Publications (Updated December 16, 2025)

1. von Heijne, G., & Teder,A. (1973) Kinetics of the Decomposition of Aqueous Chlorine Dioxide Solutions. Acta Chem.Scand. 27, 4018-4019.

2. von Heijne, G., & Blomberg,C. (1976) Kinetic Aspects of the DNA Helix-Cruciform Transition. J.theor.Biol. 63, 347-353.

3. Blomberg,C., von Heijne, G., & Nilsson,L. (1977) Description of Some Processes in Protein Synthesis From a Statistical Mechanical Point of View. Ann.Isr.Phys.Soc. 2, 970-973.

4. von Heijne, G., Nilsson,L., & Blomberg,C. (1977) Translation and Messenger RNA Secondary Structure. J.theor.Biol. 68, 321-329.

5. von Heijne, G., & Blomberg,C. (1977) The ß-structure: Inter-strand Correlations. J.Mol.Biol. 117, 821-824.

6. von Heijne, G., & Blomberg,C. (1978) Some Global ß-sheet Characteristics. Biopolymers 17, 2033-2037.

7. von Heijne, G., Nilsson,L., & Blomberg,C. (1978) Models for mRNA Translation: Theory versus Experiment. Eur.J.Biochem. 92, 397-402.

8. von Heijne, G., Blomberg,C., & Baltscheffsky,H. (1978) Early Evolution of Cellular Electron Transport: Molecular Models for the Ferredoxin-Rubredoxin-Flavodoxin Region. Origins of Life 9, 27-37.

9. Baltscheffsky,H., von Heijne, G., & Blomberg,C. (1978) Protein Secondary Structure and the Molecular Evolution of Biological Electron Transport.inMatsubara,H. & Yamanaka,T. (eds.): Evolution of Protein Molecules. Japan Scientific Societies Press. pp. 141-147.

10. von Heijne, G., Leimar,O., & Blomberg,C. (1978) On the Emergence of New Function in Primitive Proteins. J.theor.Biol. 75, 167-180.

11. von Heijne, G., & Blomberg,C. (1979) The Concentration Dependence of the Error Frequencies and Some Related Quantities in Protein Synthesis. J.theor.Biol. 78, 113-120.

12. von Heijne, G., & Blomberg,C. (1979) Trans-Membrane Translocation of Proteins: The Direct Transfer Model. Eur.J.Biochem. 97, 175-181.

13. von Heijne, G. (1980) Trans-Membrane Translocation of Proteins: A Detailed Physico-Chemical Analysis. Eur.J.Biochem. 103, 431-438.

14. von Heijne, G. (1980) A Sequence Correlation Between Oppositely Charged Residues in Secreted Proteins. Biochem.Biophys.Res.Comm. 93, 82-86.

15. Blomberg,C., von Heijne, G., & Leimar,O. (1981) Competition, Coexistence, and Irreversibility in Models of Early Molecular Evolution.inWolman,Y. (ed.): Origin of Life. Reidel Publishing Co. pp.385-392.

16. von Heijne, G. (1981) On the Hydrophobic Nature of Signal Sequences. Eur.J.Biochem. 116, 419-422.

17. von Heijne, G. (1981) Membrane Proteins: The Amino Acid Composition of Membrane-Penetrating Segments. Eur.J.Biochem. 120, 275-278.

18. von Heijne, G. (1981) Models for Trans-Membrane Translocation of Proteins. Biochem.Soc.Symp. 46, 259-273.

19. von Heijne, G., & Savageau,M. (1982) RNA Splicing: Advantages of Parallel Processing. J.theor.Biol. 98, 563-574.

20. von Heijne, G. (1982) Signal Sequences are not Uniformly Hydrophobic. J.Mol.Biol. 159, 537-541.

21. von Heijne, G. (1982) A Theoretical Study of the Attenuation Control Mechanism. J.theor.Biol. 97, 227-238.

22. von Heijne, G. (1983) Patterns of Amino Acids near Signal-Sequence Cleavage Sites. Eur.J.Biochem. 133, 17-21.

23. Flinta,C., von Heijne, G., & Johansson,J. (1983) Helical Sidedness and the Distribution of Polar Residues in Trans-membrane Helices. J.Mol.Biol. 168, 193-196.

24. von Heijne, G. (1984) How Signal Sequences Maintain Cleavage Specificity. J.Mol.Biol. 173, 243-251.

25. von Heijne, G. (1984) Analysis of the Distribution of Charged Residues in the N-terminal Region of Signal Sequences: Implications for Protein Export in Prokaryotic and Eukaryotic Cells. EMBO J. 3, 2315-2318.

26. von Heijne, G. (1985) Structural and Thermodynamic Aspects of the Transfer of Proteins Into and Across Membranes.*In* Current Topics in Membranes and Transport 24, 151-179.

27. von Heijne, G. (1985) "Theoretical Experiments" on Amino Acid and Nucleotide Sequences: Three Case-Studies. Biomed.Biochim.Acta 6, 903-911.

28. [1]von Heijne, G. (1985) Signal Sequences: The Limits of Variation. J.Mol.Biol. 184, 99-105.

29. Liljenström,H., von Heijne, G., Blomberg,C., & Johansson,J. (1985) The tRNA Cycle and Its Relation to the Rate of Protein Synthesis. Eur.Biophys.J. 12, 115-119.

30. Persson,B., Flinta,C., von Heijne, G., & Jörnvall,H. (1985) Structures of N-terminally Acetylated Proteins. Eur.J.Biochem. 152, 523-527.

31. von Heijne, G. (1985) Ribosome - SRP - Signal Sequence Interactions: The Relay Helix Hypothesis. FEBS Lett. 190, 1-5.

32. Flinta,C., Persson,B., Jörnvall,H., & von Heijne, G. (1986) Sequence Determinants of Cytosolic N-terminal Protein Processing. Eur.J.Biochem. 154, 193-196.

33. von Heijne, G. (1986) Towards a Comparative Anatomy of N-terminal Topogenic Protein Sequences. J.Mol.Biol. 189, 239-242.

34. von Heijne, G. (1986) Why Mitochondria Need a Genome. FEBS Lett. 198, 1-4.

35. Liljenström,H., & von Heijne, G. (1987) Translation Rate Modification by Preferential Codon Usage: Intragenic Position Effects. J.theor.Biol. 124, 43-55.

36. von Heijne, G. (1986) Mitochondrial Targeting Sequences May Form Amphiphilic Helices. EMBO J. 5, 1335-1342.

37. von Heijne, G. (1986) A New Method for Predicting Signal Sequence Cleavage Sites. Nucl.Acids Res. 14, 4683-4690.

38. von Heijne, G. (1986) Net N-C Charge Imbalance may be Important for Signal Sequence Function in Bacteria. J.Mol.Biol. 192, 287-290.

[1] Among the 100 most cited articles in JMB during the journal's first 50 years.

39. von Heijne, G. (1986) The Distribution of Positively Charged Residues in Bacterial Inner Membrane Proteins Correlates With the Trans-Membrane Topology. EMBO J. 5, 3021-3027.

40. von Heijne, G., Blomberg,C., & Liljenström,H. (1987) Theoretical Modelling of Protein Synthesis. J.theor.Biol. 125, 1-14.

41. von Heijne, G. (1987) SIGPEP - A Sequence Database for Secretory Signal Peptides. Protein Sequence and Data Analysis 1, 41-42.

42. von Heijne, G., & Segrest,J. (1987) The Leader Peptides of Bacteriorhodopsin and Halorhodopsin are Potential Amphipathic Helices. FEBS Lett. 213, 238-240.

43. von Heijne, G., & Uhlén,M. (1987) Homology to Region X from Staphylococcal Protein A is *not* Unique to Cell Surface Proteins. J.theor.Biol. 127, 373-376.

44. von Heijne, G. (1987) Sequence Analysis in Molecular Biology: Treasure Trove or Trivial Pursuit? Academic Press, 188pp.

45. von Heijne, G., Wickner,W., & Dalbey,R. (1988) The Cytoplasmic Domain of *Escherichia coli* Leader Peptidase is a Translocation Poison Sequence. Proc.Natl.Acad.Sci.USA 85, 3363-3366.

46. von Heijne, G., & Gavel,Y. (1988) Topological Signals in Integral Membrane Proteins. Eur.J.Biochem. 174, 671-678.

47. von Heijne, G. (1988). Determinants of Protein Sorting Into and Across Membranes. In Op den Kamp,J.A.F. (Ed) *Membrane Biogenesis*. NATO ASI Series H-16, Springer Verlag. pp. 307-322.

48. von Heijne, G. (1988) Transcending the Impenetrable: How Proteins Come to Terms with Membranes. Biochim.Biophys.Acta. 947, 307-333.

49. Gavel, Y., Nilsson,L., & von Heijne, G. (1988) Mitochondrial Targeting Sequences: Why 'Non-Amphiphilic' Peptides May Still be Amphiphilic. FEBS Letters 235, 173-177.

50. von Heijne, G. (1988) Getting Sense out of Sequence Data. Nature 333, 605-608.

51. von Heijne, G. (1988) Role of the Signal Peptide in Protein Export. ISI Atlas of Science 1, 205-209.

52. von Heijne, G. (1988) Topogenic Signals in Membrane Protein Assembly. Proceedings of the 14th International Union of Biochemistry Congress.

53. von Heijne, G., Steppuhn,J., & Herrmann,R.G. (1989) Domain Structure of Mitochondrial and Chloroplast Targeting Peptides. Eur.J.Biochem. 180, 535-545.

54. von Heijne, G. (1989) The Structure of Signal Peptides from Bacterial Lipoproteins. Protein Engineering 2, 531-534.

55. von Heijne, G., & Abrahmsén,L. (1989) Species-Specific Variation in Signal Peptide Design: Implications for Protein Secretion in Foreign Hosts. FEBS Lett. 244, 439-446.

56. von Heijne, G. (1989) Control of Topology and Mode of Assembly of a Polytopic Membrane Protein by Positively Charged Residues. Nature 341, 456-458.

57. von Heijne, G. (1989) Structure of Targeting Peptides for Organellar Protein Import. Proceedings of the VIIIth International Congress on Photosynthesis. Kluwer Academic Publishers, Dordrecht.

58. Gavel,Y., & von Heijne, G. (1990) Sequence Differences Between Glycosylated and Non-glycosylated Asn-X-Thr/Ser Acceptor Sites. Protein Engineering 3, 433-442.

59. von Heijne, G. (1990) The Signal Peptide. J.Membr.Biol. 115, 195-201.

60. Franzén,L-G., Rochaix,J-D., & von Heijne, G. (1990) Chloroplast Transit Peptides from the Green Alga *Chlamydomonas reinhardtii* Share Features with Both Mitochondrial and Higher Plant Presequences. FEBS Lett. 260, 165-168.

61. Gavel,Y., & von Heijne, G. (1990) Cleavage-site Motifs in Mitochondrial Targeting Peptides. Protein Engineering 4, 33-37.

62. Gavel,Y., & von Heijne, G. (1990) A Conserved Cleavage-Site Motif in Chloroplast Transit Peptides. FEBS Lett. 261, 455-458.

63. von Heijne, G. (1990) Protein Targeting Signals. Current Opinion in Cell Biology 2, 604-608.

64. Nilsson,IM., & von Heijne, G. (1990) Fine-tuning the Topology of a Polytopic Membrane Protein: Role of Positively and Negatively Charged Amino Acids. Cell 62, 1135-1141.

65. Bilgin,N., Lee,J.I., Zhu,H., Dalbey,R., & von Heijne, G. (1990) Mapping of Catalytically Important Domains in *Escherichia coli* Leader Peptidase. EMBO J., 9, 2717-2722.

66. von Heijne, G., & Manoil,C. (1990) Membrane Proteins: From Sequence to Structure. Protein Engineering 4, 109-112.

67. Keegstra,K., & von Heijne, G. (1990) Transport of Proteins into Chloroplasts. *In* Herrmann,R. (ed.): Plant Gene Research: Cell Organelles. Springer Verlag. pp. 353-370.

68. von Heijne, G. (1990) Signals for Protein Import into Organelles. *In* Herrmann,R.G. & Larkins,B.O. (Eds.) "Plant Molecular Biology 2". NATO ASI series A, vol. 212, pp.583-593.

69. von Heijne, G. (1991) Cleavage-sites in Protein Targeting Signals. *In* Jörnvall,H., Höög,J-O., & Gustavsson,A-M. (Eds.) "Methods in Protein Sequence Analysis", Birkhäuser Verlag, Basel. pp. 231-238.

70. Nilsson, IM. & von Heijne, G. (1991) A *de novo* Designed Signal Peptide Cleavage Cassette Functions *in vivo*. J.Biol.Chem. 266, 3408-3410.

71. von Heijne, G. (1991) Proline-kinks in Transmembrane α-helices. J.Mol.Biol. 218, 499-503.

72. von Heijne, G. (1991) Computer Analysis of DNA and Protein Sequences. Eur.J.Biochem., 199, 253-256.

73. von Heijne, G. & Nishikawa,K. (1991) Chloroplast Transit Peptides: The Perfect Random Coil? FEBS Lett. 278, 1-3.

74. Wilson,I.B.H., Gavel,Y., & von Heijne, G. (1991) Amino Acid Distributions Around O-linked Glycosylation Sites. Biochem.J. 275, 529-534.

75. Gavel,Y., Steppuhn,J., Herrmann,R. & von Heijne, G. (1991) The "Positive-Inside Rule" Applies to Thylakoid Membrane Proteins. FEBS Lett. 282, 41-46.

76. von Heijne, G., Liljeström,P., Mikus,P., Andersson,H., & Ny,T. (1991) The Efficiency of the Uncleaved Secretion Signal in the Plasminogen Activator Inhibitor Type 2 Protein Can Be Enhanced by Point Mutations that Increase Its Hydrophobicity. J.Biol.Chem 266, 15240-15243.

77. Andersson,H., & von Heijne, G. (1991) A 30 Residues Long "Export Initiation Domain" Adjacent to the Signal Sequence is Critical for Protein Translocation Across the Inner Membrane of *Escherichia coli*. Proc.Natl.Acad.Sci USA 88, 9751-9754.

78. von Heijne, G., Hirai,T., Klösgen,R-B., Steppuhn,J., Keegstra,K., Herrmann,R. (1991) CHLPEP - A Database of Chloroplast Transit Peptides. Plant Molecular Biology Reporter 9, 104-126.

79. von Heijne, G. (1992) Sequence Determinants for Protein Import Into Chloroplasts and Thylakoid Membrane Protein Assembly. *In* Clarkson,D.T. and Cooke,D.T. (eds.) *Transport and Receptor Proteins of Plant Membranes*. Plenum Press, New York, pp. 195-199.

80. von Heijne, G. (1991) Protein Targeting - Basic Concepts. In *The Encyclopedia of Human Biology*, vol.6, pp. 237-243. Academic Press.

81. von Heijne, G. (1991) DNA, RNA, and Protein Sequences. Analysis by Computer. In *The Encyclopedia of Human Biology*, vol.3., pp.163-167. Academic Press.

82. Andersson,H., Bakker,E., & von Heijne, G. (1992) Different Positively Charged Amino Acids Have Similar Effects on the Topology of a Polytopic Transmembrane Protein in *E. coli*. J.Biol.Chem. 267, 1491-1495.

83. von Heijne, G. (1992) Cleavage-Site Motifs if Protein Targeting Sequences. *In Genetic Engineering, Principles and Methods*, vol.14. Plenum Press, New York. pp. 1-11.

84. Nilsson, IM., & von Heijne, G. (1992) A Signal Peptide With a Proline Next to the Cleavage Site Inhibits Leader Peptidase When Present in a *sec*-Independent Protein. FEBS Lett. 299, 243-246.

85. von Heijne, G. (1992) Sequence Determinants of Membrane Protein Topology. *In* Neupert,W & Lill, R. (Eds.) *Membrane Biogenesis and Protein Targeting*. Elsevier, Amsterdam. pp.75-84.

86. von Heijne, G. (1994) Decoding the Signals of Membrane Protein Sequences. *In* White, S. (Ed.) *Membrane Protein Structure: Experimental Approaches*. Oxford University Press, New York. pp. 27-40.

87. [2]von Heijne, G. (1992) Membrane Protein Structure Prediction: Hydrophobicity Analysis and the 'Positive Inside' Rule. J.Mol.Biol. 225, 487-494.

88. Gavel, Y., & von Heijne, G. (1992) The Distribution of Charged Amino Acids in Mitochondrial Inner Membrane Proteins Suggests Different Modes of Membrane Integration for Nuclearly and Mitochondrially Encoded Proteins. Eur.J.Biochem. 205, 1207-1215.

89. Johansson, M., Nilsson, IM., & von Heijne, G. (1993) Positively Charged Amino Acids Placed Next to a Signal Sequence Block Protein Translocation More Efficiently in *Escherichia coli* than in Mammalian Microsomes. Mol.Gen.Genet., 239, 251-256.

90. von Heijne, G. (1993) Design of Protein Targeting Signals and Membrane Protein Engineering. *In* Wrede, P. & Schneider, G. (Eds.) *Concepts of Protein Engineering and Design*, pp. 263-279. Walter de Gruyter, Berlin.

91. Wallin, E., Wettergren, C., Hedman, F., & von Heijne, G. (1993) Fast Needleman-Wunsch Scanning of Sequence Databanks on a Massively Parallel Computer. CABIOS 9, 117-118.

92. von Heijne, G. (1992) Assembly of *Escherichia Coli* Inner Membrane Proteins: *Sec*-Dependent and *Sec*-Independent Membrane Insertion. *In* Pullman, B. & Pullman, A. (Eds.): *Membrane Proteins: Structure and Function*. Kluwer Publishers. pp. 449-455.

93. Andersson, H., & von Heijne, G. (1993) *Sec*-dependent and *Sec*-independent Assembly of *E. coli* Inner Membrane Proteins: The Topological Rules Depend on Chain Length. EMBO J. 12, 683-691.

94. von Heijne, G. (1994) Signals for Protein Targeting Into and Across Membranes. *In* Maddy, A.H., & Harris, J.R. (Eds.) *Membrane Biogenesis*. Plenum Publishing Corporation, New York, pp. 1-19.

95. Dalbey, R.E., & von Heijne, G. (1992) Signal Peptidases in Prokaryotes and Eukaryotes: A New Protease Family. TIBS 17, 474-478.

[2] Among the 100 most cited articles in JMB during the journal's first 50 years.

96. von Heijne, G. (1993) Targeting Signals and Mechanisms of Protein Insertion Into Membranes. *In* Wirtz, K.A. & Gustafsson, J-Å (Eds.) *New Developments in Lipid-Protein Interactions and Receptor Function*. NATO ASI Series, vol. A246, pp. 175-182. Plenum Publishing Corporation.

97. Cramer, W.A., Engelman, D.M., von Heijne, G., and Rees, D. (1992) Forces Involved in the Assembly and Stabilization of Membrane Proteins. FASEB J. 6, 3397-3402.

98. Nilsson, IM., and von Heijne, G. (1993) Determination of the Distance Between the Oligosaccharyl Transferase Active Site and the ER Membrane. J.Biol.Chem. 268, 5798-5801.

99. Nilsson, IM., Gafvelin, G., and von Heijne, G. (1993) Different *Sec*-Requirements for Signal Peptide Cleavage and Protein Translocation in a Model *E. coli* Protein. FEBS Lett. 318, 7-10.

100. Whitley, P., Nilsson, L., and von Heijne, G. (1993) A 3D-Model for the Membrane Domain of *Escherichia coli* Leader Peptidase Based on Disulphide Mapping. Biochemistry 32, 8534-8539.

101. Sipos, L., and von Heijne, G. (1993) Predicting the Topology of Eukaryotic Membrane Proteins. Eur. J. Biochem. 213, 1333-1340.

102. Andersson, H., and von Heijne, G. (1993) Position-specific Asp-Lys Pairing Can Affect Signal Sequence Function and Membrane Protein Topology. J. Biol. Chem. 268, 21389-21393.

103. Whitley, P., and von Heijne, G. (1995) Membrane Protein Assembly. *In* Dalbey, R. (Ed.) *Membrane Organization and Biogenesis in Prokaryotic Organisms*. JAI Press, pp. 1-16.

104. von Heijne, G. (1994) Membrane Proteins: From Sequence to Structure. Annu. Rev. Biophys. Biomol. Struct. 23, 167-192.

105. Whitley, P., and von Heijne, G. (1993) The DsbA-DsbB System Affects the Formation of Disulfide Bonds in Periplasmic but not in Intramembraneous Protein Domains. FEBS Lett. 332, 49-51.

106. von Heijne, G. (1993) Assembly of Integral Membrane Proteins. *In* Op den Kamp, J.A.F. (Ed) *Biological Membranes: Structure, Biogenesis and Dynamics*. NATO ASI Series, vol. H82, pp.199-206. Springer Verlag, Berlin.

107. von Heijne, G. (1993) Membrane Protein Assembly: Can Protein-Lipid Interactions Explain the "Positive Inside" Rule? *In* Torriani, Silver & Yagil (Eds.) *Molecular Biology of Phosphate in Microorganisms*. ASM, pp. 247-250.

108. von Heijne, G. (1996) Computer-Assisted Identification of Protein Sorting Signals and Prediction of Membrane Protein Topology and Structure. *In* Villar, H.O. (Ed.) *Advances in Computational Biology*. JAI Press, pp. 1-14.

109. von Heijne, G. (1996) Targeting Signals for Protein Import Into Mitochondria and Other Subcellular Organelles. *In* Hartl, F-U. (Ed.) *Advances in Molecular and Cell Biology*, vol. 17., pp. 1-12. JAI Press, Inc.

110. Andersson, H., and von Heijne, G. (1994) Membrane Protein Topology: Effects of $\Delta\mu_{H^+}$ on the Translocation of Charged Residues Explain the "Positive Inside" Rule. EMBO J. 13, 2267-2272.

111. Gafvelin, G., and von Heijne, G. (1994) Topological "Frustration" in Multi-Spanning *E. coli* Inner Membrane Proteins. Cell 77, 401-412.

112. von Heijne, G. (1996) Prediction of Transmembrane Protein Topology. *In* Sternberg, M. (Ed.) *Prediction of Protein Structure - A Practical Approach*, pp. 101-109. Oxford University Press.

113. Cheng, S., Cao, G., Whitley, P., von Heijne, G., Kuhn, A., and Dalbey, R.E. (1994) Synergistic Insertion of Two Hydrophobic Regions Drives *sec*-Independent Membrane Protein Assembly. J. Biol. Chem. 269, 26898-26903.

114. Nilsson, IM., Whitley, P., von Heijne, G. (1994) The C-terminal Ends of Internal Signal and Signal-Anchor Sequences are Positioned Differently in the ER Translocase. J. Cell Biol. 126, 1127-1132.

115. Andersson, H., and von Heijne, G. (1994) Positively Charged Residues Influence the Degree of *Sec*-Dependence in Protein Translocation Across the *E. coli* Inner Membrane. FEBS Lett. 347, 169-172.

116. von Heijne, G. (1994) *Sec*-Independent Protein Insertion into the Inner *E. coli* Membrane: A Phenomenon in Search of an Explanation. FEBS Lett. 346, 69-72.

117. von Heijne, G. (1994) Protein Sorting Signals: Simple Peptides with Complex Functions. *In* Jollés & Jörnvall (Eds.) *Interface Between Chemistry and Biochemistry*. Birkhäuser Verlag, pp. 67-76.

118. Claros, M.G., and von Heijne, G. (1994) TopPred II: An Improved Software For Membrane Protein Structure Predictions. CABIOS 10, 685-686.

119. Whitley, P., Zander, T., Ehrmann, M., Haardt, M., Bremer, E., and von Heijne, G. (1994) *Sec*-Independent Translocation of a 100-Residues Long Periplasmic N-Terminal Tail in the *E. coli* Inner Membrane Protein ProW. EMBO J. 13, 4653-4661.

120. von Heijne, G. (1995) Membrane Protein Assembly: Rules of the Game. BioEssays 17, 25-30.

121. Whitley, P., Nilsson, IM., and von Heijne, G. (1994) *De novo* Design of Integral Membrane Proteins. Nature Struct.Biol. 1, 858-862.

122. Sääf, A., Andersson, H., Gafvelin, G., and von Heijne, G. (1995) SecA-Dependence of the Translocation of a Large Periplasmic Loop in the *E. coli* MalF Inner Membrane Protein is a Function of Sequence Context. Mol.Membr.Biol. 12, 209-215.

123. von Heijne, G. (1995) Membrane Protein Topogenesis in *Escherichia coli*. *In* Rothman, S.S. (Ed.) *Membrane Protein Transport*, vol. 3., pp. 201-214. JAI Press.

124. Hirsch, S., Muckel, E., Heemeyer, F., von Heijne, G., and Soll, J. (1994) A Receptor Component of the Chloroplast Protein Translocation Machinery. Science 266, 1989-1992.

125. von Heijne, G. (Editor) *Signal Peptidases*. RG Landes Press (1994).

126. Nielsen, H., Engelbrecht, J., von Heijne, G., and Brunak, S. (1996) Defining a Homology Threshold for a Functional Protein Sequence Pattern: The Signal Peptide Cleavage Site. PROTEINS: Struct. Funct. Genet. 24, 165-177.

127. Dalbey, R.D., Kuhn, A., and von Heijne, G. (1995). Directionality in protein translocation across membranes: The N-tail phenomenon. Trends Cell Biol. 5, 380-383.

128. Wallin, E., and von Heijne, G. (1995) Properties of N-terminal tails in G-protein coupled receptors - A statistical study. Protein Engineer. 8, 693-698.

129. Whitley, P., Sääf, A., Gafvelin, G., Johansson, M., Wallin, E., and von Heijne, G. (1995) Membrane protein anchors and polytopic determinants. Biochem.Soc.Trans., 23,965-967.

130. Nilsson, IM., Whitley, P., and von Heijne, G. (1996) Glycosylation mapping of the interaction between topogenic sequences and the ER translocase. *In* Op den Kamp, J.A.F. (Ed) *Biological Membranes: Structure, Biogenesis and Dynamics*. NATO ASI Series H, vol. 96, pp.9-14. Springer Verlag, Berlin.

131. van Klompenburg, W., von Heijne, G., and de Kruijff, B. (1995) A quantitative assay to determine the amount of signal peptidase I in *E.coli* and the orientation of membrane vesicles. Mol.Membr.Biol. 12, 349-353.

132. Whitley, P., Gafvelin, G., and von Heijne, G. (1995) *Sec*-independent translocation of the periplasmic N-terminal tail of an *E. coli* inner membrane protein: Position-specific effects on translocation of positively charged residues and construction of a protein with a C-terminal translocation signal. J.Biol.Chem. 270, 29831-29835. (PDF)

133. Whitley, P., Nilsson, I.M., and von Heijne, G. (1996) A Nascent Secretory Protein May Traverse the Ribosome/ER-translocase Complex as an Extended Chain. J.Biol.Chem. 271, 6241-6244. (PDF)

134. Whitley, P., Grahn, E., Kutay, U., Rapoport, T.A., and von Heijne, G. (1996) A 12 residues long poly-leucine tail is sufficient to anchor syntaptobrevin to the ER membrane. J.Biol.Chem. 271, 7583-7586. (PDF)

135. Mingarro, I., Whitley, P., Lemmon, M.A., and von Heijne, G. (1996) Ala-insertion scanning mutagenesis of the glycophorin A transmembrane helix. A rapid way to map helix-helix interactions in integral membrane proteins. Protein Sci. 5, 1339-1341.

136. Gafvelin, G., Sakaguchi, M., Andersson, H., and von Heijne, G. (1997) Topological rules for membrane protein assembly in eukaryotic cells. J.Biol.Chem. 272, 6119-6127. (PDF)

137. van Klompenburg, W., Nilsson, IM., von Heijne, G., and de Kruijff, B. (1997) Anionic phospholipids are determinants of membrane protein topology. EMBO J., 16, 4261-4266. (PDF)

138. Sääf, A., Wallin, E., and von Heijne, G. (1998) Stop-transfer function of pseudo-random amino acid segments during translocation across prokaryotic and eukaryotic membranes. Eur.J.Biochem., 251, 821-829. (PDF)

139. Whitley, P., and von Heijne, G. (1997) What can glycosylation mapping tell us about membrane proteins assembly and structure? *In* Hamasaki & Mihara (Eds.): *Membrane proteins: Structure, function and expression control*. pp. 117-126.

140. von Heijne, G. (1997) Evolution of protein sorting signals. *In* Schenk, H.E.A. (Ed.): *Intertaxonic combination and symbiotic adaptation*. Tübingen, pp.191-194.

141. [3]Nielsen, H., Engelbrecht, J., Brunak, S. and von Heijne, G. (1997) Identification of prokaryotic and eukaryotic signal peptides and prediction of their cleavage sites. Prot.Engineer., 10, 1-6. (PDF)

142. Johansson, M. and von Heijne, G. (1996) Membrane topology of Kch, a putative K^+ channel from *E. coli*. J.Biol.Chem., 271, 25912-25915. (PDF)

143. Braun, P., Persson, B., Kaback, H.R. and von Heijne, G. (1997) Alanine insertion scanning mutagenesis of lactose permease transmembrane helices: Identification of a structurally and functionally important segment in helix III. J.Biol.Chem., 272, 29566-29571. (PDF)

144. Kiefer, H., Krieger, J., Olszewski, J.D., von Heijne, G., Prestwich, G.D. and Breer, H. (1996) Expression of an olfactory receptor in *E. coli*: Purification, reconstitution, and ligand binding. Biochemistry, 35, 16077-16084. (PDF)

145. Glick, B.S. and von Heijne, G. (1996) *Saccharomyces cerevisiae* mitochondria lack a bacterial-type Sec machinery. Protein Sci., 5, 2651-2652.

146. von Heijne, G. (1997) Principles of membrane protein assembly and structure. Progr.Biophys.Mol.Biol., 66, 113-139. (PDF)

147. Andersson, H., Nilsson, IM. and von Heijne, G. (1996) Calnexin can interact with N-linked glycans located close to the endoplasmic reticulum membrane. FEBS Lett., 397, 321-324.

148. de Gier, J-W.L., Mansournia, P., Valent, Q.A., Phillips, G.J., Luirink, J. and von Heijne, G. (1996) Assembly of a cytoplasmic membrane proteins in *Escherichia coli* is dependent on the signal recognition particle. FEBS Lett., 399, 307-309.

149. Wallin, E., Tsukihara, T., Yoshikawa, S., von Heijne, G. and Elofsson, A. (1997) Architecture of helix bundle membrane proteins: An analysis of cytochrome *c* oxidase from bovine mitochondria. Protein Sci., 6, 808-815.

[3] 6th most cited paper in Biology & Biochemistry 1997-2007 (Essential Science Indicators). Included among the 10 Most Important Papers in Prot. Eng. and Design 1986-2016.

150. von Heijne, G. (1997) Getting greasy: How transmembrane polypeptide segments integrate into the lipid bilayer. Mol.Microbiol., 24, 249-253.

151. Nielsen, H., Engelbrecht, J., Brunak, S. and von Heijne, G. (1997) A neural network method for identification of prokaryotic and eukaryotic signal peptides and prediction of their cleavage sites. Int. J. Neural Systems 8, 581-599. (PDF)

152. Mothes, W., Heinrich, S., Graf, R., Nilsson, IM., von Heijne, G., Brunner, J. and Rapoport, T.A. (1997) Molecular mechanism of membrane protein integration into the endoplasmic reticulum. Cell, 89, 523-533. (PDF)

153. Nilsson, IM., Sääf, A., Whitley, P., Gafvelin, G., Waller, C., and von Heijne, G. (1998) Proline-induced disruption of a transmembrane α-helix in its natural environment. J.Mol.Biol., 284, 1165-1175. (PDF)

154. Claros, M., Brunak, S., and von Heijne G. (1997) Prediction of N-terminal sorting signals. Curr. Opinion Struct. Biol. 7, 394-398.

155. Cserzö, M., Wallin, E., Simon, I., von Heijne, G., and Elofsson, A. (1997) Prediction of transmembrane α-helices in prokaryotic membrane proteins: The Dense Alignment Surface method. Protein Engineer. 10, 673-676.

156. de Gier, J-W., Valent, Q.A., von Heijne, G., and Luirink, J. (1997) The *E. coli* SRP: preferences of a targeting factor. FEBS Lett. 408, 1-4.

157. Valent, Q.A., de Gier, J-W., von Heijne, G., Kendall, D.A., ten Hagen-Jongman, C.M., Oudega, B., and Luirink, J. (1997) Nascent membrane and presecretory proteins associate with signal recognition particle and trigger factor. Mol. Microbiol. 25, 53-64.

158. Mingarro, I., de Gier, J-W., von Heijne, G., Braun, P., and Whitley, P. (1998) Membrane Protein Assembly. *In* Chapman, D. and Haris, P.I. (Eds.): *Biomembrane Structures*. IOS Press, Amsterdam, pp. 228-244.

159. Mingarro, I., Elofsson, A., and von Heijne, G. (1997) Helix-helix packing in a membrane-like environment. J. Mol. Biol., 272, 633-641. (PDF)

160. Schneider, G., Sjöling, S., Wallin, E., Wrede, P., Glaser, E., and von Heijne, G. (1998) Feature-extraction from endopeptidase cleavage sites in mitochondrial targeting peptides. PROTEINS: Struct. Funct. Genet., 30, 49-60. (PDF)

161. Mingarro, I., von Heijne, G., and Whitley, P. (1997) Membrane protein engineering. TIBTECH 15, 432-437.

162. van Klompenburg, W., Ridder, A.N.J.A., van Raalte, A.L.J., Killian, A.J., von Heijne, G., and de Kruijff, B. (1997) *In vitro* membrane integration of leader peptidase depends on the Sec machinery and anionic phospholipids and can occur post-translationally. FEBS Lett. 413, 109-114.

163. Wallin, E., and von Heijne, G. (1998) Genome-wide analysis of integral membrane proteins from eubacterial, archaean, and eukaryotic organisms. Protein Sci. 7, 1029-1038. (HTML)

164. Valent, Q.A., Scotti, P.A., High, S., de Gier, J.W.L., von Heijne, G., Lentzen, G., Wintermeyer, Oudega, B., and Luirink, J. (1998) The *E. coli* SRP and Sec targeting pathways converge at the translocon. EMBO J. 17, 2504-2512. (PDF)

165. Sonnhammer, E.L.L., von Heijne, G., and Krogh, A. (1998) A hidden Markov model for predicting transmembrane helices in protein sequences. Intell. Syst. Mol.Biol. 6, 175-182. (PDF)

166. Seshadri, K., Wallin, E., Garemyr, R., von Heijne, G., and Elofsson, A. (1998) Architecture of ß-barrel membrane proteins: Structural analysis of trimeric porins. Protein Sci. 7, 2026-2032. (HTML)

167. van Klompenburg, W., Paetzel, M., de Jong, J.M., Dalbey, R.E., Demel, R.A., von Heijne, G., and de Kruijff, B. (1998) Phosphatidylethanolamine mediates insertion of the catalytic domain of leader peptidase in membranes. FEBS Lett. 431, 75-79. (PDF)

168. Ota, K., Sakaguchi, M., von Heijne, G., Hamasaki, N., and Mihara, K. (1998) Forced transmembrane orientation of hydrophilic polypeptide segments in multispanning membrane proteins. Molecular Cell 2, 495-503. (PDF)

169. de Gier, J.W., Scotti, P.A., Sääf, A., Valent, Q.A., Kuhn, A., Luirink, J., and von Heijne, G. (1998) Differential use of the SRP-translocase targeting pathway for inner membrane protein assembly in *Escherichia coli*. Proc.Natl.Acad.Sci. USA, 95, 14646-14651. (PDF)

170. Monné, M., Nilsson, IM., Johansson, M., Elmhed, N., and von Heijne, G. (1998) Positively and negatively charged residues have different effects on the

position in the membrane of a model transmembrane helix. J.Mol.Biol., 284, 1177-1183. (PDF)

171. Nilsson, IM., and von Heijne, G. (1998) Breaking the camel's back: Proline-induced turns in a model transmembrane helix. J.Mol.Biol., 284, 1185-1189. (PDF)

172. Sääf, A., Monné, M., de Gier, JW., and von Heijne, G. (1998) Membrane topology of the 60 kDa Oxa1p homologue from *Escherichia coli*. J.Biol.Chem. 273, 30415-30418. (PDF)

173. von Heijne, G. (1998) News & Views: The life and death of a signal peptide. Nature 396, 111-112. (PDF)

174. van Geest, M., Nilsson, IM., von Heijne, G., and Lolkema, J.S. (1999) Insertion of a bacterial secondary transport protein into the ER membrane. J.Biol.Chem. 274, 2816-2823. (PDF)

175. Nielsen, H., Brunak, S., and von Heijne, G. (1999) Machine learning approaches to the prediction of signal peptides and other protein sorting signals. Prot.Engineer. 12, 3-9. (PDF)

176. [4]Emanuelsson, O., Nielsen, H., and von Heijne, G. (1999) ChloroP, a neural network-based method for predicting chloroplast transit peptides and their cleavage sites. Protein Sci. 8, 978-984. (PDF)

177. Monné, M., Hermansson, M., and von Heijne, G. (1999) A turn propensity scale for transmembrane helices. J.Mol.Biol. 288, 141-145. (PDF)

178. Monné, M., Gafvelin, G., Nilsson, R., and von Heijne, G. (1999) N-tail translocation in a eukaryotic polytopic membrane protein: Synergy between neighboring transmembrane segments. Eur.J.Biochem. 263, 264-269. (PDF)

179. Cristóbal, S., de Gier, J-W., Nielsen, H., and von Heijne, G. (1999) Competition between Sec and TAT dependent protein translocation in *Escherichia coli*. EMBO J. 18, 2982-2990. (PDF)

180. Sääf, A., Johansson, M., Wallin, E., and von Heijne, G. (1999) Divergent evolution of membrane protein topology: The *Escherichia coli* RnfA and RnfE homologues. Proc.Natl.Acad.Sci. USA 96, 8540-8544. (PDF)

[4] Second most cited European paper in plant science during 1999-2005. LabTimes, issue 1 2007.

181. Cristóbal, S., Scotti, P., Luirink, J., von Heijne, G., and de Gier, J-W. (1999) The SRP-targeting pathway does not necessarily deliver proteins to the Sec-translocase in *Escherichia coli*. J. Biol. Chem. 274, 20068-20070. (PDF)

182. Braun, P., and von Heijne, G. (1999) The aromatic residues Trp and Phe have different effects on the positioning of a transmembrane helix in the microsomal membrane. Biochemistry 38, 9778-9782. (PDF)

183. Devoto, A., Piffanelli, P., Nilsson, IM., Wallin, E., Panstruga, R., von Heijne, G., and Schulze-Lefert, P. (1999) Topology, subcellular localization and sequence diversity of the Mlo family in plants. J. Biol. Chem. 274, 34993-35004. (PDF)

184. Monné, M., Nilsson, IM., Elofsson, A., and von Heijne, G. (1999) Turns in transmembrane helices: Determination of the minimal length of a "helical hairpin" and derivation of a fine-grained turn propensity scale. J. Mol. Biol. 293, 807-814. (PDF)

185. von Heijne, G. (1999) A day in the life of Dr K. or How I learned to stop worrying and love lysozyme. A tragedy in six acts. J.Mol.Biol. 293, 367-379. (PDF)

186. Armulik, A., Nilsson, IM., von Heijne, G., and Johansson, S. (1999) Determination of the border between transmembrane and cytoplasmic domains of human integrin subunits. J.Biol.Chem. 274, 37030-37034 (PDF)

187. Nilsson, IM., Witt, S., Kiefer, H., Mingarro, I., and von Heijne, G. (2000) Distant downstream sequence determinants can control N-tail translocation during protein insertion into the ER membrane. J.Biol.Chem. 275, 6207-6213. (PDF)

188. Scotti, P.A., Urbanus, M.L., Brunner, J., de Gier, J-W., von Heijne, G., van der Does, C., Driessen, A.J.M., Oudega, B., and Luirink, J. (2000) YidC, the *E. coli* homologue of mitochondrial Oxa1p, is a component of the Sec translocase. EMBO J. 19, 542-549. (PDF)

189. von Heijne, G. (2000) Recent advances in the understanding of membrane protein assembly and structure. Quart.Rev.Biophys. 32, 285-307.

190. Nilsson, IM, and von Heijne, G. (2000) Glycosylation efficiency of Asn-X-Thr sequons depends both on the distance from the C-terminus and on the presence of a downstream transmembrane segment. J.Biol.Chem. 275, 17338-17343. (PDF)

191. [5]Emanuelsson, O., Nielsen, H., Brunak, S., and von Heijne, G. (2000) Predicting subcellular localization of proteins based on their N-terminal amino acid sequence. J.Mol.Biol. 300, 1005-1016. (PDF)

192. Sääf, A., Hermansson, M., and von Heijne, G. (2000) Formation of cytoplasmic turns between two closely spaced transmembrane helices during membrane protein integration into the ER membrane. J.Mol.Biol. 301, 191-197. (PDF)

193. Killian, J.A., and von Heijne, G. (2000) How proteins adapt to a membrane-water interface. TIBS 25, 429-434. (PDF)

194. Hasler, U., Greasley, P.J., von Heijne, G., and Geering, K. (2000) Determinants of topogenesis and glycosylation of type II membrane proteins: Analysis of Na,K-ATPase β_1 and β_3 subunits by glycosylation mapping. J.Biol.Chem. 275, 29011-29022. (PDF)

195. Chin, C-N., and von Heijne, G. (2000) Charge pair interactions in a model transmembrane helix in the ER membrane. J. Mol. Biol. 303, 1-5. (PDF)

196. von Heijne, G. (2000) Membrane permeability: Transport of peptides and proteins through membranes (Editorial overview). Curr.Op.Cell Biol. 12, 399. (PDF)

197. [6]Krogh, A., Larsson, B., von Heijne, G., and Sonnhammer, E.L.L. (2001) Predicting transmembrane protein topology with a hidden Markov model: Application to compete genomes. J.Mol.Biol. 305, 567-580. (PDF)

198. Nilsson, J., Persson, B., and von Heijne, G. (2000) Consensus prediction of membrane protein topology. FEBS Lett., 486, 267-269. (PDF)

199. Mingarro, I., Nilsson, IM, Whitley, P., and von Heijne, G. (2000) Different conformations of nascent polypeptides during translocation across the ER membrane. BioMed Central Cell Biology 1, 3. (PDF)

200. Sääf, A., Baars, L., and von Heijne, G. (2001) The internal repeats in the Na^+/Ca^{2+} exchanger-related *E. coli* protein YrbG have opposite membrane topologies. J.Biol.Chem. 276, 18905-18907. (PDF)

[5] Among the 100 most cited articles in JMB during the journal's first 50 years.
[6] Among the 100 most cited articles in JMB during the journal's first 50 years.

201. Monné, M., and von Heijne, G. (2001) Effects of 'hydrophobic mismatch' on the location of transmembrane helices in the ER membrane. FEBS Lett. 496, 96-100. (PDF)

202. von Heijne, G. (2001) Signal peptides. *In* Encyclopedia of the Human Genome. MacMillan Press.

203. Emanuelsson, O., von Heijne, G., and Schneider, G (2001) Analysis and prediction of mitochondrial targeting peptides. Methods in Cell Biol. 65, 175-187.

204. Nilsson, IM., Ohvo-Rekilä, H., Slotte, J.P., Johnson, A.E., and von Heijne, G. (2001) Inhibition of protein translocation across the ER membrane by sterols. J.BiolChem. 276, 41748-41754.

205. Hermansson, M., Monné, M., and von Heijne, G. (2001) Formation of 'helical hairpins' during membrane protein assembly into the endoplasmic reticulum membrane. Role of the N- and C-terminal flanking regions. J.Mol.Biol. 313, 1171-1179.

206. Drew, D.E., von Heijne, G., Nordlund, P., and de Gier, J-W.,L (2001) Green Fluorescent Protein as an indicator to monitor membrane protein overexpression in *Escherichia coli*. FEBS Lett. 207, 220-224.

207. Peltier, J-B., Emanuelsson, O., Kalume, D.E., Ytterberg, J., Friso, G.,Rudella, A., Liberles, D.A., Söderberg, L., Roepstorff, P., von Heijne, G., and van Wijk, K.J. (2002) Central functions of the lumenal and peripheral thylakoid proteome of *Arabidopsis thaliana* determined by experimentation and genome-wide prediction. Plant Cell 14, 211-236.

208. Liberles, D.A., Thoren, A., von Heijne G., and Elofsson, A. (2002) The use of phylogenetic profiles for gene predictions. Curr.Genomics 3, 131-137.

209. Drew, D., Sjöstrand, D., Nilsson, J., Urbig, T., Chin, C., de Gier, J-W., and von Heijne, G. (2002) Rapid topology mapping of *E. coli* inner membrane proteins by prediction and PhoA/GFP fusion analysis. Proc.Natl.Acad.Sci.USA 99, 2690-2695.

210. von Heijne, G. (2003) Membrane protein assembly *in vivo*. Adv.Prot.Chem. 63, 1-18.

211. Emanuelsson, O., and von Heijne, G. (2001) Prediction of organellar targeting signals. Biochem.Biophys. Acta 1541, 114-119.

212. Hedman, M., de Loof, H., von Heijne, G., and Elofsson, A. (2002) Improved detection of homologous membrane proteins by inclusion of information from topology predictions. Prot. Sci. 11, 652.

213. Nilsson, IM., Johnson, A.E., and von Heijne, G. (2002) Cleavage of a tail-anchored protein by signal peptidase. FEBS Lett. 516. 106-108.

214. Chin, C., von Heijne, G., and de Gier, J-W. (2002) Membrane proteins: Shaping up. TIBS 27, 231-234.

215. Vilar, M., Saurí, A., Monné, M., Marcos, J.F., von Heijne, G., Pérez-Payá, E., and Mingarro, I. (2002) Insertion and topology of a plant viral movement protein in the endoplasmic reticulum membrane. J.Biol.Chem. 277, 23447-23452.

216. von Heijne, G. (2002) Bioinformatics of Membrane Proteins. In Mewes, Seidel & Weiss (Eds.) "Bioinformatics and Genome Analysis", Springer Verlag, pp. 17-27.

217. Nilsson, J., Persson, B., and von Heijne, G. (2002) Prediction of partial membrane protein topologies using a consensus approach. Prot.Sci. 11, 2974-2980.

218. Hessa, T., Monné, M., and von Heijne, G. (2003) Stop-transfer efficiency of marginally hydrophobic segments depends on the length of the C-terminal tail. EMBO Rep. 4, 178-183.

219. Kim, H., Melén, K., and von Heijne, G. (2003) Topology models for 37 *Saccharomyces cerevisiae* membrane proteins based on C-terminal reporter fusions and prediction. J.Biol.Chem. 278, 10208-10213.

220. Melén, K., Krogh, A., and von Heijne, G. (2003) Reliability measures for membrane protein topology prediction algorithms. J.Mol.Biol. 327, 735-744.

221. Lundin, M., Monné, M., Widell, A., von Heijne, G., and Persson, M.A.A. (2003) Topology of the membrane associated Hepatitis C virus NS4B protein. J.Virol. 77, 5428-5438.

222. Nilsson, IM., Kelleher, D.J., Miao, Y., Shao, Y., Kreibich, G., Gilmore, R., von Heijne, G., and Johnson, A.E. (2003) Photocrosslinking of nascent chains to the STT3 subunit of the oligosaccharyltransferase complex. J. Cell Biol. 161, 715-725.

223. Emanuelsson, O., Elofsson, A., von Heijne, G., and Cristobal, S. (2003) *In silico* prediction of the peroxisomal proteome in fungi, plants and animals. J.Mol.Biol. 330, 443-456.

224. Andersson, H., D'Antona, A.M., Kendall, D.A., von Heijne, G., and Chin, C-N. (2003). Membrane assembly of the cannabinoid receptor 1: Impact of a long N-terminal tail. Mol.Pharmacol. 64, 570-577.

225. Kim, H., von Heijne, G., Caputo, G.A., and Lennarz, W.J. (2003) Determination of membrane topology of Ost4p, and its subunit interactions in the oligosaccharyltransferase complex in *Saccharomyces cerevisiae*. Proc.Natl.Acad.Sci. USA 100, 7460-7464.

226. Nilsson, IM., Johnson, A., and von Heijne, G. (2003) How hydrophobic is alanine? J.Biol.Chem. 278, 29389-29393.

227. Juncker, A.S., Wilenbrock, H., von Heijne, G., Brunak, S., Nielsen, H., and Krogh, A. (2003) Prediction of lipiprotein signal peptides in Gram-negative bacteria. Prot.Sci. 12, 1652-1662.

228. Westerlund, I., von Heijne, G., and Emanuelsson, O. (2003) LumenP - a neural network predictor for protein localization in the thylakoid lumen. Prot.Sci. 12, 2360-2366.

229. Hermansson, M., and von Heijne, G. (2003) Inter-helical hydrogen bond formation during membrane protein integration into the ER membrane. J.Mol.Biol. 334, 803-809.

230. Rapp, M., Drew, D., Daley, D.O., Nilsson, J., Carvalho, T., Melén, K., de Gier, J.W., and von Heijne, G. (2004) Experimentally based topology models for *E. coli* inner membrane proteins. Prot.Sci. 13, 937-945.

231. Stefansson, A., Armulik, A., Nilsson, IM., von Heijne, G., and Johansson., S. (2004) Determination of N- and C-terminal borders of the transmembrane domain of integrin subunits. J.Biol.Chem. 279, 21200-21205.

232. [7]Dyrløv-Bendtsen, J., Nielsen, H., von Heijne, G., and Brunak, S. (2004) Improved prediction of signal peptides – SignalP 3.0. J.Mol.Biol. 340, 783-795.

233. Kerje, S., Sharma, P., Gunnarsson, U., Kim, H., Bagchi, S., Fredriksson, R., Schütz, K., Jensen, P., von Heijne, G., Okimoto, R., and Andersson, L., (2004) The *Dominant white, Dun* and *Smoky* color variants in chicken are associated with insertion/deletion polymorphisms in the *PMEL17* gene. Genetics 168, 1507-1518.

234. Monné, M., Hessa, T., Thissen, L., and von Heijne, G. (2005) Competition between neighboring topogenic signals during membrane protein insertion into the ER. FEBS J. 272, 28-36.

235. White, S.H., and von Heijne, G. (2004) The machinery of membrane protein assembly. Curr.Opinion Struct.Biol. 14, 397-404.

236. Granseth, G., von Heijne, G., and Elofsson, A. (2005) A Study of the membrane-water interface region of membrane proteins. J.Mol.Biol. 346, 377-385.

237. Dyrløv-Bendtsen, J., Juhl Jensen, L., Blom, N., von Heijne, G., and Brunak, S. (2004) Feature-based prediction of non-classical and leaderless protein secretion. Prot.Eng.Des.Sel. 17, 349-356.

238. [8]Hessa, T., Kim., H., Bihlmaier, K., Lundin, C., Boekel, J., Andersson, H., Nilsson, I.M., White, S.H., and von Heijne, G. (2005) Recognition of transmembrane helices by the endoplasmic reticulum translocon. Nature 433, 377-381.

239. Hessa, T., White, S.H., and von Heijne, G. (2005) Membrane insertion of a potassium channel voltage sensor. Science 307, 1427.

240. Ding, B., Kull, B., Liu, Z., Mottagui-Tabara, S., Thonberg, H., Gu, H.F., Brookes, A.J., Grundemar, L., Karlsson, C., Hamsten, A., Arner, P., Östensson, C.G., Efendic, S., Monné, M., von Heijne, G., Eriksson, P., and Wahlestedt, C. (2005) Human neuropeptide Y signal peptide gain-of-function polymorphism associated with increased body mass index: possible mode of function. Regul.Pept.127, 45-53.

[7] Red Hot Science Papers, Science watch Nov/Dec 2005. Among the 100 most cited articles in JMB during the journal's first 50 years.
[8] "Hot Paper", The Scientist May 2007

241. Tie, J-L., Nicchitta, C., von Heijne, G., and Stafford, D.W. (2005) Membrane topology mapping of vitamin K epoxide reductase by *in vitro* translation/cotranslocation. J.Biol.Chem. 280, 16410-16416.

242. White, S.H., and von Heijne, G. (2005) Transmembrane helices before, during, and after insertion. Curr.Op.Struct.Biol. 15, 378-386.

243. Daley, D.O., Rapp, M., Granseth, E., Melén, K., Drew, D., and von Heijne, G. (2005) Global topology analysis of the *Escherichia coli* inner membrane proteome. Science 308, 1321-1323.

244. Nilsson, J., Persson, B., and von Heijne, G. (2005) Comparative analysis of amino acid distributions in integral membrane proteins from 107 genomes. PROTEINS: Structure, Function, and Bioinformatics 60, 606-616.

245. Kim, H., von Heijne, G., and Nilsson, I.M. (2005) Membrane topology of the STT3 subunit of the oligosaccharyl transferase complex. J.Biol.Chem. 280, 20261-20267.

246. Bernsel, A., and von Heijne, G. (2005) Improved membrane protein toplogy prediction by domain assignments. Prot.Sci. 14, 1723-1728.

247. Médigue, C., Krin, E., Pascal, G., Barbe, V., Bernsel, A., Bertin, P.N., Cheung, F., Cruveiller, S., D'Amico, S., Duilio, A., Fang, G., Feller, G., Ho, C., Mangenot, S., Marino, G., Nilsson, J., Parilli, E., Rocha, E.P.C., Rouy, Z., Sekowska, A., Tutino, M.L., Vallenet, D., von Heijne, G., and Danchin, A. (2005) Coping with cold: the genome of the versatile marine Antarctica bacterium *Pseudoalteromonas haloplanktis* TAC125. Genome Res. 15, 1325-1335.

248. Pasche, B., Knobloch, T.J., Bian, Y., Liu, J., Phukan, S., Rosman, D., Kaklamani, V., Baddi, L., Frankel, W., Prior, T.W., Schuller, D.E., Agrawal, A., Lang, J., Dolan, M.E., Vokes, E.E., Lane, W.S., Huang, C.C., Caldes, T., Di Cristofano, A., Hampel, H., Nilsson, I.M., von Heijne, G., Fodde, R., Murty, V.V.V.S., de la Chapelle, A., Weghorst, C.M. (2005) Somatic Acquisition and Signaling of *TGFBR1**6A in Cancer. J.Am.Med.Assoc. 294, 1634-1646.

249. Granseth, E., Daley, D.O., Rapp, M., Melén, K., and von Heijne, G. (2005) Experimentally constrained topology models for 51,208 bacterial inner membrane proteins. J.Mol.Biol. 352, 489–494.

250. White, S., and von Heijne, G. (2005) Do protein-lipid interactions determine the recognition of transmembrane helices at the ER translocon? Biochem.Soc.Trans. 33, 1012-1015.

251. von Heijne, G. (2005) Perspective: Translocation of anthrax toxin - Lord of the Rings. Science 309, 709.

252. Laudon, H., Hansson, E.M., Melén, K., Bergman, A., Farmery, M.R., Winblad, B., Lendahl, U., von Heijne, G. and Näslund, J. (2005) A nine transmembrane domain topology for presenilin 1. J.Biol.Chem. 280, 35352-35360.

253. Stenberg, F., Chovanec, P., Maslen, S.L., Robinson, C.V., Ilag, L., von Heijne, G., and Daley, D.O. (2005) Protein complexes of the *Escherichia coli* cell envelope. J.Biol.Chem. 280, 34409-34419.

254. White, S.H., Hessa, T., and von Heijne, G. (2005) Lipid bilayers, translocons and the shaping of polypeptide structure. *In* Tamm, K. (ed.) "Protein-lipid interactions: From membrane domains to cellular networks", Wiley-VCH.

255. Freites, J.A., Tobias, D.J., von Heijne, G., and White, S.H. (2005) Interface connections of a transmembrane voltage sensor. Proc.Natl.Acad.Sci. USA 102, 15059-15064.

256. Luirink, J., von Heijne, G., Houben, E., and de Gier, J-W. (2005) Biogenesis of inner membrane proteins in *Escherichia coli*. Annu.Rev.Microbiol. 59, 329-355.

257. von Heijne, G. (2005) News and views: Helices on the move. Nature Struct.Molec.Biol. 12, 834-835.

258. Villarejo, A., Burén, S., Larsson, S., Déjardin, A., Monné, M., Rudhe, C., Karlsson, J., Jansson, S., Lerouge, P., Rolland, N., von Heijne, G., Grebe, M., Bako, L., and Samuelsson, G. (2005) A route through the endoplasmic reticulum for proteins targeted to the higher plant chloroplast. Nature Cell Biol. 7, 1224-1231.

259. Karamyshev, A.L., Kelleher, D.J., Gilmore, R., Johnson, A.E., von Heijne, G., and Nilsson, I-M. (2005) Mapping the interaction of the STT3 subunit of the oligosaccharyl transferase complex with nascent polypeptide chains. J.Biol.Chem. 280, 40489–40493.

260. Björklund, A., Thorén, A., von Heijne, G., and Elofsson, A. (2006) The use of phylogenetic profiles for gene predictions revisited. Curr Genom 7, 79-86.

261. Marani, P., Wagner, S., Baars, L., Genevaux, P., de Gier, J-W., Nilsson, I.M., Casadio, R., and von Heijne, G. (2006) New *Escherichia coli* outer membrane proteins identified through prediction and experimental verification. Prot.Sci. 15, 884-889.

262. Rapp, M., Seppälä, S., Granseth, E., and von Heijne, G. (2006) Identification and evolution of dual topology membrane proteins. Nature Struct.Mol.Biol. 13, 112-116.

263. Lundin, C., Nordström, R., Wagner, K., Windpassinger, C., Andersson, H., von Heijne, G., and Nilsson, IM. (2006) Membrane topology of the human seipin protein. FEBS Lett. 280, 2281-2284.

264. Amico, M., Finelli, M., Rossi, I., Zauli, A., Elofsson, A., Viklund, H., von Heijne, G., Jones, D., Krogh, A., Fariselli, P., Martelli, P.L., and Casadio, R. (2006) PONGO: A web server for multiple predictions of all-alpha transmembrane proteins. Nucl.Acid.Res. 34, W169-W172.

265. Kim, H., Melén, K., Österberg, M., and von Heijne, G. (2006) A global topology map of the *Saccharomyces cerevisiae* membrane proteome. Proc.Natl.Acad.Sci. USA 103, 11142-11147.

266. Österberg, M., Kim, H., Warringer, J., Melén, K., Blomberg, A., and von Heijne, G. (2006) Phenotypic effects of membrane protein overexpression in *Saccharomyces cerevisiae*. Proc.Natl.Acad.Sci. USA 103, 11148-11153.

267. Meindl-Beinker, N.M., Lundin, C., Nilsson, IM., White, S.H., and von Heijne, G. (2006) Asn- and Asp-mediated interactions between transmembrane helices during translocon-mediated membrane protein assembly. EMBO Rep. 7, 1111-1116.

268. von Heijne, G. (2006) Membrane-protein topology. Nature Rev.Mol.Cell.Biol. 7, 909-918.

269. Rapp, M., Seppälä, S., Granseth, E., and von Heijne, G. (2007) Emulating membrane protein evolution by rational design. Science 315, 1282-1284.

270. Elofsson, A., and von Heijne, G. (2007) Membrane protein structure: Prediction vs. reality. Annu.Rev.Biochem. 76, 125-140.

271. von Heijne, G. (2007) The membrane-protein universe - what's out there and why bother? J.Int.Med. 261, 543-557.

272. Emanuelsson, O., Brunak, S., von Heijne, G., and Nielsen, H. (2007) Locating proteins in the cell using TargetP, SignalP, and related tools. Nature Protocols 2, 953-971.

273. von Heijne, G. (2007) Formation of transmembrane helices *in vivo* – is hydrophobicity all that matters? J.Gen.Physiol. 129, 353-356.

274. Zhang, L., Sato, Y., Hessa, T., von Heijne, G., Lee , J-K., Kodama , K., Sakaguchi, M., and Uozumi, N. (2007) Contribution of hydrophobic and electrostatic interactions to the membrane integration of the Shaker K^+ channel voltage sensor domain. Proc.Natl.Acad.Sci. USA 104, 8263-8268.

275. Granseth, E., Seppälä, S., Rapp, M., Daley, D.O., and von Heijne, G. (2007) Membrane protein structural biology – How far can the bugs take us?. Mol.Membr.Biol. 24, 329-332.

276. Stenberg, F., von Heijne, G., and Daley, D.O. (2007) Assembly of the cytochrome bo_3. J.Mol.Biol. 371, 765-773.

277. von Heijne, G. (2007) Membrane proteins up for grabs. Nature Biotech. 25, 646.

278. Lundin, C., Johansson, S., Johnson, A.E., Näslund, J., von Heijne, G., and Nilsson, IM. (2007) Stable insertion of Alzheimer Aβ peptide into the ER membrane strongly correlates with its length. FEBS Lett. 581, 3809-3813.

279. Newstead, S., Kim, H., von Heijne, G., Iwata, S., and Drew, D. (2007) High-throughput fluorescent-based optimization of eukaryotic membrane protein overexpression and purification in *Saccharomyces cerevisiae*. Proc.Natl.Acad.Sci. USA 104, 13936-13941.

280. Hessa, T., Meindl-Beinker, N.M., Bernsel, A., Kim, H., Sato, Y., Lerch-Bader, M., Nilsson, IM., White, S.H., and von Heijne, G. (2007) Molecular code for transmembrane-helix recognition by the Sec61 translocon. Nature 450, 1026-1030.

281. White, S.H., and von Heijne, G. (2008) How translocons select transmembrane helices. Ann.Rev.Biophys.Biomolec.Struct. 37, 23-42

282. Xie, K., Hessa, T., Seppälä, S., Rapp, M., von Heijne, G., and Dalbey, R. (2007) features of transmembrane segments that promote the lateral release from the translocase into the lipid phase. Biochemistry 46, 15153-15161.

283. Lundin, C., Käll, L., Kreher, S.A., Kapp, K., Sonnhammer, E.L., Carlson, J.R., von Heijne, G., and Nilsson, IM. (2007) Membrane topology of the *Drosophila* OR83b odorant receptor. FEBS Lett. 581, 5601-5604.

284. Lerch-Bader, M., Lundin, C., Kim, H., Nilsson, IM., and von Heijne, G. (2008) Contribution of positively charged flanking residues to the insertion of transmembrane helices into the endoplasmic reticulum. Proc.Natl.Acad.Sci. USA 105, 4127-4132.

285. Drew, D., Newstead, S., Sonoda, Y., Kim, H., von Heijne, G., and Iwata, S. (2008) GFP-based optimization scheme for the overexpression and purification of eukaryotic membrane proteins in *Saccharomyces cerevisiae*. Nature Protocols 5, 784-798.

286. Bernsel, A., Viklund, H., Falk, J., Lindahl, E., von Heijne, G., and Elofsson, A. (2008) Prediction of membrane-protein topology from first principles. Proc.Natl.Acad.Sci. USA 105, 7177-7181.

287. Cassel, M., Seppälä, S., and von Heijne, G. (2008) Confronting fusion-protein based membrane protein topology mapping with reality: the *Escherichia coli* ClcA H^+/Cl^- exchange transporter. J.Mol.Biol. 381, 860-866.

288. von Heijne, G., and Rees, D. (2008) Membranes: reading between the lines. Curr.Op.Struct.Biol. 18, 403-405.

289. Lundin, C., Kim, H., Nilsson, IM., White, S.H., and von Heijne, G. (2008) The molecular code for protein insertion in the ER membrane is similar for N_{in}-C_{out} and N_{out}-C_{in} transmembrane helices. Proc.Natl.Acad.Sci. USA 105, 15702-15707.

290. Hessa, T., Reithinger, J.H., von Heijne, G., and Kim, H. (2009) Quantitative analysis of transmembrane helix integration in the endoplasmic reticulum in *S. cerevisiae*. J.Mol.Biol. 386, 1222-1228.

291. Juncker, A.S., Jensen, L.J., Pierleoni, A., Bernsel, A., Tress, M.L., Bork, P., von Heijne, G., Valencia, A., Ouzounis, C.A., Casadio, R., and Brunak, S. (2009) Sequence-based feature prediction and annotation of proteins. Genome Biol. 10, 206.

292. Enquist, K., Fransson, M., Boekel, C., Bengtsson, I., Geiger, K., Lang, L., Pettersson, A., Johansson, S., von Heijne, G., and Nilsson, I.M. (2009) Membrane-integration characteristics of two ABC transporters, CFTR and P-glycoprotein. J.Mol.Biol. 387, 1153-1164.

293. Jaud, S., Fernández-Vidal, M., Nilsson, I.M., Meindl-Beinker, N.M., Hübner, N., Tobias, D.J., von Heijne, G., and White, S.H. (2009) Insertion of short transmembrane helices by the Sec61 translocon. Proc.Natl.Acad.Sci. USA 106, 11588-11593.

294. Fagerberg, L., Jonasson, K., von Heijne, G., Uhlén, M., and Berglund, L. (2010) Prediction of the human membrane proteome. Proteomics 10, 1141-1149.

295. Sakata, S., Kurokawa, T., Nørholm, M.H.H., Takagi, M., Okochi, Y., von Heijne, G., and Okamura, Y. (2010) Activities of the voltage-gated proton channel truncated in S4. Proc.Natl.Acad.Sci. USA 107, 2313-2318.

296. Hedin, L., Öjemalm, K., Bernsel, A., Hennerdal, A., Illergård, K., Karl Enquist, K., Kauko, A., Cristobal, S., von Heijne, G., Lerch-Bader, M., Nilsson, IM., and Elofsson, A. (2010) Membrane insertion of marginally hydrophobic transmembrane helices depends on sequence context. J.Mol.Biol. 396, 221-229.

297. [9]Daniels, R., Mellroth, P., Bernsel, A., Neiers, F., Normark, S., von Heijne, G., and Henriques-Normark, B. (2010) Gram-positive bacteria cope with oxidative pressure by two distinct strategies. J.Biol.Chem. 285, 3300-3309.

298. Langel, Ü., Cravatt, B.F., Gräslund, A., von Heijne, G., Niessen, S., and Zorko, M. (2009) Introduction to peptides and proteins. CRC Press, Boca Raton.

299. Kauko, A., Hedin, L., Thebaud, E., Cristobal, S., Elofsson, A., and von Heijne, G. (2010) Repositioning of transmembrane α-helices during membrane protein folding. J.Mol.Biol. 397, 190-201.

300. Strömqvist, J., Skoog, K., Daley, D., Widengren, J., and von Heijne, G. (2010) Estimating Z-ring radius and contraction in dividing *Escherichia coli.* Mol.Microbiol. 76, 151-158.

[9] JBC "Paper of the Week"

301. Seppälä, S., Slusky, J.S., Loris-Garcerá, P., Rapp, M., and von Heijne, G. (2010) Control of membrane protein topology by a single C-terminal residue. Science 328, 1698-1700.

302. Schow, E.V., Freites, J.A., Cheng, P., Bernsel, A., von Heijne, G., White, S.H. and Tobias, D.J. (2011) Arginine in membranes: The connection between molecular dynamics simulations and translocon-mediated insertion experiments. J.Membr.Biol. 239, 35-48.

303. Nørholm, M.H.N., Cunningham, F., Deber, C.M., and von Heijne, G. (2011) Converting a marginally hydrophobic soluble protein into a membrane protein. J.Mol.Biol. 407, 171-179.

304. Calado Botelho, S., Österberg, M., Reichert, A.S., Yamano, K., Björkholm, P., Endo, T., von Heijne, G., and Kim. H. (2011) TIM23-mediated insertion of transmembrane α-helices into the mitochondrial inner membrane. EMBO J. 30, 1003-1011.

305. Österberg, M., Calado Botelho, S., von Heijne, G., and Kim, H. (2011) Charged flanking residues control the efficiency of membrane insertion of the first transmembrane segment in mitochondrial Mgm1p. FEBS Lett. 585, 1238-1242.

306. Öjemalm, K., Higuchi, T., Jiang, Y., Langel, Ü., Nilsson, IM., White, S.H., Suga, H., and von Heijne, G. (2011) Apolar surface area determines the efficiency of translocon-mediated membrane protein integration into the endoplasmic reticulum. Proc.Natl.Acad.Sci. USA 108:E359-E364.

307. Nørholm, M.H.N., Shulga, Y.V., Aoki, S., Epand, R.M., and von Heijne, G. (2011) Flanking residues help determine if a hydrophobic segment adopts a monotpoic or bitopic topology in the membrane. J.Biol.Chem. 286, 25284-25290.

308. von Heijne, G. (2011) Membrane proteins: From bench to bits. Biochem. Soc.Trans. 39, 747-750.

309. Nørholm, M.H., Light, S., Virkki, M.T., Elofsson, A., von Heijne, G., and Daley, D.O. (2012) Manipulating the genetic code for membrane protein production: What have we learnt so far? BBA – Biomembranes 1818, 1091-1096..

310. Nordahl Petersen, T., Brunak, S., von Heijne, G., and Nielsen, H. (2011) SignalP 4.0 – Discriminating signal peptides from transmembrane regions. Nature Meth. 8, 785-786.

311. von Heijne, G. (2011) Introduction to the theme "Membrane protein folding". Annu.Rev.Biochem.80, 157-160.

312. Contreras, F.-X., Ernst, A.M., Haberkant, P., Björkholm, P., Lindahl, E., Gönen, B., Tischer, C., Elofsson, A., von Heijne, G., Thiele, C., Pepperkok, R., Wieland, F., and Brügger, B. (2012) Molecular recognition of a single sphingolipid species by a protein's transmembrane domain. Nature 481, 525-529.

313. Skoog, K., Söderström, B., Widengren, J., von Heijne, G., and Daley, D.O. (2012) Sequential closure of the cytoplasm and then the periplasm during cell division in *Escherichia coli*. J.Bacteriol. 194, 584-586.

314. Öjemalm, K., Halling, K.K., Nilsson, IMN., and von Heijne, G. (2012) Orientational preferences of neighboring helices can drive ER insertion of a marginally hydrophobic transmembrane helix. Mol.Cell 45, 529-540.

315. Tarry, M., Skaar, K., von Heijne, G., Draheim, R., and Högbom, M. (2012) Production of human tetraspanin proteins in *Escherichia coli*. Prot.Expr.Purif. 82, 373-379.

316. Galian, C., Björkholm, P., Bulleid, N., and von Heijne, G. (2012) Efficient glycosylphosphatidylinositol (GPI) modification of membrane proteins requires a C-terminal anchoring signal of marginal hydrophobicity. J.Biol.Chem. 287, 16399-16409.

317. Lloris-Garcerá, P., Bianchi, F., Slusky, J.S.G., Seppälä, S., Daley, D.O., von Heijne, G. (2012) Antiparallel dimers of the small multidrug-resistance protein EmrE are more stable than parallel dimers. J.Biol.Chem. 287, 26052-26059.

318. Toddo, S., Söderström, B., Palombo, I., von Heijne, G., Nørholm, M.H.H., and Daley, D.O. (2012) Application of split-GFP for topology mapping membrane proteins in *Escherichia coli*. Prot.Sci. 21, 1571-1576.

319. [10]Ismail, N., Hedman, R., Schiller, N., and von Heijne, G. (2012) A bi-phasic pulling force acts on transmembrane helices during translocon-mediated membrane integration. Nature Struct. Molec. Biol. 19, 1018-1023.

320. Lee, H., Min, J., von Heijne, G., and Kim, H. (2012) Glycosylatable GFP as a compartment-specific membrane topology reporter. Biochem. Biophys. Res. Comm. 427, 780-784.

321. Öjemalm, K., Watson, H., Roboti, P., Cross, B.C.S., Warwicker, J., von Heijne, G., and High, S. (2013) Positional editing of transmembrane domains during ion channel assembly. J. Cell Sci. 126, 464-472.

322. Calado Botelho, S., Tatsuta, T., von Heijne, G., and Kim. H. (2013) Dislocation by the m-AAA protease increases the threshold hydrophobicity for retention of transmembrane helices in the inner membrane of yeast mitochondria. J. Biol. Chem. 288, 4792-4798.

323. Öjemalm, K., Calado Botelho, S., Stüdle, C., and von Heijne, G. (2013) Quantitative analysis of SecYEG-mediated insertion of transmembrane α-helices into the bacterial inner membrane. J Mol Biol 425, 2813-2822.

324. Nørholm, M.H.H.., Toddo, S., Virkki, M.T.I., Light, S., von Heijne, G., and Daley, D.O. (2013) Improved production of membrane proteins in *Escherichia coli* by synonymous codon substitutions in the coding region. FEBS Lett 587:2352-2358.

325. Lloris-Garcerá, P., Slusky, J.S.G., Seppälä, S., Prieß, M., Schäfer, L.V., and von Heijne, G. (2013) *In vivo* Trp-scanning of the Small Multidrug Resistance protein EmrE confirms 3D structure models. J Mol Biol 425, 4642-4651.

326. Cymer., F., and von Heijne, G. (2013) Co-translational folding of membrane proteins probed by arrest-peptide mediated force measurements. Proc Natl Acad Sci USA 110, 14640-14645.

327. Reithinger, J.H., Yim, C., Björkholm, P., von Heijne, G., and Kim, H. (2013) A short C-terminal tail prevents mis-targeting of hydrophobic mitochondrial membrane proteins to the ER. FEBS Lett 587, 3480-3486.

[10] Editor's Choice, Science 19 October 2012

328. Karamyshev, A.L., Patrick, A.E., Karamysheva, Z.N., Griesemer, D.S., Hudson, H., Tjon-Kon-Sang, S., Nilsson, I.M., Otto, H., Liu, O., Rospert, S., von Heijne, G., Johnson, A.E., and Thomas, P.J. (2014) Inefficient SRP interaction with a nascent chain triggers a mRNA quality control pathway. Cell 156, 146-157.

329. Söderström, B., Skoog, K., Blom, H., Weiss, D.S., von Heijne, G., and Daley, D. (2014) Disassembly of the divisome in *Escherichia coli*: Evidence that FtsZ dissociates before compartmentalization. Mol Microbiol 92, 1-9.

330. Lloris-Garcera, P., Seppälä, S., Slusky, J.S.G., Rapp, M., and von Heijne, G. (2014) Why have Small Multidrug-Resistance proteins not evolved into fused, internally duplicated structures? J Mol Biol 426, 2246-2254.

331. Cymer, F., Ismail, N., and von Heijne, G. (2014) Weak pulling forces exerted on N_{in}-orientated transmembrane segments during co-translational insertion into the inner membrane of *Escherichia coli*. FEBS Lett. 588, 1930-1934.

332. Virkki, M., Boekel, C., Illergård, K., Peters, C., Shu, N., Tsirigos, K.D., Elofsson, A., von Heijne*, G., and Nilsson*, IM. (2014) Large tilts in transmembrane helices can be induced during tertiary structure formation. J Mol Biol 426, 2529-2538. (*corresponding authors)

333. Björkholm. P., Ernst, A.M., Hacke, M., Wieland, F., Brügger, B., and von Heijne, G. (2014) Identification of novel sphingolipid-binding motifs in mammalian membrane proteins. BBA-Biomembranes 1838, 2066-2070.

334. Nilsson, IM., Lara, P., Hessa, T., Johnson, A.E., von Heijne, G., and Karamyshev, A.L. (2015) The code for directing proteins for translocation across ER membrane: SRP cotranslationally recognizes specific features of a signal sequence. J Mol Biol 427, 1191-1201.

335. Ulmschneider, M.B., Ulmschneider, J.P., Schiller, N., Wallace, B.A., von Heijne, G., and White, S.H. (2014) Spontaneous transmembrane helix insertion mimics translocon-guided insertion thermodynamically. Nature Commun, 5, 4863.

336. Ezure, T., Nanatani, K., Suzuki, S., Sato, Y., Aizawa, K., Souma, S., Ito, M., Hohsaka, T., von Heijine, G., Utsumi, T., Abe, K., Ando, E., Uozumi, N. (2014)

A cell-free translocation system using extracts of cultured insect cells to yield functional membrane proteins. PLoS ONE, DOI:10.1371/journal.pone.0112874.

337. Nørholm, M., von Heijne, G., and Draheim, R. (2015) 'Forcing the issue' – Aromatic tuning facilitates stimulus-independent modulation of a two-component signaling circuit. ACS Synthetic Biology 4, 474-481.

338. Vargas-Uribe, M., Rodnin, M.V., Öjemalm, K., Delgado, A., Kyrychenko, A., Nilsson, IM., Posokhov, Y.O., Makhatadze, G., von Heijne, G., and S. Ladokhin, A.S. (2015) Thermodynamics of membrane insertion and refolding of the diphtheria toxin T-domain. J Membr Biol, 248, 383–394.

339. Cymer, F., von Heijne, G., and White, S.H. (2015) Mechanisms of integral membrane protein insertion and folding. J Mol Biol 427, 999-1022.

340. Ismail, N., Hedman, R., Lindén, M., and von Heijne, G. (2015) Charge-driven dynamics of nascent chain movement through the SecYEG translocon. Nature Struct Molec Biol 22, 145-149.

341. Uhlén, M., Linn Fagerberg, L., Hallström, B.M., Lindskog, C., Oksvold, P., Mardinoglu, A., Sivertsson, Å., Kampf, C., Sjöstedt, E., Asplund, A., Olsson, IM., Edlund, K., Lundberg, E., Navani, S., Al-Khalili Szigyarto, C., Odeberg, J., Djureinovic, D., Ottosson Takanen, J., Hober, S., Alm, T., Berling, H., Tegel, H., Mulder, J., Rockberg, J., Nilsson, P., Schwenk, J.M., Hamsten, M., von Feilitzen, K., Forsberg, M., Persson, L., Johansson, F., Zwahlen, M., von Heijne, G., Nielsen, J., and Pontén, F. (2015). Tissue-based map of the human proteome. Science 347, 394 & 1260419-1 – 1260419-9.

342. Botelho, S.C., Enquist, K., von Heijne, G., and Draheim, R.R. (2015) Differential repositioning of the second transmembrane helices from *E. coli* Tar and EnvZ upon moving the flanking aromatic residues. Biochem. Biophys. Acta 1848, 615-621.

343. Goel, S., Palmkvist, M., Kirsten Moll, K., Joannin, N., Lara, P., Akhouri, R., Moradi, N., Öjemalm, K., Westman, M., Angeletti, D., Kjellin, H., Lehtiö, J., Hult, A.K., Olsson, M.L., von Heijne, G., Nilsson, IM., and Wahlgren, M. (2015) RIFINs are adhesins implicated in severe *Plasmodium falciparum* malaria. Nature Med. 21, 314-317.

344. Stone, T.A., Schiller, N., von Heijne, G., and Deber, C.M. (2015) Hydrophobic blocks facilitate lipid compatibility and translocon recognition of transmembrane protein sequences. Biochemistry 54, 1465–1473.

345. Cymer, F., Hedman, R., Ismail, N., and von Heijne, G. (2015) Exploration of arrest-peptide sequence space reveals arrest-enhanced variants. J Biol Chem 290, 10208–10215.

346. Nilsson, O.B., Hedman, R., Marino, J., Wickles, S., Bischoff, L., Johansson, M., Müller-Lucks, A., Trovato, F., Puglisi, J.D., O'Brien, E., Beckmann, R., and von Heijne, G. (2015) Cotranslational protein folding inside the ribosome exit tunnel. Cell Reports 12, 1533-1540.

347. Nilsson, O.B., Müller-Lucks, A., Kramer, G., Bukau, B., and von Heijne, G. (2016) Trigger Factor reduces the force exerted on the nascent chain by a cotranslationally folding protein. J Mol Biol 428, 1356-1364.

348. Marino, J., von Heijne, G., and Beckmann, R. (2016) Small protein domains fold inside the ribosome exit tunnel. FEBS Lett 590, 655-660.

349. Baeza-Delgado, C., von Heijne, G., Marti-Renom, M.A., and Mingarro, I. (2016) Biological insertion of computationally designed short transmembrane segments. Scientific Reports, DOI: 10.1038/srep23397.

350. Söderström, B., Mirzadeh, K., Toddo, S., von Heijne, G., Skoglund, U., and Daley, D.O. (2016) Coordinated disassembly of the divisome complex in *Escherichia coli*. Mol Microbiol 101, 425-438.

351. Schibich, D., Gloge, F., Pöhner, I., Björkholm, P., Wade, R.C., von Heijne, G., Bukau, B., and Kramer, G. (2016) Genome-wide profiling of SRP interaction with nascent polypeptides. Nature 536, 219-223.

352. Öjemalm, K., Higuchi, T., Lara, P., Lindahl, E., Suga, H., and von Heijne, G. (2016) Energetics of side-chain snorkeling in transmembrane helices probed by non-proteinogenic amino acids. Proc Natl Acad Sci USA 113, 10559-10564.

353. Stone, T.A., Schiller, N., Workewych, N., von Heijne, G., and Deber , C.M. (2016) Hydrophobic clusters raise the threshold hydrophilicity for insertion of transmembrane sequences *in vivo*. Biochemistry 55, 5772-5779.

354. Mishima, E., Sato, Y., Nanatani, K., Hoshi, N., Lee, J-K., Schiller, N., von Heijne, G., Sakaguchi, M., and Uozumi, N. (2016) The topogenic function of S4 promotes membrane insertion of the voltage-sensor domain in the KvAP channel. Biochem J 473, 4361-4372.

355. Farías-Rico, J.A., Goetz, S.K., Marino, J. and von Heijne, G. (2016) Mutational analysis of protein folding inside the ribosome exit tunnel. FEBS Lett 591:155-163.

356. Nilsson, O.B., Nickson, A.A., Hollins, J.J., Wickles, S., Steward, A., Beckmann, R., von Heijne[11], G., and Clarke[11], J. (2017) Cotranslational folding of spectrin domains via partially structured states. Nature Struct Molec Biol 24, 221-225.

357. Ulmschneider, M.B., Ulmschneider , J.P., Freites, J.A., von Heijne, G., Tobias, D.J., and White, S.H. (2017) Transmembrane helices containing a charged arginine are thermodynamically stable. Eur Biophys J, 46, 627-637.

358. Su, T., Cheng, J., Sohmen, D., Hedman, R., Berninghausen, O., von Heijne, G., Wilson, D.N., and Beckmann, R. (2017) The force-sensing peptide VemP employs extreme compaction and secondary structure formation to induce ribosomal stalling. eLife 6:e25642.

359. Renault, H., De Marothy, M.T.I., Jonasson, G., Lara, P., André, F., Nilsson, I.M., von Heijne, G., and Werck-Reichhart, D. (2017) Gene duplication leads to altered membrane topology of a cytochrome P450 enzyme in seed plants. Mol Biol and Evol, 34, 2041-2056.

360. Fluman[12], N., Tobiasson, V., and von Heijne[12], G. (2017) Stable membrane topologies of small dual-topology membrane proteins. Proc Natl Acad Sci USA 114, 7987-7992.

361. Snapp, E.L., McCaul, N., Quandte, M., Cabartova, Z., Bontjer, I., Källgren, C., Nilsson, IM., Land, A., von Heijne, G., Sanders, R.W., and Braakman, I. (2017) Structure and topology around the cleavage site regulate post-translational cleavage of the HIV-1 gp160 signal peptide. eLife 6:e26067, DOI: 10.7554/eLife.26067.

[11] Corresponding authors
[12] Corresponding authors

362. von Heijne, G. (2018) Reflections: Membrane protein serendipity. J Biol Chem, 293, 3470 –3476.

363. Notari, L., Martinez-Carranza, M., Farías-Rico, J.A., Stenmark, P., and von Heijne, G. (2018) Cotranslational folding of a pentarepeat β-helix protein. J Mol Biol 430, 5196-5206.

364. Tian, P., Steward, A., Kudva, R., Su, T., Shilling, P. J., Nickson, A. A., Hollins, J. J., Beckmann, R., von Heijne, G., Best, R., and Clarke, J. (2018) The folding pathway of an Ig domain is conserved on and off the ribosome. Proc Natl Acad Sci USA 115, E11284-E11293.

365. Kudva, R., Pardo-Avila, F., Carroni, M., Bernstein, H.D., and von Heijne, G. (2018) The shape of the ribosome exit tunnel affects cotranslational protein folding. eLife 2018;7:e36326.

366. Niesen, M.J.M., Müller-Lucks, A., Hedman, R., von Heijne, G., and Miller III, T.F. (2018) Forces on nascent polypeptides during membrane insertion and translocation via the Sec translocon. Biophys J 115, 1885-1894.

367. Orrell, K.E., Tellgren-Roth, Å., Di Bernardo, M., Zhang, Z., Cuviello, F., Lundqvist, J., von Heijne, G., Nilsson, IM., and Melnyk, R.A. (2018) Direct detection of membrane-inserting fragments defines the translocation pores of a family of pathogenic toxins. J Mol Biol 430, 3190-3199.

368. Farías-Rico, J.A., Ruud Selin, F., Myronidi, I., Frühauf, M., von Heijne, G. (2018) Effects of protein size, thermodynamic stability, and net charge on cotranslational folding on the ribosome. Proc Natl Acad Sci USA 115, E9280-E9287.

369. Almagro Armenteros, J.J., Tsirigos, K.D., Kaae Sønderby, C., Nordahl Petersen, T., Winther, O., Brunak, S., von Heijne, G., and Nielsen, H. (2019) SignalP 5.0: improved signal peptide predictions across the tree of life using deep neural networks. Nature Biotech 37, 420-423.

370. Bañó-Polo, M., Baeza-Delgado, C., Tamborero, S., Hazel, A., Grau, B., Nilsson, IM., Whitley, P., Gumbart, J.C., von Heijne, G., and Mingarro, I. (2018)

Transmembrane but not soluble helices fold inside the ribosome tunnel. Nature Comm 9, article 5246. doi:10.1038/s41467-018-07554-7.

371. Kemp, G., Kudva, R., de la Rosa, A., and von Heijne, G. (2019) Force-profile analysis of the cotranslational folding of HemK and filamin domains: Comparison of biochemical and biophysical folding assays. J Mol Biol 431, 1308-1314.

372. Lara, P., Tellgren-Roth, Å., Behesti, H., Horn, Z., Schiller, N., Enquist, K., Cammenberg, M., Liljenström, A., Hatten, M.E., von Heijne[13], G., and Nilsson[13], IM. (2019) Astrotactins 1 and 2 have similar membrane topology and mature via endoproteolytic cleavage catalyzed by signal peptidase. J Biol Chem 294, 4538-4545.

373. Nielsen, H., Tsirigos, K.D., Brunak, S., and von Heijne, G. (2019) A brief history of protein sorting prediction. The Protein Journal 38, 200-216.

374. Tikhonova, E.B., Karamysheva, Z.N., von Heijne, G., and Karamyshev, A.L. (2019) Silencing of aberrant secretory protein expression by disease-associated mutations. J Mol Biol 431, 2567-2580.

375. Shanmuganathan, V., Schiller, N., Magoulopoulou, A., Cheng, J., Braunger, K., Cymer, F., Berninghausen, O., Beatrix, B., Kohno, K., von Heijne[14], G. and Beckmann[14], R. (2019) Structural and mutational analysis of the ribosome-arresting human XBP1u. eLife 8:e46267.

376. Kudva, R., Vogt, A., Denks, K., and von Heijne, G. (2019) Isolation of ribosome-associated nascent chains of soluble proteins produced in *Escherichia coli*. Protocols.io, dx.doi.org/10.17504/protocols.io.23fggjn.

377. Seurig, M., Ek, M., von Heijne[15], G., and Fluman[15], N. (2019) Dynamic membrane topology in an unassembled membrane protein. Nature Chem Biol 15, 945-948.

[13] Corresponding authors
[14] Corresponding authors
[15] Corresponding authors

378. [16]Almagro Armenteros, J., Salvatore, M., Winther, O., Emanuelsson, O., von Heijne, G., Elofsson, A., and Nielsen, H. (2019) Detecting sequence signals in targeting peptides using deep learning. Life Science Alliance 2, e201900429.

379. Lee, S, Lee, H., Yoo, S., Leva, R., van der Laan, M., von Heijne, G., and Kim, H. (2020) Mgr2 regulates membrane insertion of marginal stop-transfer signals in the mitochondrial inner membrane. FEBS Lett 954, 1081-1087.

380. Andersson, A., Kudva, R., Magoulopoulou, A., Lejarre, Q., Lara, P., Xu, P., Goel, S., Pissi, J., Ru, X., Hessa, T., Wahlgren, M., von Heijne, G., Nilsson, I.M., and Tellgren-Roth, Å. (2020) Membrane integration and topology of RIFIN and STEVOR proteins of the *Plasmodium falciparum* parasite. FEBS J 287, 2744-2762.

381. Kemp, G., Nilsson, O.B., Tian, P., Best, R.B., and von Heijne, G. (2020) Cotranslational folding cooperativity of contiguous domains of α-spectrin. Proc Natl Acad Sci USA 117, 14119-14126.

382. Elfageih, R., Karyolaimos, A., Kemp, G., de Gier, JW., von Heijne[17], G., Kudva[17], R. (2020) Cotranslational folding of alkaline phosphatase in the periplasm of *Escherichia coli*. Protein Sci 29, 2028-2037.

383. Nicolaus, F., Metola, A., Mermans, D., Liljenström, A., Krč, A., Abdullahi, S.M., Matthew Zimmer[4], Miller III, T.F., von Heijne, G. (2021) Residue-by-residue analysis of cotranslational membrane protein integration *in vivo*. eLife 10:e64302.

384. Sandhu, H. Hedman, R., Cymer,F., Kudva, R., Ismail, N., von Heijne, G. (2021) Cotranslational folding of a periplasmic protein domain in *Escherichia coli*. J Mol Biol 433, 167047.

385. Wruck, F., Tian, P., Kudva, R., Best, R.B., von Heijne, G., Tans, S.J., Katranidis, A. (2021) The ribosome modulates folding inside the ribosomal exit tunnel. Commun Biol 4:523.

386. von Heijne, G. (2021) Introduction to the theme on membrane channels. Annu Rev Biochem, in press.

[16] Most cited paper in Life Science Alliance as of 2025
[17] Corresponding authors

387. Su, T., Kudva, R., Becker, T., Buschauer, R., Komar, T., Berninghausen, O., von Heijne, G., Cheng, J., and Beckmann, R. (2021) Structural basis of L-tryptophan-dependent inhibition of Release Factor 2 by the TnaC arrest peptide. Nucl Acid Res 49, 9539-9547.

388. von Heijne, G. (2021) Molten globules lure transmembrane helices away from the membrane (Commentary). Proc Natl Acad Sci USA 118: e2112899118.

389. Teufel, F., Almagro Armenteros, J.J., Rosenberg Johansen, A., Halldór Gislason, M., Irby Pihl, S., Tsirigos, K.D., Winther, O., Brunak, S., von Heijne, G., Nielsen, H. (2022) SignalP 6.0 achieves signal peptide prediction across all types using protein language models. Nature Biotech, https://doi.org/10.1038/s41587-021-01156-3.

390. Di Palma, F., Decherchi, S., Pardo-Avila, F., Succi, S., Levitt, M., von Heijne[18], G., Cavalli[18], A. (2022) Probing interplays between human XBP1u translational arrest peptide and 80S ribosome. J Chem Theory Comput 18, 1905-1914.

391. White, S.H., von Heijne, G., and Engelman, D.A. (2022; Japanese edition 2025) Cell boundaries: How membranes and their proteins work (1st edition). Garland Science (New York). 564 pages.

392. Nicolaus, F., Ibrahimi, F., den Besten, A., and von Heijne, G. (2022) Upstream charged and hydrophobic residues impact the timing of membrane insertion of transmembrane helices. FEBS Lett 596, 1004-1012.

393. Mermans, D., Nicolaus, F., Fleisch, K., and von Heijne, G. (2022) Cotranslational folding and assembly of the dimeric *E. coli* inner membrane protein EmrE. Proc Natl Acad Sci USA 119, e2205810119.

394. Mermans, D., Nicolaus, F., Baygin, A., and von Heijne, G. (2023) Cotranslational folding of human growth hormone *in vitro* and in *Escherichia coli*. FEBS Lett 597, 1355-1362.

395. Westerfield[18], J.M., Kozojedová, P., Juli, C., Metola, A., and von Heijne[18], G. (2025) Cotranslational membrane insertion of the voltage-sensitive K^+ channel KvAP. Proc Natl Acad Sci USA 122, e2412492122.

[18] Corresponding authors

396. Nielsen, H., Teufel, F., Brunak, S., and von Heijne, G. (2024) SignalP: The evolution of a web server. *In* Lisacek, F. (ed.), Protein Bioinformatics, Methods in Molecular Biology, vol. 2836, pp. 331-367. https://doi.org/10.1007/978-1-0716-4007-4_17.

397. Chung, Y., Yim, C., Pereira, G., Son, S., Ravnkilde, L., Mazurkiewicz, L.E., Weeks, A.M., Förster, F., von Heijne, G., de Souza, P.C.T., and Kim, H. (2024). Spc2 modulates substrate- and cleavage site-selection in the yeast signal peptidase complex**.** J Cell Biol 223, e202211035. https://doi.org/10.1083/jcb.202211035.

398. Pardo-Avila, F., Kudva, R., Levitt, M., and von Heijne, G. (2024) Single-residue effects on the behavior of a nascent polypeptide chain inside the ribosome exit tunnel. BioRxiv, https://doi.org/10.1101/2024.08.20.608737.

399. Grau, B., Kormos, R., Bañó-Polo, M., Chen, K., García-Murria, M.J., Hajredini, F., Sánchez del Pino, M.M., Jo, H., Martínez-Gil, L., von Heijne, G., DeGrado, W.F., and Mingarro, I. (2025) Sequence-dependent scale for translocon-mediated insertion of interfacial helices in membranes. Sci Adv 11, eads6804. DOI: 10.1126/sciadv.ads6804

400. Westerfield, J., Nicolaus, F., Swanstrom R., von Heijne, G. (2025) Cotranslational folding and maturation of HIV-1 protease. BioRxiv https://doi.org/10.1101/2025.08.27.672612.