CURRICULUM VITAE

Evgeny Nudler, Ph.D.

Investigator, Howard Hughes Medical Institute
Julie Wilson Anderson Professor
Biochemistry and Molecular Pharmacology
New York University School of Medicine
The Alexandria Center for Life Science
450 E, 29th Street, #303, New York, NY 10016
212-263-7431
evgeny.nudler@nyumc.org
http://nudlerlab.info/

Education

Year	Degree	Field	Institution
1989	B.A.	Biology	Division of Biology, Moscow State University, Moscow, USSR
1992	M.S.	Genetics	Department of Genetics, Moscow State University, Russia
1995	Ph.D.	Biochemistry	Institute of Molecular Genetics, Russian Academy of Sciences

Postdoctoral Training

Dates	Specialty	Mentor	Place of Training
1995-1997	Molecular Biology	Dr. A. Goldfarb	Public Health Research Institute, New York

Academic Appointments

1997-2003	Assistant Professor, New York University School of Medicine, New York, NY
2003-2005	Associate Professor (tenured), New York University School of Medicine
2005-2008	Professor, Dept. of Biochemistry, NYU School of Medicine
2008-	Julie Wilson Anderson Professor, NYU School of Medicine
2013-	Investigator, Howard Hughes Medical Institute
2024-	Founding Director, Center for Unified Structural Proteomics (CUSP)

Awards/Honors

1997	The Helen Hay Whitney Foundation research fellowship (declined)
1998	The Searle Scholar Award
2001	The Irma T. Hirschl Career Scientist Award
2002	The Edward Mallinckrodt, Jr. Foundation Research Award
2002	Fogarty International Research Collaboration Award
2004	Keynote Lecture: The RNA Biochemistry Symposia. Blaubeuren, Germany
2004	United States-Israel Bi-national Science Foundation Award
2006	The Dynasty Foundation Award
2006	NIH Director's Pioneer Award
2008	Crain's "40 Under 40" Alumni
2008	Julie Wilson Anderson Professorship (endowment chair)
2009	The Vilcek Foundation Finalist Prize
2010	Keynote Lecture: The Harden Conference on Transcription. Cambridge, UK
2010	The Blavatnik Award, New York Academy of Science
2011	The Robertson Foundation Award
2012	Biogerontology Research Foundation Award
2013	Investigator, Howard Hughes Medical Institute

2013 Honorary Professor, Moscow Institute of Physics and Technology
2013 Master Scientist, NYU Langone Medical Center
2014 Dean's Honor Lecture, NYU School of Medicine
2016 The Neil Welker Memorial Award
2016 Engelhardt Memorial Lecture, IMB, Russian Academy of Science
2016 Elected Foreign Member, Russian Academy of Sciences
2017 Elected Fellow, American Academy of Arts and Sciences
2018 Glenn Award for Research in Biological Mechanisms of Aging
2024 Blavatnik Family Foundation Award

Research Statement

Our most significant contributions include:

1. RNA polymerase (RNAP) *backtracking* and *ratcheting*: In 1997 we described back-and-forth sliding of RNAP along DNA and RNA (Nudler *Cell* 1997). Our group then showed that this universal phenomenon, which we called "backtracking", plays a key role in controlling gene expression (e.g. Proshkin *Science* 2010), genome instability (e.g. Dutta *Cell* 2011), and DNA repair (e.g. Epshtein *Nature* 2014). We were also first to demonstrate that RNAP is a *Brownian ratchet* machine (Bar-Nahum *Cell* 2005). Our findings explained in mechanistical detail how RNAP translocates and responds to regulatory signals and elongation factors. More recently, we have shown that RNAP II exhibits persistent backtracking over distances exceeding 20nt in human cells. This prolonged backtracking phenomenon frequently manifests near promoters and splicing junctions, exerting significant influence over the expression of a multitude of genes. Notably, histone genes emerge as particularly susceptible to persistent backtracking, underscoring the necessity for resolving such events promptly to ensure timely expression during cell division (Yang *Mol Cell* 2024).

2. Transcription termination and antitermination in bacteria: We have uncovered the mechanistical principles of the termination process in bacteria and formulated models explaining the molecular pathways leading to both intrinsic and Rho-dependent transcription termination (Gusarov *Mol Cell*, 1999; Epshtein *Mol Cell* 2007; Epshtein *Nature* 2010; Hao *Mol Cell* 2021). We also studied how these processes are regulated in the cell and formulated mechanistical models of factor-dependent (Gusarov *Cell* 2001) and factor-independent (Mironov *Cell* 2002; Sedlyarova *Mol Cell* 2017) modes of regulation. Our studies uncovered novel functions of Rho, such as silencing of horizontally transferred genes (Cardinal *Science* 2008) and preserving genomic integrity (Dutta *Cell* 2011). We also found that Rho functions as a global regulator of transcription, acting at 5'UTRs of numerous genes, and that sRNAs control Rho termination genome-wide, thus establishing sRNAs as transcription elongation factors (Sedlyarova *Cell* 2016).

3. Transcription-driven DNA repair: In 2014 we found that the key DNA repair helicase UvrD binds RNAP during elongation and forces it to slide backward along DNA (Epshtein *Nature* 2014). By inducing backtracking, UvrD exposes DNA lesions shielded by RNAP, allowing the repair enzymes to access the damage sites. We also showed that bacterial alarmone ppGpp contributes to UvrD-mediated TCR by rendering RNAP backtracking-prone (Kamarthapu *Science* 2016; Weaver *NSMB* 2023). Because backtracking is a shared feature of all cellular RNAPs, this mechanism enables RNAP to function as a global DNA damage scanner in bacteria and eukaryotes. More recently we showed that RNAP serves as a platform for the assembly of functional nucleotide excision repair (NER) complexes (Bharati *Nature* 2022). Contrary to the conventional dogma, we show that TCR accounts for most chromosomal NER events and is largely independent of Mfd – a DNA translocase thought to be necessary and sufficient for TCR (Bharati *Nature* 2022; Martinez *Nat Commun* 2022). We also discovered that ribonucleotide

excision repair (RER) is driven by transcription in *E. coli* (Hao *Cell* 2023).

4. *Riboswitches*: In 2002, we discovered the first ligand-sensing mRNAs that regulate biosynthetic genes in *B. subtilis* (Mironov *Cell* 2002). Simultaneously, Breaker and colleagues reported similar findings in *E. coli*. Since then, dozens of riboswitches have been described in bacteria and eukaryotes where they control numerous genes. We have shown that riboswitches can activate and suppress gene expression acting at the level of transcription termination, translation initiation, and modulating alternative splicing and mRNA stability (reviewed in Serganov and Nudler *Cell* 2013).

5. Eukaryotic RNA *thermosensor*: In 2006 we isolated a complex composed of the translation elongation factor eEF1A1 and a novel non-coding RNA (HSR1) that is required for activation of heat shock genes in mammals (Shamovsky *Nature* 2006). We have shown that HSR1 serves as a molecular thermosensor. We also showed that eEF1A1 orchestrates the whole process of heat shock response, from transcription activation to mRNA stabilization, transport, and translation (Vera *eLife* 2014). These findings provide a new paradigm of cellular adaptation to stress, with far-reaching clinical implications in neurodegeneration and cancer.

6. *Gas-defense system* in bacteria: We showed that endogenously produced gases NO and H_2S protect bacteria from oxidative stress, immune attack, and many antibiotics (Gusarov *Science* 2009; Shatalin *Science* 2011). These results support the emerging concept of antibiotic killing, which relies in part on oxidative damage, and establish NO- and H_2S-producing enzymes as promising targets for antimicrobial therapy. We also discovered the critical role of endogenous H_2S in bacterial tolerance, including the formation of persister cells and biofilms (Shatalin *Science* 2021). In a separate line of investigation, we showed that NO produced by bacteria inside their host diffuses into animal tissues where it activates a defined set of genes that protect the host from environmental stress and extend its lifespan (Gusarov *Cell* 2013).

Bibliography:

1. Gragerov A., Nudler E., Komissarova N., Gaitanaris G. A., Gottesman M. E., Nikiforov V. (1992) Cooperation of GroEL/GroES and DnaK/DnaJ heat shock proteins in preventing protein misfolding in Escherichia coli. **Proc Natl Acad Sci USA 89**: 10341-10344.
2. Kashlev M., Nudler E., Goldfarb A., White T., Kutter E. (1993) Bacteriophage T4 Alc protein: a transcription termination factor sensing local modification of DNA. **Cell 75**: 147-154.
3. Bezanilla M., Drake B., Nudler E., Kashlev M., Hansma P. K., Hansma H. G. (1994) Motion and enzymatic degradation of DNA in the atomic force microscope. **Biophysical J 67**: 2454-2459.
4. Nudler E., Goldfarb A., Kashlev M. (1994) Discontinuous mechanism of transcription elongation. **Science 265**: 793-796.
5. Nudler E., Kashlev M., Nikiforov V., Goldfarb A. (1995) Coupling between transcription termination and RNA polymerase inchworming. **Cell 81**: 351-357.
6. Nudler E., Avetissova E., Markovtsov V., Goldfarb A. (1996) Transcription processivity: protein DNA interactions holding together the elongation complex. **Science 273**: 211-217.
7. Kashlev M., Nudler E., Severinov K., Borukhov S., Komissarova N., Goldfarb A. (1996) His-tagged RNA polymerase and transcription in solid phase. **Methods Enzymol 274**: 326-334.
8. Nudler E., Mustaev A., Lukhtanov E. and Goldfarb A. (1997). The RNA/DNA hybrid maintains the register of transcription by preventing backtracking of RNA polymerase. **Cell**

89: 33-41.

9. Korzheva N, Mustaev A, Nudler E, Nikiforov V, and Goldfarb A. (1998) Mechanistic model of the elongation complex of Escherichia coli RNA polymerase. **Cold Spring Harb Symp Quant Biol 63**: 337-345
10. Nudler E., Gusarov I., Avetissova E., Kozlov M., and Goldfarb A. (1998). Topology of transcription elongation complex in Escherichia coli. **Science 281**: 424-428.
11. Nudler E. (1999). Transcription elongation: structural basis and mechanisms. **J Mol Biol 288**: 1-12.
12. Gusarov I. and Nudler E. (1999). The mechanism of intrinsic transcription termination. **Mol Cell 3**: 495-504.
13. Nedospasov A., Rafikov R., Beda N., and Nudler E. (2000). An autocatalytic mechanism of protein nitrosylation. **Proc Natl Acad Sci USA 97:** 13543-13548.
14. Bar-Nahum G. and Nudler E. (2001). Isolation and characterization of sigma 70-retaining transcription elongation complexes from Escherichia coli. **Cell 106**: 443-451
15. Gusarov I. and Nudler E. (2001) Control of intrinsic transcription termination by N and NusA: the basic mechanisms. **Cell 107**: 437-449.
16. Rafikova O., Rafikov R., and Nudler E. (2002) Catalysis of S-nitrosothiols formation by serum albumin: the mechanism and implication in vascular control. **Proc Natl Acad Sci USA 99**: 5913-5918.
17. Nudler E. and Gottesman M. (2002). Transcription termination and antitermination in Escherichia coli. **Genes Cells 7**: 755-768.
18. Kandel E. and Nudler E. (2002). Template switching by RNA polymerase II in vivo: evidence and implications from a retroviral system. **Mol Cell 10:** 1495-1502.
19. Mironov A.S., Gusarov I., Rafikov R., Lopez L.E., Kreneva R., Perumov D, and Nudler E. (2002). Sensing small molecules by nascent RNA: a mechanism to control transcription in bacteria. **Cell 111:** 747-756**.**
20. Nudler E., Gusarov I., and Bar-Nahum G. (2003) Methods of walking with the RNA polymerase. **Methods Enzymol 371**: 160-169.
21. Nudler E., Avetissova E., Korzheva, N. and Mustaev A. (2003) Characterization of protein-nucleic acid interactions that are required for transcription processivity. **Methods Enzymol 371:** 179-190.
22. Nudler E., and Gusarov I. (2003) Analysis of the intrinsic transcription termination mechanism and its control. **Methods Enzymol 371:** 369-382.
23. Epshtein V., Mironov A. S., and Nudler E. (2003) The riboswitch-mediated control of sulfur metabolism in bacteria. **Proc Natl Acad Sci USA 100:** 5052-5056.
24. Epshtein V., and Nudler E. (2003) Cooperation between RNA polymerase molecules in transcription elongation. **Science 300:** 801-805.
25. Borukhov S. and Nudler E. (2003) RNA polymerase holoenzyme: structure, function, and biological implications. **Curr Opin Microbiol 6:** 93-100.
26. Epshtein V., Toulmé F., Rahmouni, A. R., Borukhov, S. and Nudler E. (2003). Transcription through the roadblocks: the role of RNA polymerase cooperation. **EMBO J. 22**: 4719-4727.
27. Nudler E. and Mironov A. S. (2004) The riboswitch control of bacterial metabolism. **Trends**

Biochem Sci 29: 11-17.

28. Bergig O., Barash D., Nudler E., and Kedem K. (2004) STR2: a structure to string approach for locating G-box riboswitch shapes in pre-selected genes. **In Silico Biol 4**: 593-604.
29. Rafikova, O., Sokolova, E., Rafikov, R., and Nudler, E. (2004) Control of plasma NO bioactivity by perfluorocarbons: physiological mechanisms and clinical implications. **Circulation 110**: 3573-3580.
30. Bar-Nahum G., Epshtein V., Ruckenstein A. E., Rafikov R., Mustaev A., and Nudler E. (2005). A ratchet mechanism of transcription elongation and its control. **Cell 120**: 183-193.
31. Gusarov I. and Nudler E. (2005) NO-mediated cytoprotection: instant adaptation to oxidative stress in bacteria. **Proc Natl Acad Sci USA 102:** 13855-13860.
32. Tadigotla V.R., O'Maoileidigh D., Sengupta M.A., Epshtein V., Ebright R.H., Nudler E., and Ruckenstein A.E. (2006) Thermodynamics and kinetics based identification of transcriptional pauses. **Proc Natl Acad Sci USA 103:** 4439-4444.
33. Shamovsky I., Ivannikov M., Kandel E., Gershon D., and Nudler E. (2006) RNA-mediated response to heat shock in mammalian cells. **Nature 440**: 556-560.
34. Mirkin E.V., Roa D.C., Nudler E., and Mirkin S.M. (2006) Transcription regulatory elements are punctuation marks for DNA replication. **Proc Natl Acad Sci USA 103:** 7276-7281.
35. Nudler, E. (2006) Flipping riboswitches. **Cell 126**: 19-22.
36. Wade J.T., Roa D.C., Grainger D.C., Hurd D., Busby S.J.W., Struhl K., and Nudler E. (2006). Extensive functional overlap between sigma factors in Escherichia coli. **Nature Struct Mol Biol 13**: 806-814.
37. Shamovsky I., and Nudler E. (2006) Gene control by large non-coding RNAs. **Science (STKE) 355**, pe40.
38. Hausladen A., Rafikov R., Angelo M., Singel D.J., Nudler E., and Stamler J.S. (2007) Assessment of nitric oxide signals by triiodide chemiluminescence. **Proc Natl Acad Sci USA 104**: 2157-2162.
39. Epshtein V., Cardinale C., Ruckenstein A.E., Borukhov S., and Nudler E. (2007) Allosteric path to transcription termination. **Mol Cell 28**: 991-1001.
40. Bocobza S., Shapira M., Nudler E., and Aharoni A. (2007) Riboswitch-dependent gene regulation and its evolution in the plant kingdom. **Genes Dev 21**: 2874 - 2879.
41. Shatalin K., Gusarov I., Avetissova E., Shatalina Y., McQuade L., Lippard S.J. and Nudler E. (2007) Bacillus anthracis-derived nitric oxide is essential for pathogen virulence and survival in macrophages **Proc. Natl Acad Sci USA 105**:1009-1013.
42. Shamovky, I. and Nudler, E. (2008) Modular RNA heats up. **Mol Cell 29**: 415-417.
43. Borukhov, S. and Nudler, E. (2008) RNA polymerase: a vehicle of transcription. **Trends Microbiol 16**: 126-134.
44. Shamovsky, I. and Nudler, E. (2008). New insights into the mechanism of heat shock response activation. **Cell Mol Life Sci 65**: 851-1005.
45. Cardinale, C.J., Washburn, R., Tadiogotia, V.R., Brown, L.M., Zavadil, J., Gottesman, M.E. and Nudler, E. (2008). Termination factor Rho and its cofactors NusA and NusG silence foreign DNA in *E. coli.* **Science 320**: 935-938.

46. Gusarov, I., Starodubtseva, M., Wang, Z., Mcuate, L., Lippard, S.J., Stuehr, D. and Nudler, E. (2008). Bacterial NO-synthases operate without a dedicated redox partner. **J Biol Chem 283**: 13140 - 13147.

47. Svetlov V. and Nudler E. (2008). Jamming the ratchet of transcription. **Nature Struct Mol Biol 15**: 777-779.

48. Belogurov G.A., Vassylyeva M. N., Sevostyanova A., Xiang A.X., Lira R., Webber S.E., Klyuyev S., Nudler E., Artsimovitch I., and Vassylyev D.G. (2009). Transcription inactivation through local refolding of the RNA polymerase structure. **Nature 457**: 332-335.

49. Nudler E. (2009) Mechanics of Transcription Termination. In *RNA Polymerases as Molecular Motors* (The Royal Society of Chemistry; Paris, France).

50. Shen X., Banga S, Liu Y., Xu L., Gao P., Shamovsky I., Nudler E., and Luo Z. (2009). Targeting eEF1A by a *Legionella pneumophila* effector leads to inhibition of protein synthesis and induction of host stress response. **Cell Microbiol 11**: 911-926.

51. Shamovsky I. and Nudler E. (2009) Isolation and characterization of the heat shock RNA-1 (HSR1). **Methods Mol Biol 540:** 265-279.

52. Mironov A., Epshtein V., and Nudler E. (2009) Transcriptional approaches to riboswitch studies. **Methods Mol Biol 540**: 39-51.

53. Nudler E. (2009) RNA polymerase active center: the molecular engine of transcription. **Annu Rev Biochem 78**: 335-361.

54. Gusarov I., Shatalin K., Starodubtseva M., and Nudler E. (2009) Endogenous nitric oxide protects bacteria against a wide spectrum of antibiotics. **Science 325**: 1380-1384.

55. Svetlov V., and Nudler E. (2009) Macromolecular micromovements: how RNA polymerase translocates. **Curr Opin Struct Biol 19**: 701-717.

56. Epshtein V., Dutta D., Wade J., and Nudler E. (2010). An allosteric mechanism of Rho-depended transcription termination. **Nature 463**: 245-249.

57. Proshkin S., Rahmouni A.R., Mironov A., and Nudler E. (2010). Cooperation between translating ribosomes and RNA polymerase in transcription elongation. **Science 328**: 504-508.

58. O'Maoileidigh, D., Tadigotla, V., Nudler E. and Ruckenstein A.E. (2011) A unified model of transcription elongation: What have we learned from single-molecule experiments? **Biophysical J**. **100:** 1157-1166.

59. Svetlov V. and Nudler E. (2011). Clamping the clamp of RNA polymerase. **EMBO J**. **31:** 1190-1191.

60. Dutta D., Shatalin K., Epshtein V., Gottesman M. E., and Nudler E. (2011). Linking RNA polymerase backtracking to genome instability in E. coli. **Cell 146**: 533-543.

61. Artsimovitch I., Svetlov V., Nemetski S.M., Epshtein V., Cardozo T. and Nudler E. (2011). Tagetitoxin inhibits RNA polymerase through trapping of the trigger loop. **J Biol Chem 286**: 40395-40400.

62. Garbuz D.G., Astakhova L.N., Zatsepina O.G., Arkhipova I.R., Nudler E., and Evgen'ev M.B. (2011) Functional Organization of hsp70 Cluster in Camel (Camelus dromedarius) and Other Mammals. **PLoS One 6(11)**: e27205.

63. Shatalin K., Shatalina E., Mironov A., and Nudler E. (2011). H_2S: a universal defense against antibiotics in bacteria. **Science 334**: 986-990.

64. Svetlov V., Artsimovitch I., and Nudler E. (2012) On the mechanism of tagetitoxin inhibition of transcription. **Transcription 3**: 51-55.
65. Hollands K., Proshkin S., Sklyarova S., Epshtein V., Mironov A., Nudler E*., and Groisman E. A*. (2012). Riboswitch control of Rho-dependent transcription termination. **Proc Natl Acad Sci USA 109**: 5376-5381.
66. Gusarov I. and Nudler E. (2012). S-Nitrosylation signaling in Escherichia coli. **Science Signal 5** (228):pe26.
67. Nudler E. (2012). RNA polymerase backtracking in gene regulation and genome instability. **Cell 149**:1438-1445.
68. Svetlov V. and Nudler E. (2012). Unfolding the bridge between transcription and translation. **Cell 150**: 243-245.
69. Bobkova N, Guzhova I, Margulis B, Nesterova I, Medvedinskaya N, Samokhin A, Alexandrova I, Garbuz D, Nudler E, Evgen'ev M. (2012). Dynamics of endogenous Hsp70 synthesis in the brain of olfactory bulbectomized mice. **Cell Stress Chaperones 18**:109-18.
70. Nedialkov YA, Nudler E, and Burton ZF. (2012). RNA polymerase stalls in a post-translocated register and can hyper-translocate. **Transcription 3**: 260-269.
71. Nedialkov YA, Opron K, Assaf F, Artsimovitch I, Kireeva ML, Kashlev M, Cukier RI, Nudler E, and Burton ZF. (2012) The RNA polymerase bridge helix YFI motif in catalysis, fidelity and translocation. **Biochim Biophys Acta**. **1829**: 187-198.
72. Svetlov V, and Nudler E. (2013). Basic mechanism of transcription by RNA polymerase II. **Biochim Biophys Acta 1829**: 20-28.
73. van Sorge NM, Beasley FC, Gusarov I, Gonzalez DJ, von Köckritz-Blickwede M, Anik S, Borkowski A, Dorrestein PC, Nudler E, and Nizet V. (2013). Methicillin-resistant Staphylococcus aureus bacterial nitric oxide synthase affects antibiotic sensitivity and skin abscess development. **J Biol Chem**. **288**: 6417-6426.
74. Serganov A. and Nudler E. (2013) A decade of riboswitches. **Cell 152**: 17-24.
75. Svetlov V. and Nudler E. (2013) Looking for a promoter in 3D. **Nature Stuct Mol Biol 20,** 141-142.
76. Luhachack L., Nudler E. (2013) H2S as a bacterial defense against antibiotics; in *Hydrogen Sulfide and its Therapeutic Applications*, pp 173-180; Springer Vienna.
77. Gusarov I., Gautier L., Smolentseva O., Shamovsky I., Eremina S., Mironov A., and Nudler E. (2013). Bacterial nitric oxide extends the lifespan of C. elegans. **Cell 152**: 818-830.
78. Kozlov M, Nudler E, Nikiforov V, Mustaev A. (2013) Reactive rifampicin derivative able to damage transcription complex. **Bioconjug Chem 24**: 443-447.
79. McGary K, and Nudler E. (2013) RNA polymerase and the ribosome: the close relationship. **Curr Opin Microbiol 16**:112-117.
80. Helmrich A, Ballarino M, Nudler E, and Tora L. (2013) Transcription-replication encounters, consequences and genomic instability. **Nature Struct Mol Biol 20**: 412-428.
81. Bobkova N.V., Garbuz D.G., Nesterova I., Medvinskaya N., Samokhin A., Alexandrova I., Yashin V., Karpov V., Kukharsky M.S., Ninkina N.N., Smirnov A.A., Nudler E*., and Evgen'ev M. (2014). Therapeutic effect of exogenous Hsp70 in mouse models of Alzheimer`s disease. **J Alzheimers Dis. 38**: 425-435.

82. Epshtein V., Kamarthapu V., McGary K., Svetlov V., Ueberheide B., Proshkin S., Mironov A., and Nudler E. (2014) UvrD facilitates DNA repair by pulling RNA polymerase backwards**. Nature 505**, 372–377.

83. Proshkin S., Mironov A., and Nudler E. (2014) Riboswitches in regulation of Rho-dependent transcription termination. **Biochim Biophys Acta**. **1839**: 974-977.

84. Kulikova AA, Tsvetkov PO, Indeykina MI, Popov IA, Zhokhov SS, Golovin AV, Polshakov VI, Kozin SA, Nudler E, Makarov AA. (2014). Phosphorylation of Ser8 promotes zinc-induced dimerization of the amyloid-β metal-binding domain. **Mol Biosyst**. **10**: 2590-6.

85. Luhachack L, Nudler E. (2014). Bacterial gasotransmitters: an innate defense against antibiotics. **Curr Opin Microbiol**. **21C**: 13-17.

86. Vera M., Pani B., Griffiths L. A., Muchardt C., Abbott C. M., Singer R. H., and Nudler E. (2014). Translation elongation factor eEF1A1 couples transcription to translation during heat shock response. **eLife 3**: e03164.

87. Mejia YX, Nudler E, Bustamante C. (2015). Trigger loop folding determines transcription rate of Escherichia coli's RNA polymerase. **Proc Natl Acad Sci U S A 112**: 743-748.

88. Kamarthapu V, Nudler E. (2015). Rethinking transcription coupled DNA repair. **Curr Opin Microbiol**. **24C**: 15-20.

89. Sekine SI, Murayama Y, Svetlov V, Nudler E, Yokoyama S. (2015). The Ratcheted and Ratchetable Structural States of RNA Polymerase Underlie Multiple Transcriptional Functions. **Mol Cell 57**: 408-421.

90. Sekine S, Murayama Y, Svetlov V, Nudler E, Yokoyama S. (2015) Ratcheting of RNA polymerase toward structural principles of RNA polymerase operations. **Transcription 6**: 56-60.

91. Bobkova NV, Evgen'ev M, Garbuz DG, Kulikov AM, Morozov A, Velmeshev D, Medvinskaya N, Nesterova I, Pollock A, and Nudler E. (2015). Exogenous Hsp70 delays senescence and improves cognitive function in aging mice. **Proc Natl Acad Sci U S A**. **112**: 16006-16011.

92. Lazarev VF, Nikotina AD, Mikhaylova ER, Nudler E, Polonik SG, Guzhova IV, and Margulis BA. (2016). Hsp70 chaperone rescues C6 rat glioblastoma cells from oxidative stress by sequestration of aggregating GAPDH. **Biochem Biophys Res Commun**. **470**: 766-71.

93. Kamarthapu V., Epshtein V., Benjamin B., Proshkin S., Mironov A., Cashel M., and Nudler E. (2016). ppGpp couples transcription to DNA repair in E. coli. **Science 352**: 993-996.

94. Jee J., Rasouly A., Shamovsky I., Akivis Y., Steinman S., Mishra B., and Nudler E. (2016). Rates and mechanisms of bacterial mutagenesis from maximum-depth sequencing. **Nature 534**: 693-696.

95. Lechpammer M, Tran YP, Wintermark P, Martínez-Cerdeño V, Krishnan VV, Ahmed W, Berman RF, Jensen FE, Nudler E, and Zagzag D. (2016). Upregulation of cystathione β-synthase and p70S6K/S6 in neonatal hypoxic ischemic brain injury. **Brain Pathol. 27**: 449-458.

96. Sedlyarova N, Shamovsky I, Bharati BK, Epshtein V, Chen J, Gottesman S, Schroeder R, and Nudler E. (2016). sRNA-Mediated Control of Transcription Termination in E. coli. **Cell 167**: 111-121.

97. Chung MC, Alem F, Hamer SG, Narayanan A, Shatalin K, Bailey C, Nudler E, and Hakami RM. (2017). S-nitrosylation of peroxiredoxin 1 contributes to viability of lung epithelial cells

during Bacillus anthracis infection. **Biochim Biophys Acta**. **1861**(1 Pt A): 3019-3029.

98. Rasouly A., Pani B., and Nudler E. (2017). A magic spot in genome maintenance. **Trends Genet 33**: 58-67.

99. Mironov A, Seregina T, Nagornykh M, Luhachack L, Korolkova N, Lopes L.E., Kotova V, Zavilgelsky G, Shakulov R, Shatalin K, and Nudler E. (2017). A Mechanism of H_2S-mediated Protection Against Oxidative Stress in *E. coli.* **Proc Natl Acad Sci U S A 114**: 6022-6027.

100. Sedlyarova N, Rescheneder P, García A.M, Popitsch N, Rziha N, Bilusic I, Epshtein V, Zimmermann B, Lybecker M, Sedlyarov V, Schroeder R, and Nudler E. (2017). Natural RNA polymerase aptamers regulate transcription in *E. coli*. **Mol Cell 67**: 30-43.

101. Epshtein V., Kamarthapu V., and Nudler E. (2017). Strategies and methods of transcription-coupled repair studies in vitro and in vivo. **Methods Enzymol 591**: 287-306.

102. Pani B. and Nudler E. (2017). Mechanistic insights into transcription-coupled DNA repair. **DNA Repair (Amst) 56**: 42-50.

103. Gusarov I, Pani B, Gautier L, Smolentseva O, Eremina S, Shamovsky I, Katkova-Zhukotskaya O, Mironov A, and Nudler E. (2017). Glycogen controls Caenorhabditis elegans lifespan and resistance to oxidative stress. **Nature Commun**. **8:** 15868.

104. Smolentseva O, Gusarov I, Gautier L, Shamovsky I, DeFrancesco AS, Losick R, and Nudler E. (2017). Mechanism of biofilm-mediated stress resistance and lifespan extension in C. elegans. **Sci Rep 7**(1): 7137.

105. Demo G.,[#] Rasouly A[#], Vasilyev N., Svetlov V., Loveland A. B., Diaz-Avalos R., Grigorieff N., Nudler E*, and Korostelev A.A.* (2017) Structure of RNA polymerase bound to 30S ribosomal subunit. **eLife 6**: pii e28560.

106. Gusarov I. and Nudler E. (2018). Protein-S-nitrosylation: enzymatically controlled, but intrinsically unstable, post-translational modification. **Mol Cell 69**: 351-353.

107. Rasouli A. and Nudler E. (2018). Antibiotic killing through oxidized nucleotides. **Proc Natl Acad Sci U S A 115:** 1967-1969.

108. Ekimova IV, Plaksina DV, Pastukhov YF, Lapshina KV, Lazarev VF, Mikhaylova ER, Polonik SG, Pani B, Margulis BA, Guzhova IV, and Nudler E. (2018) New HSF1 inducer as a therapeutic agent in a rodent model of Parkinson's disease. **Exp Neurol 306:** 199-208. PMID: 29704482.

109. Svetlov V. and Nudler E. (2018). Reading of the non-template DNA by transcription elongation factors. **Mol Microbiol**. PMID: 29757477.

110. Gusarov I. and Nudler E. (2018). Glycogen at the crossroad of stress resistance, energy maintenance, and pathophysiology of aging**. BioEssays 40**(9): e1800033.

111. Abolhasani Khaje N., Mobley C.K., Misra S.K., Miller L., Li Z., Nudler E, and Sharp J.S. (2018). Variation in FPOP Measurements Is Primarily Caused by Poor Peptide Signal Intensity. **J Am Soc Mass Spectrom 29**: 1901-1907.

112. Bodnar N.O., Kim K.H., Ji Z., Wales T.E., Svetlov V., Nudler E., Engen J.R., Waltz T. and Rappaport T.A. (2018) Structure of the Cdc48 ATPase with its ubiquitin-binding cofactor Ufd1/Npl4. **Nature Struct Mol Biol 25**: 616-62.

113. Toliver-Kinsky T, Cui W, Törö G, Lee SJ, Shatalin K, Nudler E, and Szabo C. (2018) H_2S: a Bacterial Defense Mechanism Against the Host Immune Response. **Infect Immun**. **87**(1)

pii: e00272-18. PMID: 30323021.

114. Schneider JA, Craven TW, Kasper AC, Yun C, Haugbro M, Briggs EM, Svetlov V, Nudler E, Knaut H, Bonneau R, Garabedian MJ, Kirshenbaum K, and Logan SK. (2018). Design of Peptoid-peptide Macrocycles to Inhibit the β-catenin TCF Interaction in Prostate Cancer. **Nature Commun**. Oct 23;9(1):4396. PMID: 30352998

115. Svetlov V. and Nudler E. (2018) Analysis of the impact of molecular motions on the efficiency of XL-MS and the physical boundaries of distance restraints in hybrid structural biology. **bioRxiv** 379289; doi: https://doi.org/10.1101/379289

116. Svetlov V. and Nudler E. (2018) An automated workflow for the discovery and docking simulation of the protein-protein complexes using *in vivo* chemical cross-linking. **bioRxiv** 373829; doi: https://doi.org/10.1101/373829.

117. Valencia-Sánchez MI, De Ioannes P, Wang M, Vasilyev N, Chen R, Nudler E, Armache JP, and Armache KJ. (2019). Structural Basis of Dot1L Stimulation by Histone H2B Lysine 120 Ubiquitination. **Mol Cell 74**:1010-1019.

118. Rasouly A, and Nudler E. (2019). Reactive oxygen species as the long arm of bactericidal antibiotics. **Proc Natl Acad Sci U S A**. **116**: 9696-9698.

119. Hou L., Wang Y., Liu Y., Zhang N., Shamovsky I., Nudler E., Tian B., and Dynlacht B. D. (2019). Paf1 regulates RNA polymerase II progression by modulating the elongation rate. **Proc Natl Acad Sci U S A 116**: 14583-14592.

120. Luhachack L., Shamovsky I., and Nudler E. (2019) YcjW: a transcription factor that controls the emergency generator of H_2S in E. coli. **Nature Commun. 10** (1): 2868.

121. Chou H-T., Apelt L., Farrell D.P., White S.R., Woodsmith J., Svetlov V., Goldstein J.S., Nager A.R., Muller J., Dollfus H., Nudler E., Stelzl U., DiMaio F., Walz T., and Nachury M. V. (2019). The molecular architecture of the BBSome and its implications for facilitated transition zone crossing. **Structure 27**(9): 1384-1394.

122. Magán A, Amman F, El-Isa F, Hartl N., Shamovsky I, Nudler E., Schroeder R, and Sedlyarova N. (2019). iRAPs curb antisense transcription in *E. coli*. **Nucleic Acids Res 47**(20): 10894-10905.

123. Svetlov V. and Nudler E. (2019). Towards the unified principles of transcription termination. **EMBO J**. Dec 30:e104112. doi: 10.15252/embj.2019104112.

124. Wu X, Siggel M, Ovchinnikov S, Mi W, Svetlov V, Nudler E, Liao M, Hummer G, Rapoport TA. (2020). Structural basis of ER-associated protein degradation mediated by the Hrd1 ubiquitin ligase complex. **Science 368**(6489):eaaz2449. doi:10.1126/science.aaz2449

125. Mironov A, Seregina T, Shatalin K, Nagornykh M, Shakulov R, and Nudler E (2020). CydDC functions as a cytoplasmic cystine reductase to sensitize *Escherichia coli* to oxidative stress and aminoglycosides **Proc Natl Acad Sci USA 117**: 23565-23570.

126. Hao Z, Epshtein V, Kim KH, Proshkin S, Svetlov V, Kamarthapu V, Bharati B, Mironov A, Walz T, and Nudler E. (2021). Pre-termination Transcription Complex: Structure and Function. **Mol Cell 81**(2):281-292. Epub 2020 Dec 8. PMID: 33296676.

127. Grau D, Zhang Y, Lee CH, Valencia-Sánchez M, Zhang J, Wang M, Holder M, Svetlov V, Tan D, Nudler E, Reinberg D, Walz T, and Armache KJ. (2021). Structures of monomeric and dimeric PRC2:EZH1 reveal flexible modules involved in chromatin compaction. **Nature Commun. 12**(1):714. doi: 10.1038/s41467-020-20775-z. PMID: 33514705; PMCID:

PMC7846606.

128. Rabow Z, Morningstar T, Showalter M, Heil H, Thongphanh K, Fan S, Chan J, Martínez-Cerdeño V, Berman R, Zagzag D, Nudler E, Fiehn O, and Lechpammer M. (2021). Exposure to DMSO during infancy alters neurochemistry, social interactions, and brain morphology in long-evans rats. **Brain Behav**. Apr 10:e02146. doi: 10.1002/brb3.2146. PMID: 33838015.

129. Valencia-Sánchez MI, Abini-Agbomson S, Wang M, Lee R, Vasilyev N, Zhang J, De Ioannes P, La Scola B, Talbert P, Henikoff S, Nudler E, Erives A, and Armache KJ. (2021). The structure of a virus-encoded nucleosome. **Nature Struct Mol Biol**. **12**: 714. PMID: 33927388.

130. Wang B., Svetlov V., Wolf YI., Koonin EV., Nudler E., and Artsimovitch I. (2021). Allosteric activation of SARS-CoV-2 RdRp by remdesivir triphosphate and other phosphorylated nucleotides. **mBio**. Jun 29;12(3):e0142321. PMID: 34154407.

131. Shatalin K., Nuthanakanti A., Kaushik A., Shishov D., Peselis A., Shamovsky I., Pani B., Lechpammer M., Vasiliev N., Rebatchouk D., Shatalina E., Mironov A., Fedichev P., Serganov A., and Nudler E. (2021). Inhibitors of bacterial H_2S biogenesis targeting antibiotic resistance and tolerance. **Science** 372(6547):1169-1175. PMID: 34112687.

132. Gusarov I, Shamovsky I, Pani B, Gautier L, Eremina S, Katkova-Zhukotskaya O, Mironov A, Makarov AA, Nudler E. (2021). Dietary thiols accelerate aging of C. elegans. **Nature Commun 12**(1):4336. PMID: 34267196.

133. Lazarev VF, Tsolaki M, Mikhaylova ER, Benken KA, Shevtsov MA, Nikotina AD, Lechpammer M, Mitkevich VA, Makarov AA, Moskalev AA, Kozin SA, Margulis BA, Guzhova IV, Nudler E. (2021). Extracellular GAPDH Promotes Alzheimer Disease Progression by Enhancing Amyloid-β Aggregation and Cytotoxicity. **Aging Dis**. **12**: 1223-1237. PMID: 34341704

134. Briggs EM, Mita P, Sun X, Ha S, Vasilyev N, Leopold ZR, Nudler E, Boeke JD, Logan SK. (2021). Unbiased proteomic mapping of the LINE-1 promoter using CRISPR Cas9. **Mob DNA**. **12**(1):21. doi: 10.1186/s13100-021-00249-9. PMID: 34425899

135. Ruff SE, Vasilyev N, Nudler E, Logan SK, Garabedian MJ. (2021). PIM1 phosphorylation of the androgen receptor and 14-3-3 ζ regulates gene transcription in prostate cancer. **Commun Biol**. 4(1):1221. doi: 10.1038/s42003-021-02723-9.

136. Rasouly A, Shamovsky Y, Epshtein V, Tam K, Vasilyev N, Hao Z, Quarta G, Pani B, Li L, Vallin C, Shamovsky I, Krishnamurthy S, Shtilerman A, Vantine S, Torres VJ, Nudler E. (2021). Analyzing the fitness cost of antibiotic resistance to identify targets for combination antimicrobials. **Nature Microbiol**. Oct 25. doi: 10.1038/s41564-021-00973-1. Epub ahead of print. PMID: 34697460.

137. Hao Z, Svetlov V, Nudler E. (2021). Rho-dependent transcription termination: a revisionist view. **Transcription**. Oct 27:1-11. doi: 10.1080/21541264.2021.1991773. PMID: 34705601.

138. Muto T, Guillamot M, Yeung J, Fang J, Bennett J, Nadorp B, Lasry A, Redondo LZ, Choi K, Gong Y, Walker CS, Hueneman K, Bolanos LC, Barreyro L, Lee LH, Greis KD, Vasyliev N, Khodadadi-Jamayran A, Nudler E, Lujambio A, Lowe SW, Aifantis I, Starczynowski DT. (2022). TRAF6 functions as a tumor suppressor in myeloid malignancies by directly targeting MYC oncogenic activity. **Cell Stem Cell 29**: 298-314.e9. PMID: 35045331.

139. Martinez B., Bharati B.K., Epshtein V., and Nudler E. (2022). Pervasive transcription-coupled DNA repair in *E. coli.* **Nature Commun 13**(1):1702. doi: 10.1038/s41467-022-

28871-y. PMID: 35354807; PMCID: PMC8967931.

140. Bharati B.K., Gowder M., Zheng F., Alzoubi K., Svetlov V., Kamarthapu V., Weaver J.W., Epshtein V., Vasilyev N., Shen L., Zhang Y., and Nudler E. (2022). Crucial role and mechanism of transcription-coupled DNA repair in bacteria. **Nature 604**: 152-159. PMID: 35355008.

141. Escobar TM, Yu JR, Liu S, Lucero K, Vasilyev N, Nudler E, Reinberg D. (2022). Inheritance of repressed chromatin domains during S phase requires the histone chaperone NPM1. **Science Adv**. Apr 29;8(17):eabm3945. PMID: 35476441; PMCID: PMC9045712.

142. Nadon JF, Epshtein V, Cameron E, Samatov MR, Vasenko AS, Nudler E, and Lafontaine DA. (2022). Site-specific photolabile roadblocks for the study of transcription elongation in biologically complex systems. **Commun Biol**. **5**(1):457. PMID: 35552496.

143. Cai SW, Zinder JC, Svetlov V, Bush MW, Nudler E, Walz T, and de Lange T. (2022). Cryo-EM structure of the human CST-Polα/primase complex in a recruitment state. **Nature Struct Mol Biol**. May 16. Epub ahead of print. PMID: 35578024.

144. Patlán-Vázquez AG, Ayala-García VM, Vallin C, Cortés J, Vásquez-Morales SG, Robleto EA, Nudler E, Pedraza-Reyes M. (2022). Dynamics of Mismatch and Alternative Excision-Dependent Repair in Replicating *Bacillus subtilis* DNA Examined Under Conditions of Neutral Selection. **Front Microbiol**. doi: 10.3389/fmicb.2022.866089. PMID: 35847079.

145. Rasouly A, Nudler E. (2022). The very hungry bactericidal antibiotics. **Proc Natl Acad Sci U S A**. **119**(28):e2208035119. PMID: 35867771.

146. Mitkevich VA, Barykin EP, Eremina S, Pani B, Katkova-Zhukotskaya O, Polshakov VI, Adzhubei AA, Kozin SA, Mironov AS, Makarov AA, and Nudler E. (2023). Zn-dependent β-amyloid Aggregation and its Reversal by the Tetrapeptide HAEE. **Aging Dis**.**14**: 309-318. PMID: 37008059.

147. Weaver JW, Proshkin S, Duan W, Epshtein V, Gowder M, Bharati BK, Afanaseva E, Mironov A, Serganov A, and Nudler E. (2023). Control of transcription elongation and DNA repair by alarmone ppGpp. **Nature Struct Mol Biol**. Mar 30. doi: 10.1038/s41594-023-00948-2. Epub ahead of print. PMID: 36997761.

148. Rasouly A, and Nudler E. (2023). RNA polymerase and ppGpp deliver a one-two punch to antibiotics. **Mol Cell 83**:1204-1205. PMID: 37084711.

149. Hao, Z., Gowder, M., Proshkin, S., Bharati, B.K., Epshtein, V., Svetlov, V., Shamovsky, I., and Nudler, E. (2023). RNA Polymerase Drives Ribonucleotide Excision DNA Repair in *E. coli.* **Cell 186**: 2425-2437. PMID: 37196657.

150. Abini-Agbomson S, Gretarsson K, Shih RM, Hsieh L, Lou T, De Ioannes P, Vasilyev N, Lee R, Wang M, Simon MD, Armache JP, Nudler E, Narlikar G, Liu S, Lu C, Armache KJ. (2023). Catalytic and non-catalytic mechanisms of histone H4 lysine 20 methyltransferase SUV420H1. **Mol Cell 83**:2872-2883.e7. PMID: 37595555.

151. Thomas JF, Valencia-Sánchez MI, Tamburri S, Gloor SL, Rustichelli S, Godínez-López V, De Ioannes P, Lee R, Abini-Agbomson S, Gretarsson K, Burg JM, Hickman AR, Sun L, Gopinath S, Taylor HF, Sun ZW, Ezell RJ, Vaidya A, Meiners MJ, Cheek MA, Rice WJ, Svetlov V, Nudler E, Lu C, Keogh MC, Pasini D, Armache KJ. (2023). Structural basis of histone H2A lysine 119 deubiquitination by Polycomb repressive deubiquitinase BAP1/ASXL1. **Science Adv**. **9**(32):eadg9832. doi: 10.1126/sciadv.adg9832. PMID: 37556531.

152. Nudler E. (2023). Transcription-coupled global genomic repair in E. coli. **Trends Biochem Sci** doi: 10.1016/j.tibs.2023.07.007**.**

153. Yang K.B., Cameranesi M., Gowder M., Martinez C., Shamovsky Y., Epshtein V., Hao Z., Nguyen T., Nirenstein E., Shamovsky I., Rasouly A., and Nudler E. (2023). High resolution landscape of an antibiotic binding site. **Nature** 622: 180-187.

154. Li J, Krause GJ, Gui Q, Kaushik S, Rona G, Zhang Q, Liang FX, Dhabaria A, Anerillas C, Martindale JL, Vasilyev N, Askenazi M, Ueberheide B, Nudler E, Gorospe M, Cuervo AM, Pagano M. (2023). A noncanonical function of SKP1 regulates the switch between autophagy and unconventional secretion. **Science Adv**. doi: 10.1126/sciadv.adh1134. PMID: 37831778.

155. Pani B, and Nudler E. Bacterial histones unveiled. (2023) **Nature Microbiol**. **8**:1939-1941. PMID: 37857818.

156. Sokolova V, Miratsky J, Svetlov V, Brenowitz M, Vant J, Lewis T, Dryden K, Lee G, Sarkar S, Nudler E, Singharoy A, and Tan D. (2023) Structural mechanism of HP1α-dependent transcriptional repression and chromatin compaction. **Structure**, **32**(11):2094-2106. PMID: 39383876

157. Vasilyev N., Liu M., Epshtein V., Shamovsky I., and Nudler E. (2024) General Transcription Factor from E. coli with a Distinct Mechanism of Action. **Nature Struct Mol Biol 31**: 141-149. PMID: 38177674.

158. Yang KB, Rasouly A, Epshtein V, Martinez C, Nguyen T, Shamovsky I, and Nudler E. (2024). Persistence of backtracking by human RNA polymerase II. **Mol Cell 84**: 897-909 PMID: 38340716.

159. Seregina T, Shakulov R, Shatalin K, Sklyarova S, Petrushanko I, Mitkevich V, Makarov A, Mironov A, and Nudler E. (2025). Pentose Phosphate Pathway Protects *E. coli* from Antibiotic Lethality. **mBio 16**(8):e0065425. PMID: 40600718.

160. Rasouly A, Nudler E. (2025). In the shadow of antibiotics. **Proc Natl Acad Sci U S A**. **122**(7):e2426773122. PMID: 39928882

161. Prakash A, Kalita A, Bhardwaj K, Mishra RK, Ghose D, Kaur G, Verma N, Pani B, Nudler E, and Dutta D. (2024). Rho and riboswitch-dependent regulations of mntP gene expression evade manganese and membrane toxicities. **J Biol Chem**. **300**:107967. PMID: 39510182.

162. Varghese A, Gusarov I, Gamallo-Lana B, Dolgonos D, Mankan Y, Shamovsky I, Phan M, Jones R, Gomez-Jenkins M, White E, Wang R, Jones D, Papagiannakopoulos T, Pacold ME, Mar AC, Littman DR, and Nudler E. (2025) Unraveling cysteine deficiency-associated rapid weight loss. **Nature 643**: 776-784. PMID: 40399674.

163. Pani B and Nudler E. (2025). Transcription-coupled repair: protecting genome across generations. **Curr Opin Genet Dev**. Aug 5;94:102385. doi: 10.1016/j.gde.2025.102385. Epub ahead of print. PMID: 40768825.

164. Gavrilov AA, Shamovsky I, Zhegalova I, Proshkin S, Shamovsky Y, Evko G, Epshtein V, Rasouly A, Blavatnik A, Lahiri S, Rothenberg E, Razin SV, and Nudler E. (2025). Elementary 3D organization of active and silenced E. coli genome. **Nature**. doi: 10.1038/s41586-025-09396-y. Epub ahead of print. PMID: 40804527.