagonist Antalarmin on behavioral and endocrine responses to stress. *Endocrinology*, **140**, 79-86, 1999.
71. Kim, P.J., Cole, M.A., Kalman, B.A. and Spencer, R.L. Evaluation of RU28318 and RU40555 as selective mineralocorticoid receptor and glucocorticoid receptor antagonists, respectively: receptor measures and functional studies. *Journal of Steroid Biochemistry and Molecular Biology*, **67**, 213-222, 1998.
72. Miller, A.H., Spencer, R.L., Pearce, B.D., Pisell, T.L., Azrieli, Y., Tanapat, P., Moday, H., Rhee, R. and McEwen, B.S. Glucocorticoid receptors are differentially expressed in the cells and tissues of the immune system. *Cellular Immunology*, **186**, 45-54, 1998.
73. Herman, J.P. and Spencer, R.L. Regulation of hippocampal glucocorticoid receptor gene transcription and protein expression in vivo. *Journal of Neuroscience*, **18**, 7462-7473, 1998.
74. Spencer, R.L., Kim, P.J., Kalman, B.A. and Cole, M.A. Evidence for mineralocorticoid receptor facilitation of glucocorticoid receptor dependent regulation of hypothalamic-pituitary-adrenal axis activity. *Endocrinology*, **139**, 2718-2726, 1998.
75. Ronchi, E., Spencer, R.L., Krey, L.C. and McEwen, B.S. Effects of photoperiod on brain corticosteroid receptors and the stress response in the golden hamster (*Mesocricetus auratus*). *Brain Research*, **780**, 348-351, 1998.
76. Galea, L.A.M., McEwen, B.S., Tanapat, P., Deak, T., Spencer, R.L. and Dhabhar, F.S. Sex differences in dendritic atrophy of CA3 pyramidal neurons in response to chronic restraint stress. *Neuroscience*, **81**, 689-698, 1997.
77. Deak, T., Meriwether, J.L., Fleshner, M., Spencer, R.L., Abouhamze, A., Moldawer, L.L., Grahm, R.E., Watkins, L.R., and Maier, S.F. Evidence that brief stress may induce the acute phase response in rats. *Am J Physiol*, **273**, R1998-R2004, 1997.
78. Spencer, R.L., Moday, H.J., and Miller, A.H. Maintenance of basal ACTH levels by corticosterone and RU28362, but not aldosterone: relationship to available type I and type II corticosteroid receptor levels in brain and pituitary. *Stress*, **2**, 51-64, 1997.
79. Miller, A.H., Spencer, R.L., Pearce, B.D., Pisell, T.L., Tanapat, P., Leung, J.J., Dhabhar, F.S., McEwen, B.S. and Biron, C.A. 1996 Curt P. Richter Award. Effects of viral infection on corticosterone secretion and glucocorticoid receptor binding in immune tissues. *Psychoneuroendo*, **22**, 455-474, 1997.
80. Kalman, B.A., Kim, P.J., Cole, M.A., Chi, M.S. and Spencer, R.L. Diazepam attenuation of restraint stress-induced corticosterone levels is enhanced by prior exposure to repeated restraint. *Psychoneuroendo*, **22**, 349-360, 1997.
81. Spencer, R.L. and McEwen, B.S. Impaired adaptation of the hypothalamic-pituitary-adrenal axis to chronic ethanol stress in aged rats. *Neuroendocrinology*, **65**, 353-359, 1997.

82. Dhabhar, F.S., McEwen, B.S. and Spencer, R.L. Adaptation to prolonged or repeated stress—comparison between rat strains showing intrinsic differences in reactivity to acute stress. *Neuroendocrinology*, **65**, 360-368, 1997.
83. McEwen, B.S., Biron, C.A., Brunson, K.W., Bulloch, K., Chambers, W.H., Dhabhar, F.S., Goldfarb, R.H., Kitson, R.P., Miller, A.H., Spencer, R.L. and J.Weiss. The role of adrenocorticoids as modulators of immune function in health and disease: neural, endocrine, and immune interactions. *Brain Res Rev*, **23**, 79-133, 1997.
84. Dhabhar, F.S., Miller, A.H., McEwen, B.S. and Spencer, R.L. Stress-induced changes in blood leukocyte distribution: role of adrenal steroid hormones. *J Immunol*, **157**, 1638-1644, 1996.
85. Spencer, R.L., Miller, A.H., Moday, H., McEwen, B.S., Blanchard, R.J., Blanchard, D.C. and Sakai, R.R. Chronic social stress produces reductions in available splenic type II corticosteroid receptor binding and plasma corticosteroid binding globulin levels. *Psychoneuroendo*, **21**, 95-109, 1996.
86. Fleshner, M., Spencer, R.L., Deak, T., Watkins, L.R. and Maier, S.F. A long-term increase in basal levels of corticosterone and a decrease in corticosteroid binding globulin (CBG) following acute stressor exposure. *Endocrinology*, **136**, 5336-5342, 1995.
87. Dhabhar, F.S., Miller, A.H., McEwen, B.S. and Spencer, R.L. Effects of stress on immune cell distribution—dynamics and hormonal mechanisms. *J Immunol*, **154**, 5511-5527, 1995.
88. O'Steen, W.K., Spencer, R.L. and McEwen, B.S. Analysis of severe photoreceptor loss and Morris water maze performance in aged rats. *Behav Brain Res*, **68**, 151-158, 1995.
89. Spencer, R.L., O'Steen, W.K. and McEwen, B.S. Water maze performance of aged Sprague-Dawley rats in relation to retinal morphological measures. *Behav Brain Res*, **68**, 139-150, 1995.
90. Orange, J.S., Salazar-Mather, T.P., Opal, S.M., Spencer, R.L., Miller, A.H., McEwen, B.S. and Biron, C.A. Mechanisms of Il-12-mediated toxicities during experimental viral infections: role of TNF and glucocorticoids. *Journal of Experimental Medicine*, **181**, 901-914, 1995.
91. Dhabhar, F.S., Miller, A.H., McEwen, B.S. and Spencer, R.L. Differential activation of adrenal-steroid receptors in neural and immune tissues of Sprague Dawley, Fischer 344, and Lewis Rats. *J. Neuroimmunology*, **56**, 77-90, 1995.
92. Blanchard, D.C., Spencer, R.L., Weiss, S.M., Blanchard, R.J., McEwen, B.S. and Sakai, R.R. Visible burrow system as a model of chronic social stress: behavioral and neuroendocrine correlates. *Psychoneuroendocrinology*, **20**, 117-134, 1995.
93. Miller, A.H., Spencer, R.L., Hassett, J., Kim, C., Rhee, R., Cuirea, D., Dhabhar, F., McEwen, B. and Stein, M. Effects of selective type I and II adrenal steroid receptor agonists on immune cell distribution. *Endocrinology*, **135**, 1934-1944, 1994.
94. Dhabhar, F.S., Miller, A.H., Stein, M., McEwen, B.S. and Spencer, R.L. Diurnal and acute stress-induced changes in distribution of peripheral blood leukocyte subpopulations. *Brain Behavior and Immunity*, **8**, 66-79, 1994.
95. Chao, H.M., Spencer, R.L., Frankfurt, M and McEwen, B.S. The effects of aging and hormonal manipulations on amyloid precursor protein APP695 mRNA expression in the rat hippocampus. *J Neuroendo*, **6**, 517-521, 1994.
96. Akompong, T., Spencer, R.L. and McEwen, B.S. Cytosolic phospholipase C activity: II. relationship to concanavalin A-induced phosphatidylinositol-turnover in splenocytes. *Journal of Cellular Biochemistry*, **56**,409-417, 1994.

97. Akompong, T., Spencer, R.L. and McEwen, B.S. Cytosolic phospholipase C activity: I. evidence for coupling with cytosolic guanine nucleotide-binding protein, Gi-alpha. *Journal of Cellular Biochemistry*, **56**,397-408, 1994.
98. McEwen, B.S., Cameron, H., Chao, H.M., Gould, E., Luine, V., Magarinos, A.M., Pavlides, C., Spencer, R.L., Watanabe, Y., Woolley, C. Resolving a mystery: progress in understanding the function of adrenal steroid receptors in hippocampus. In Progress in Brain Research, vol. 100, pp. 149-155, edited by Floyd E. Bloom, Elsevier: Amsterdam, 1994.
99. Akompong, T., Spencer, R.L. and McEwen, B.S. Glucocorticoids inhibit soluble phospholipase C activity and cytosolic Gi α immunoreactivity in spleen. *Endocrinology*, **133**, 1963-1970, 1993.
100. Miller, A.H., Spencer, R.L., Husain, A., Rhee, R., McEwen, B.S., and Stein, M. Differential expression of type I adrenal steroid receptors in immune tissues is associated with tissue specific regulation of type II receptors by aldosterone. *Endocrinology*, **133**, 2133-2140, 1993.
101. Spencer, R.L., Miller, A.H., Moday, H., Stein, M. and McEwen, B.S. Diurnal differences in basal and acute stress levels of type I and type II adrenal steroid receptor activation in neural and immune tissues. *Endocrinology*, **133**, 1941-1950, 1993.
102. Dhabhar, F.S., McEwen, B.S. and Spencer, R.L. Stress response, adrenal steroid receptor levels and corticosteroid-binding globulin — a comparison between Sprague-Dawley, Fischer 344 and Lewis rats. *Brain Research*, **616**, 89-98, 1993.
103. Luine, V.N., Spencer, R.L. and McEwen, B.S. Effects of chronic corticosterone ingestion on spatial memory performance and hippocampal serotonergic function. *Brain Research*, **616**, 65-70, 1993.
104. Miller, A.H., Spencer, R.L., McEwen, B.S. and Stein, M. Depression, adrenal steroids, and the immune system. *Ann Med*, **25**, 481-487, 1993.
105. Miller, A.H., Spencer, R.L., Pulera, M., Kang, S., McEwen, B.S. and Stein, M. Adrenal steroid receptor activation in rat brain and pituitary following dexamethasone: implications for the dexamethasone suppression test. *Biological Psychiatry*, **32**, 850-869, 1992.
106. Chao, H.M., Spencer, R.L., Sakai, R.R. and McEwen, B.S. The expression of growth-associated protein GAP-43 mRNA in the rat hippocampus in response to adrenalectomy and aging. *Molecular and Cellular Neurosciences*, **3**, 529-535, 1992.
107. McEwen BS, Angulo J, Cameron H, Chao HM, Daniels D, Gannon MN, Gould E, Mendelson S, Sakai R, Spencer R. Paradoxical effects of adrenal steroids on the brain: protection versus degeneration. *Biol Psychiatry*. 1992 Jan 15;31(2):177-99. doi: 10.1016/0006-3223(92)90204-d. Review
108. Woolley, C.S., Gould, E., Sakai, R.R., Spencer, R.L. and McEwen, B.S. Effects of aldosterone or RU28362 treatment on adrenalectomy-induced cell death in the dentate gyrus of the adult rat. *Brain Research*, **554**, 312-315, 1991.
109. Miller, A.H., Spencer, R.L., Kim, C., McEwen, B.S. and Stein, M. Adrenal steroid receptor activation in vivo and immune function. *American Journal of Physiology*, **261**, E126-E131, 1991.
110. Spencer, R.L., Miller, A.H., Stein, M. and McEwen, B.S. Corticosterone regulation of type I and type II adrenal steroid receptors in brain, pituitary, and immune tissue. *Brain Research*, **549**, 236-246, 1991.

111. Owen, T.L., Spencer, R.L. and Duckles, S.P. Effect of age on cold acclimation in rats: metabolic and behavioral responses. *American Journal of Physiology*, **260**, R284-R289, 1991.
112. Young, E.A., Spencer, R.L. and McEwen, B.S. Changes at multiple levels of the hypothalamic-pituitary-adrenal axis following repeated electrically induced seizures. *Psychoneuroendocrinology*, **15**, 165-172, 1990.
113. Spencer, R.L. and McEwen, B.S. Adaptation of the hypothalamic-pituitary-adrenal axis to chronic ethanol stress. *Neuroendocrinology*, **52**, 481-489, 1990.
114. Miller, A.H., Spencer, R.L., Stein, M. and McEwen, B.S. Adrenal steroid receptor binding in spleen and thymus after stress or dexamethasone. *American Journal of Physiology*, **259**, E405-E412, 1990.
115. Gannon, M.N., Spencer, R.L., Lundbland, J.R., McEwen, B.S. and Roberts, J.L. Pharmacological characteristics of type II glucocorticoid binding sites in AtT20 pituitary cell culture. *Journal of Steroid Biochemistry*, **36**, 83-88, 1990.
116. Spencer, R.L., Young, E., Choo, P. and McEwen, B.S. Adrenal steroid type I and type II receptor binding: estimates of in vivo receptor number, occupancy, and activation with varying level of steroid. *Brain Research*, **514**, 37-48, 1990.
117. Spencer, R.L. and Burks, T.F. Alteration of thermoregulatory set point with opioid agonists. *Journal of Pharmacology and Experimental Therapeutics*, **252**, 696-705, 1990.
118. McEwen BS, Spencer RL, Chapman S, Ganem J, O'Steen WK. [Neuroendocrine aspects of cerebral aging](#). *Int J Clin Pharmacol Res.* 1990;10(1-2):7-14. Review. PubMed PMID: 2201658.
119. Spencer, R.L., Hruby, V.J. and Burks, T.F. Body temperature response profiles for selective mu, delta, and kappa opioid agonists in restrained and unrestrained rats. *Journal of Pharmacology and Experimental Therapeutics*, **246**, 92-101, 1988.
120. Spencer, R.L., Deupree, D., Hsiao, S., Mosberg, H.I., Hruby, V., Burks, T.F. and Porreca, F. Centrally-administered opioid selective agonists inhibit drinking in the rat. *Pharmacology, Biochemistry and Behavior*, **25**, 77-82, 1986.
121. Marques, P.R., Spencer, R.L. Burks, T.F. and McDougal, J.N. Behavioral thermoregulation, core temperature, and motor activity: simultaneous quantitative assessment in rats after dopamine and prostaglandin E₁. *Behavioral Neuroscience*, **98**, 858-867, 1984.
122. Hsiao, S. and Spencer, R.L. Analysis of licking responses in rats: effects of cholecystokinin and bombesin. *Behavioral Neuroscience*, **97**, 234-245, 1983.

Book Chapters and Published Lectures:

1. Spencer, R.L., Chun, L.E., Hartsock, M.J. and Woodruff, E.R. Neurobiology of Stress-Health Relationships. In *The Encyclopedia of Health Psychology*, Editor-in-chief, Lee M. Cohen. Wiley-Blackwell, 2020, pp 21-35.
2. Spencer, R.L. and Bland, S. Chapter 5: Hippocampus and Hippocampal Neurons. In *Stress: Physiology, Biochemistry, and Pathology Volume 3 of the Handbook of Stress Series*, Editor, George Fink, Academic Press, Elsevier, London, 2019.
3. Spencer, R.L. and Bland, S. Hippocampal neurons. In *Encyclopedia of Stress*, 2nd edition, ed. by Frink. Elsevier, London, 2007.
4. Spencer, R.L., Kalman, B.A. and Dhabhar, F.S. Role of endogenous glucocorticoids in immune system function: regulation as well as counterregulation. In [Handbook of Physiology. Coping with the Environment: Neural and Endocrine Mechanisms](#), ed. by

- B.S. McEwen, Section 7, Volume IV, pp.381-424, Oxford University Press, Oxford, 2001.
5. Miller, A.H. and Spencer, R.L. Immune system and central nervous system interactions. In Comprehensive Textbook of Psychiatry/VI, 6th edition, ed. by H.I. Kaplan and B.J. Sadock, pp. 112-127, Williams and Wilkins, Baltimore, 1995.
 6. Spencer, R. Exploring brain interactions with the immune system: corticosteroids and their receptors. *Advances*, **10**, 33-40, 1994. [Transcription of lecture delivered to the Boston Behavioral Immunology Study Group, May 10, 1994]
 7. McEwen, B.S., Sakai, R.R. and Spencer, R.L. Adrenal steroid effects on the brain: versatile hormones with good and bad effects. In Hormonally Induced Changes in Mind and Brain, ed. by J. Schulkin, pp. 157-189, Academic Press, Inc., San Diego, 1993.
 8. McEwen, B.S., Chao, H.M., Gannon, M.N. and Spencer, R.L. Characterization of brain adrenal steroid receptors and their involvement in the stress response. In Stress: Neurobiology and Neuroendocrinology, ed. by M. Brown, G.F. Koob and C. Rivier, pp. 275-292, Marcel Dekker, Inc., New York, 1991.
 9. Spencer, R.L., Miller, A.H., Sakai, R. and McEwen, B.S. Neuroendocrinology of stress and aging. In Aging of the Brain: Cellular and Molecular Aspects of Brain Aging and Alzheimer's Disease, ed. by T. Nagatsu & O. Hayaishi, pp. 37-51, Japan Scientific Societies Press and Karger, Tokyo, 1990.
 10. Spencer, R.L., Miller, A.H., Young, E.A. and McEwen, B.S. Stress-induced changes in the brain: implications for aging. In Stress and the Aging Brain, ed. by G. Nappi et al, pp. 17-29, Raven Press, 1990.
 11. McEwen, B., Chao, H., Spencer, R., Brinton, R., MacIsaac, L., and Harrelson, A. Corticosteroid receptors in brain: relationship of receptors to effects in stress and aging. In the Hypothalamic-Pituitary-Adrenal Axis Revisited, ed. by W.F. Ganong, M.F., Dallman and J.L. Roberts, pp.394-401, New York Academy of Sciences, New York, 1987.

Service to Profession (1994-present)

Scientific Meeting/Session Organizer

- Invited Instructor for a Neurosciences Mini-Course, Psychoneuroimmunology Research Society, Galveston, Tx, April 28, 1999; 2 hr presentation and compiled a detailed hand-out packet for attendees on "Neurobiology of the stress response: with a focus on the hypothalamic-pituitary-adrenal axis"
- Organized and Chaired a Panel Discussion for an informal Special Interest Social at the Society for Neuroscience Annual Meeting, Nov 2000. "Psychoneuroimmunology: Are the P and the N and the I Getting Their Fair Share of Attention?"
- Organized and Chaired session: "Recent advances in corticosteroid receptor function in the brain: a comparative perspective", 2001 Workshop on Steroid Hormones and Brain function; Breckenridge, CO, April 2, 2001
- Co-organizer for Workshop on The Neuroendocrinology of Stress, June 1-3, 2005 in San Diego.
- Organized session on Stress, Hippocampus and Plasticity
- Co-organizer and Chair of Local Organizing Committee for Neurobiology of Stress Workshop 2010, June 15-18 in Boulder, CO.
- Program Committee and Session Chair for Neurobiology of Stress Workshop 2012, June 12-15, Philadelphia, PA.

Co-investigator and author of an NSF grant application (Funded Fall 2015) for conference support for Trainees to attend the 2016 Neurobiology of Stress Workshop, Newport Beach, CA.

Symposium Organizer/Chair and Speaker: “The role of extra-suprachiasmatic nucleus brain clocks in circadian regulation of brain function. Time matters!”, Annual Society for Neuroscience Meeting, Nov 2017, Washington D.C.

Journal Editorial Advisory Board Member

Stress: The International Journal on the Biology of Stress

Grant Reviewer

NIH Initial Review Group Regular member:

BNRS (Behavioral Neuroendocrinology, Neuroimmunology, Rhythms and Sleep) Regular Member October 2021-June 2025 (3 meetings per year commitment)

NIH Initial Review Group ad hoc member:

BDCN-4 (Brain Disorders and Clinical Neuroscience), Feb 1999

BDCN-5 (Brain Disorders and Clinical Neuroscience), June 1999

IFCN-2 (Integrative, Functional and Cognitive Neuroscience), June 2002

RPHB-B, Feb 2004

CNBT (Clinical neuroimmunology and brain tumors), June 2004

MESH (Biobehavioral Mechanisms of Stress, Emotion and Health), June 2006, summer 2007

F02A (Fellowships: Behavioral Neuroscience), Feb 2007

F02A (Fellowships: Behavioral Neuroscience), June 2007

F02A (Fellowships: Behavioral Neuroscience) July 2008

Social Psychology and Interpersonal Processes (SPIP), Oct 2008

F02A (Fellowships; Behavioral Neuroscience) March 2009

NNB (Neuroendocrinology, Neuroimmunology and Behavior) June 2009

NIH Special Emphasis grant review panel June 2009

F02A(Fellowships: Behavioral Neuroscience) July 2011

MNG (Molecular Neurogenetics) Sept 2014

NSF IOS grant review panel Sept 2015

ZAT1 JM(06) (NCCIH Training and Education panel) Nov 2019

NNRS (Neuroendocrinology, Neuroimmunology, Rhythms and Sleep) June 2020

ZAT1 JM(06) (NCCIH Training and Education panel) July 2020

NNRS (Neuroendocrinology, Neuroimmunology, Rhythms and Sleep) October 2020