

Chapter 93

Thermoregulation

Dean L. Kellogg, Jr.

REFERENCES

1. Romanovsky AA: Thermoregulation: Some concepts have changed. Functional architecture of the thermoregulatory system. *Amer J Physiol Regulatory Integrative Comp Physiol* **293**:R37-R46, 2007
2. Sell H, Deshaies Y, Richard D: The brown adipocyte: Update on its metabolic role. *International J Biochem & Cell Biol* **36**:2098-2104, 2004
3. Au-Yong ITH et al: Brown adipose tissue and seasonal variation in humans. *Diabetes* **58**:2583-2587, 2009
4. Kellogg DL, Jr: In vivo mechanisms of cutaneous vasodilation and vasoconstriction in humans. *J Appl Physiol* **100**:1709-1718, 2006
5. Rowell LB: Human cardiovascular adjustments to exercise and thermal stress. *Physiol Rev* **54**:75-159, 1974
6. Donadio V et al: Skin sympathetic adrenergic innervation: An immunofluorescence confocal study. *Ann Neurol* **59**:376-381, 2006
7. Johnson JM, Proppe DW: Cardiovascular adjustments to heat stress. In: *Handbook of physiology-environmental physiology*, edited by M Fregly, and C Blatteis. New York, Oxford University Press, 1996, p. 215-243
8. Sato K: The physiology, pharmacology, and biochemistry of the eccrine sweat gland. *Rev Physiol Biochem Pharmacol* **79**:51-131, 1977
9. Sato F et al: Functional and morphological changes in the eccrine sweat gland with heat acclimation. *J Appl Physiol* **69**:232-236, 1990
10. Sato K, Sato F. Nonisotonicity of simian eccrine primary sweat induced in vivo. *Am J Physiol* **252**:R1099-1105, 1987
11. Porter AMW: Why do we have apocrine and sebaceous glands? *J R Soc Med* **94**:236-237, 2001
12. Welch G et al: Nonselective NOS inhibition blunts the sweat response to exercise in a warm environment. *J Appl Physiol* **106**:796-803, 2009
13. Heath ME: Neuropeptide Y and Y1 receptor agonists increase blood flow through arteriovenous anastomoses in the rat tail. *J Appl Physiol* **85**:301-309, 1998
14. Hashim MA, Tadepalli AS: Cutaneous vasomotor effects of neuropeptide Y. *Neuropeptides* **29**:263-271, 1995
15. Padilla SL et al: Peptidergic modulation of the sympathetic contraction in the rabbit ear: Effects of temperature. *Br J Pharmacol* **121**:21-28, 1997
16. Wallengren J: Vasoactive peptides in the skin. *J Investigative Derm Symp Proceedings* **2**:49-55, 1997
17. Charkoudian N: Skin blood flow in adult human thermoregulation: How it works, when it does not, and why. *Mayo Clin Proc* **78**:603-612, 2003
18. Rowell LB: *Human Circulation: Regulation during Physical Stress*. New York, Oxford Univ. Press, 1986
19. Lewis T, Pickering GW: Vasodilation in the limbs in response to warming the body; with evidence for sympathetic vasodilator nerves in man. *Heart* **16**:33-51, 1931
20. Grant RT, Holling HE: Further observations on the vascular responses of the human limb to body warming; evidence for sympathetic vasodilator nerves in the normal subject. *Clin Sci* **3**:273-285, 1938
21. Edholm OG, Fox RH, MacPherson RK: Vasomotor control of the cutaneous blood vessels in the human forearm. *J Physiol Lond* **139**:455-465, 1957
22. Roddie IC, Shepherd JT, Whelan RF: The vasomotor nerve supply of the human forearm. *Clin Sci* **16**:67-74, 1957
23. Kellogg DL, Jr., Johnson JM, Kosiba WA: Selective abolition of adrenergic vasoconstrictor responses in skin by local iontophoresis of bretylium. *Am J Physiol* **257**:H1599-1606, 1989
24. Roddie IC: Sympathetic vasodilation in human skin. *J Physiol* **548**:336-337, 2003.
25. Fox RH, Hilton SM: Bradykinin formation in human skin as a factor in heat vasodilation. *J Physiol (London)* **142**:219-232, 1958
26. Frewin DB, McConnell DJ, Downey JA: Is a kininogenase necessary for human sweating? *Lancet* **2**:744, 1973
27. Brengelmann GL et al: Absence of active vasodilation associated with congenital absence of sweat glands in humans. *Am J Physiol* **240**:H571-H575, 1981

28. Nolano M et al: Ross Syndrome: A rare or a misknown disorder of thermoregulation? A skin innervation study on 12 subjects. *Brain* **129**:2119-2131, 2006
29. Sugenoya J et al: Vasodilator component in sympathetic nerve activity destined for the skin of the dorsal foot of mildly heated humans. *J Physiol* **507**:603-610, 1998
30. Kamijo Y-I, Lee K, Mack GW: Active cutaneous vasodilation in resting humans during mild heat stress. *J Appl Physiol* **98**:829-837, 2005
31. Hökfelt TM et al: Peptidergic neurons. *Nature* **284**:515-521, 1980
32. Roddie IC, Shepherd JT, Whelan RF. The contribution of constrictor and dilator nerves to the skin vasodilation during body heating. *J Physiol (London)* **136**:489-497, 1957.
33. Vaalasti A, Tainio H, Rechartd L: Vasoactive Intestinal Polypeptide (VIP)-like immunoreactivity in the nerves of human axillary sweat glands. *J Investigative Dermatol* **85**:246-248, 1985
34. Hartschuh W et al: VIP-immunoreactivity in the skin of various mammals: Immunohistochemical, radioimmunological, and experimental evidence for a dual localization in cutaneous nerves and Merkel cells. *Peptides* **5**:239-245, 1984
35. Tainio H: Cytochemical localization of VIP-stimulated adenylate cyclase activity in human sweat glands. *Br J Dermatol* **116**:323-328, 1987
36. Yamashita Y et al: Local effect of vasoactive intestinal polypeptide on human sweat-gland function. *Japanese J Physiol* **37**:939-936, 1987
37. Kellogg DL, Jr et al: Cutaneous active vasodilation in humans is mediated by cholinergic nerve co-transmission. *Circ Res* **77**:1222-1228, 1995
38. Bennett LA et al: Evidence for a role for vasoactive intestinal peptide in active vasodilation in the cutaneous vasculature in humans. *J Physiol* **552**:223-232, 2003
39. Bennett LA, Kellogg DL Jr, Saad A, Stephens DP, Johnson JM: Possible role for VIP in cutaneous active vasodilation during heat stress. *The FASEB J* **15**:A474, 2001
40. Itoh N et al: Human preprovasoactive intestinal polypeptide contains a novel PHI-27-like peptide, PHM-27. *Nature* **304**:547-549, 1983
41. Wong BJ, Minson CT: Neurokinin-1 receptor desensitization attenuates cutaneous active vasodilation in humans. *J Physiol* **577**:1043-1051, 2006
42. Wong BJ, Tublitz NJ, Minson CT: Neurokinin-1 receptor desensitization to consecutive microdialysis infusions of substance P in humans. *J Physiol* **568**:1047-1056, 2005
43. Taylor WF, DiCarlo SE, Bishop VS: Neurogenic vasodilator control of rabbit ear blood flow. *Am J Physiol Regulatory Integrative Comp Physiol* **262**:R766-R770, 1993
44. Taylor WF, Bishop VS: A role for nitric oxide in active thermoregulatory vasodilation. *Am J Physiol* **264**:H1355-H1359, 1993
45. Doherty DK, Liu Y, Kellogg DL, Jr.: Endothelin B2 receptors contribute to resting vascular tone in humans. *J Investigative Med* **46**:59A, 1998
46. Shastry S et al: Effects of nitric oxide synthase inhibition on cutaneous vasodilation during body heating in humans. *J Appl Physiol* **85**:830-834, 1998
47. Dietz NM et al: Is nitric oxide involved in cutaneous vasodilation during body heating in humans? *J Appl Physiol* **76**:2047-2053, 1994
48. Kellogg DL, Jr, Liu Y, Crandall CG: Mechanisms of Cutaneous Active Vasodilation. In: *1998 International Symposium on Human Biometeorology*, edited by M Shibata, M Iriki, and IY Fuji-Yoshida. Yamanashi, Japan, Yamanashi Institute of Environmental Sciences, 1999
49. Farrell DM, Bishop VS: Permissive role for nitric oxide in active thermoregulatory vasodilation in rabbit ear. *Am J Physiol* **269**:H1613-H1618, 1995
50. Crandall CG, MacLean DA: Cutaneous interstitial nitric oxide concentration does not increase during heat stress in humans. *J Appl Physiol* **90**:1020-1024, 2001
51. Kellogg DL, Jr. et al: Nitric oxide mediates increases in skin blood flow during local warming in humans. *The FASEB J* **11**:A43, 1997
52. Wilkins BW et al: Nitric oxide is not permissive for cutaneous active vasodilation in humans. *J Physiol* **548**:963-969, 2003
53. Shastry S et al: Effects of atropine and L-NAME on cutaneous blood flow during body heating in humans. *J Appl Physiol* **88**:467-472, 2000
54. Shibasaki M et al: Acetylcholine released from cholinergic nerves contributes to cutaneous vasodilation during heat stress. *J Appl Physiol* **93**:1947-1951, 2002
55. Wilkins BW et al: Mechanisms of vasoactive intestinal peptide-mediated vasodilation in human skin. *J Appl Physiol* **97**:1291-1298, 2004

56. Kellogg DL, Jr, Zhao JL, Wu Y: Neuronal nitric oxide synthase mechanisms in the cutaneous vasculature of humans in vivo. *J Physiol (London)* **586**:847-857, 2008
57. Kellogg DL, Jr, Zhao JL, Wu Y: Endothelial nitric oxide synthase control mechanisms in the cutaneous vasculature of humans in vivo. *Am J Physiol Heart Circ Physiol* **295**:H123-129, 2008
58. Kellogg DL, Jr, Zhao JL, Wu Y: Roles of nitric oxide synthase isoforms in cutaneous vasodilation induced by local warming of the skin and whole body heat stress in humans. *J Appl Physiol* **107**:1438-1444, 2009
59. Johnson JM et al: Reflex regulation of sweat rate by skin temperature in exercising humans. *J Appl Physiol* **56**:1283-1288, 1984
60. Barcroft H, Edholm OG: The effect of temperature on blood flow and deep temperature in the human forearm. *J Physiol (London)* **102**:5-20, 1943
61. Minson CT, Berry LT, Joyner MJ: Nitric oxide and neurally mediated regulation of skin blood flow during local heating. *J Appl Physiol* **91**:1619-1626, 2001
62. Golay S et al: Local heating of human skin causes hyperemia without mediation by cholinergic muscarinic receptors of prostanoids. *J Appl Physiol* **97**:1781-1786, 2004
63. Kellogg DL, Jr. et al: Mechanisms of control of skin blood flow during prolonged exercise in humans. *Am J Physiol Heart Circ Physiol* **265**:H562-H568, 1993
64. Aoki K, Stephens DP, Johnson JM: Diurnal variation in cutaneous vasodilator and vasoconstrictor systems during heat stress. *Am J Physiol Regul Integr Comp Physiol* **281**:R591-R595, 2001
65. Stewart JM et al: Cutaneous neuronal nitric oxide is specifically decreased in postural tachycardia syndrome. *Am J Physiol Heart Circ Physiol* **293**:H2161-H2167, 2007
66. Garcia-Cardena G et al: Dynamic activation of endothelial nitric oxide synthase by Hsp90. *Nature* **393**:812-824, 1998
67. Shastry S, Joyner MJ: Geldanamycin attenuates NO-mediated dilation in human skin. *Am J Physiol Heart Circ Physiol* **282**:H232-H236, 2002
68. Adson AW, Brown GE: Calorimetric studies of the extremities following sympathetic ramisectomy and ganglionectomy. *Am J Med Sci* **170**:232, 1935
69. Fox RH, Edholm OG: Nervous control of the cutaneous circulation. *Br Med Bull* **19**:110-114, 1963
70. Greenfield ADM: The circulation through the skin. In: *Handbook of Physiology, Circulation*, edited by WF Hamilton, P Dow. Washington, DC, Am Physiol Soc, 1963, p. 1325-1351
71. Blair DA et al: Peripheral vascular effects of bretylium tosylate in man. *Br J Pharmacol* **15**:466-475, 1960
72. Kenney WL et al: Alpha 1-adrenergic blockade does not alter control of skin blood flow during exercise. *Am J Physiol* **260**:H855-H861, 1991
73. Haeusler G et al: On the mechanism of the adrenergic nerve blocking action of bretylium. *Naunyn-Schmiedebergs Arch Pharmak* **265**:260-277, 1979
74. Ekenvall L, Lindblad LE: Is vibration white finger a primary sympathetic nerve injury? *Br J Ind Med* **43**:702-706, 1986
75. Stephens DP et al: Neuropeptide Y antagonism reduces reflex cutaneous vasoconstriction in humans. *Am J Physiol Heart Circ Physiol* **287**:H1401-H1409, 2004
76. Johnson JM et al: Sympathetic, sensory, and non-neural contributions to the cutaneous vasoconstrictor response to local cooling. *Am J Physiol Heart Circ Physiol* **288**:1573-1579, 2005
77. Kellogg DL, Jr. et al: Atrial natriuretic peptide, vasoactive intestinal peptide, and skin blood flow during heat stress in humans. *The FASEB J* **10**:A8:1996
78. Hodges GJ et al: Role of sensory nerves in the cutaneous vasoconstrictor response to local cooling in humans. *Am J Physiol Heart Circ Physiol* **293**:H784-H789, 2007
79. Flavahan NA: The role of vascular alpha-2-adrenoreceptors as cutaneous thermosensors. *News Physiol Sci* **6**:251-255, 1991
80. Bailey SR et al: Rho kinase mediates cold-induced constriction of cutaneous arteries. *Circ Res* **94**:1367-1374, 2004
81. Bailey SR et al: Reactive oxygen species from smooth muscle mitochondria initiate cold-induced constriction of cutaneous arteries. *Am J Physiol Heart Circ Physiol* **289**:H253-H250, 2005
82. Chotani MA et al: Silent alpha-2c-adrenergic receptors enable cold-induced vasoconstriction in cutaneous arteries. *Am J Physiol Heart Circ Physiol* **278**:H1075-H1083, 2000
83. Johnson JM et al: Regulation of the cutaneous circulation. *Fed Proc* **45**:2841-2850, 1986
84. Freedman RR et al: Local temperature modulates alpha-1 and alpha-2 adrenergic vasoconstriction in men. *Am J Physiol Heart Circ Physiol* **263**:H1197-H1200, 1993

85. Yamazaki F et al: Rate dependency and role of nitric oxide in the vascular response to direct cooling in human skin. *J Appl Physiol* **100**:42-50, 2006
86. Hodges GJ et al: The involvement of nitric oxide in the cutaneous vasoconstrictor response to local cooling in humans. *J Physiol (London)* **573.3**:849-857, 2006
87. Sawka MN, Wenger CB, Pandolf KB: Thermoregulatory responses to acute exercise-heat stress and heat acclimation. In: *Handbook of Physiology Section 4: Environmental physiology*, edited by M Fregly, C Blatteis. New York, Oxford University Press, 1996, p. 157-185
88. Young AJ: *Homeostatic responses to prolonged cold exposure: human cold acclimatization*. In: *Handbook of Physiology Section 4: Environmental physiology*, edited by M Fregly, C Blatteis. New York, Oxford University Press. 1996, p. 419-38
89. Thompson CS, Kenney WL: Altered neurotransmitter control of reflex vasoconstriction in aged human skin. *J Physiol* **558**:697-704, 2004
90. Kenney WL et al: Age and hypohydration independently influence the peripheral vascular response to heat stress. *J Appl Physiol* **68**:1902-1908, 1990