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Photoperiodic encoding by the neuronal network of the suprachiasmatic nucleus

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REFERENCES

- Abe,M., Herzog,E.D., Yamazaki,S., Straume,M., Tei,H., Sakaki,Y., Menaker,M., and Block,G.D. (2002). Circadian rhythms in isolated brain regions. *J. Neurosci.* 22, 350-356.
- Abraham,U., Prior,J.L., Granados-Fuentes,D., Piwnica-Worms,D.R., and Herzog,E.D. (2005). Independent circadian oscillations of *Period1* in specific brain areas in vivo and in vitro. *J. Neurosci.* 25, 8620-8626.
- Abrahamson,E.E. and Moore,R.Y. (2001). Suprachiasmatic nucleus in the mouse: retinal innervation, intrinsic organization and efferent projections. *Brain Res.* 916, 172-191.
- Abrahamson,E.E. and Moore,R.Y. (2006). Lesions of suprachiasmatic nucleus efferents selectively affect rest-activity rhythm. *Mol. Cell Endocrinol.* 252, 46-56.
- Aida,R., Moriya,T., Araki,M., Akiyama,M., Wada,K., Wada,E., and Shibata,S. (2002). Gastrin-releasing peptide mediates photic entrainable signals to dorsal subsets of suprachiasmatic nucleus via induction of *Period* gene in mice. *Mol. Pharmacol.* 61, 26-34.
- Akiyama,M., Kouzu,Y., Takahashi,S., Wakamatsu,H., Moriya,T., Maetani,M., Watanabe,S., Tei,H., Sakaki,Y., and Shibata,S. (1999). Inhibition of light- or glutamate-induced *mPer1* expression represses the phase shifts into the mouse

- circadian locomotor and suprachiasmatic firing rhythms. *J. Neurosci.* *19*, 1115-1121.
- Albrecht,U., Sun,Z.S., Eichele,G., and Lee,C.C. (1997). A differential response of two putative mammalian circadian regulators, mper1 and mper2, to light. *Cell* *91*, 1055-1064.
- Albus,H., Bonnefont,X., Chaves,I., Yasui,A., Doczy,J., van der Horst,G.T., and Meijer,J.H. (2002). Cryptochrome-deficient mice lack circadian electrical activity in the suprachiasmatic nuclei. *Curr. Biol.* *12*, 1130-1133.
- Albus,H., Vansteensel,M.J., Michel,S., Block,G.D., and Meijer,J.H. (2005). A GABAergic mechanism is necessary for coupling dissociable ventral and dorsal regional oscillators within the circadian clock. *Curr. Biol.* *15*, 886-893.
- Allada,R., Emery,P., Takahashi,J.S., and Rosbash,M. (2001). Stopping time: the genetics of fly and mouse circadian clocks. *Annu. Rev. Neurosci.* *24*, 1091-1119.
- Asai,M., Yamaguchi,S., Isejima,H., Jonouchi,M., Moriya,T., Shibata,S., Kobayashi,M., and Okamura,H. (2001). Visualization of mPer1 transcription in vitro: NMDA induces a rapid phase shift of mPer1 gene in cultured SCN. *Curr. Biol.* *11*, 1524-1527.
- Aschoff,J. and Pohl,H. (1978). Phase relations between a circadian rhythm and its zeitgeber within the range of entrainment. *Naturwissenschaften* *65*, 80-84.
- Aton,S.J., Colwell,C.S., Harmar,A.J., Waschek,J., and Herzog,E.D. (2005). Vasoactive intestinal polypeptide mediates circadian rhythmicity and synchrony in mammalian clock neurons. *Nat. Neurosci.* *8*, 476-483.
- Aton,S.J., Huettnner,J.E., Straume,M., and Herzog,E.D. (2006). GABA and Gi/o differentially control circadian rhythms and synchrony in clock neurons. *Proc. Natl. Acad. Sci. U. S. A* *103*, 19188-19193.
- Bao,A.M., Meynen,G., and Swaab,D.F. (2008). The stress system in depression and neurodegeneration: focus on the human hypothalamus. *Brain Res. Rev.* *57*, 531-553.
- Barnard,A.R., Hattar,S., Hankins,M.W., and Lucas,R.J. (2006). Melanopsin regulates visual processing in the mouse retina. *Curr Biol* *16*, 389-395.
- Bayliss,D.A. and Barrett,P.Q. (2008). Emerging roles for two-pore-domain potassium channels and their potential therapeutic impact. *Trends Pharmacol. Sci.* *29*, 566-575.

- Beersma,D.G., van Bunnik,B.A., Hut,R.A., and Daan,S. (2008). Emergence of circadian and photoperiodic system level properties from interactions among pacemaker cells. *J. Biol. Rhythms* 23, 362-373.
- Belenky,M.A., Yarom,Y., and Pickard,G.E. (2008). Heterogeneous expression of gamma-aminobutyric acid and gamma-aminobutyric acid-associated receptors and transporters in the rat suprachiasmatic nucleus. *J. Comp Neurol.* 506, 708-732.
- Belle,M.D., Diekman,C.O., Forger,D.B., and Piggins,H.D. (2009). Daily electrical silencing in the mammalian circadian clock. *Science* 326, 281-284.
- Bendova,Z. and Sumova,S. (2006). Photoperiodic regulation of PER1 and PER2 protein expression in rat peripheral tissues. *Physiol. Res.* 55, 623-632.
- Bergeron,H.E., Danielson,B., Biggs,K.R., and Prosser,R.A. (1999). TTX blocks baclofen-induced phase shifts of the mammalian circadian pacemaker in vitro. *Brain Res.* 841, 193-196.
- Berson,D.M., Dunn,F.A., and Takao,M. (2002). Phototransduction by retinal ganglion cells that set the circadian clock. *Science* 295, 1070-1073.
- Best,J.D., Maywood,E.S., Smith,K.L., and Hastings,M.H. (1999). Rapid resetting of the mammalian circadian clock. *J. Neurosci.* 19, 828-835.
- Biello,S.M., Golombek,D.A., and Harrington,M.E. (1997). Neuropeptide Y and glutamate block each other's phase shifts in the suprachiasmatic nucleus in vitro. *Neuroscience* 77, 1049-1057.
- Bouskila,Y. and Dudek,F.E. (1993). Neuronal synchronization without calcium-dependent synaptic transmission in the hypothalamus. *Proc. Natl. Acad. Sci. U. S. A.* 90, 3207-3210.
- Brown,T.M., Banks,J.R., and Piggins,H.D. (2006). A novel suction electrode recording technique for monitoring circadian rhythms in single and multiunit discharge from brain slices. *J. Neurosci.* 156, 173-181.
- Brown,T.M., Colwell,C.S., Waschek,J.A., and Piggins,H.D. (2007). Disrupted neuronal activity rhythms in the suprachiasmatic nuclei of vasoactive intestinal polypeptide-deficient mice. *J. Neurophysiol.* 97, 2553-2558.
- Brown,T.M., Hughes,A.T., and Piggins,H.D. (2005). Gastrin-releasing peptide promotes suprachiasmatic nuclei cellular rhythmicity in the absence of

- vasoactive intestinal polypeptide-VPAC2 receptor signaling. *J. Neurosci.* 25, 11155-11164.
- Brown,T.M. and Piggins,H.D. (2007). Electrophysiology of the suprachiasmatic circadian clock. *Prog. Neurobiol.* 82, 229-255.
- Brown,T.M. and Piggins,H.D. (2009). Spatiotemporal Heterogeneity in the Electrical Activity of Suprachiasmatic Nuclei Neurons and their Response to Photoperiod. *J. Biol. Rhythms* 24, 44-54.
- Bunger,M.K., Wilsbacher,L.D., Moran,S.M., Clendenin,C., Radcliffe,L.A., Hogenesch,J.B., Simon,M.C., Takahashi,J.S., and Bradfield,C.A. (2000). *Mop3* is an essential component of the master circadian pacemaker in mammals. *Cell* 103, 1009-1017.
- Burgoon,P.W., Lindberg,P.T., and Gillette,M.U. (2004). Different patterns of circadian oscillation in the suprachiasmatic nucleus of hamster, mouse, and rat. *J. Comp. Physiol. A Neuroethol Sens Neural Behav. Physiol* 190, 167-171.
- Cao,G. and Nitabach,M.N. (2008). Circadian control of membrane excitability in *Drosophila melanogaster* lateral ventral clock neurons. *J. Neurosci.* 28, 6493-6501.
- Card,J.P. and Moore,R.Y. (1984). The suprachiasmatic nucleus of the golden hamster: immunohistochemical analysis of cell and fiber distribution. *Neuroscience* 13, 415-431.
- Carr,A.J., Johnston,J.D., Semikhodskii,A.G., Nolan,T., Cagampang,F.R., Stirland,J.A., and Loudon,A.S. (2003). Photoperiod differentially regulates circadian oscillators in central and peripheral tissues of the Syrian hamster. *Curr. Biol.* 13, 1543-1548.
- Challet,E., Scarbrough,K., Penev,P.D., and Turek,F.W. (1998). Roles of suprachiasmatic nuclei and intergeniculate leaflets in mediating the phase-shifting effects of a serotonergic agonist and their photic modulation during subjective day. *J. Biol. Rhythms* 13, 410-421.
- Cheng,M.Y., Bullock,C.M., Li,C., Lee,A.G., Bermak,J.C., Belluzzi,J., Weaver,D.R., Leslie,F.M., and Zhou,Q.Y. (2002). Prokineticin 2 transmits the behavioural circadian rhythm of the suprachiasmatic nucleus. *Nature* 417, 405-410.

- Choi,H.J., Lee,C.J., Schroeder,A., Kim,Y.S., Jung,S.H., Kim,J.S., Kim,d.Y., Son,E.J., Han,H.C., Hong,S.K., Colwell,C.S., and Kim,Y.I. (2008). Excitatory actions of GABA in the suprachiasmatic nucleus. *J. Neurosci.* 28, 5450-5459.
- Colwell,C.S. (2005). Bridging the gap: coupling single-cell oscillators in the suprachiasmatic nucleus. *Nat. Neurosci.* 8, 10-12.
- Colwell,C.S., Foster,R.G., and Menaker,M. (1991). NMDA receptor antagonists block the effects of light on circadian behavior in the mouse. *Brain Res.* 554, 105-110.
- Colwell,C.S., Michel,S., Itri,J., Rodriguez,W., Tam,J., Lelievre,V., Hu,Z., Liu,X., and Waschek,J.A. (2003). Disrupted circadian rhythms in VIP- and PHI-deficient mice. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 285, R939-R949.
- Colwell,C.S., Ralph,M.R., and Menaker,M. (1990). Do NMDA receptors mediate the effects of light on circadian behavior? *Brain Res.* 523, 117-120.
- Daan,S., Mellow,M., and Roenneberg,T. (2002). External time--internal time. *J. Biol. Rhythms* 17, 107-109.
- Daan,S. and Pittendrigh,C.S. (1976a). A functional analysis of circadian pacemakers in nocturnal rodents. II. The variability of phase response curves. *J. Comp. Physiol.* 106, 267-290.
- Daan,S. and Pittendrigh,C.S. (1976b). A functional analysis of circadian pacemakers in nocturnal rodents. III. Heavy Water and Constant Light: Homeostasis of Frequency? *Journal of Comparative Physiology ? A* 106, 267-290.
- Dacey,D.M., Liao,H.W., Peterson,B.B., Robinson,F.R., Smith,V.C., Pokorny,J., Yau,K.W., and Gamlin,P.D. (2005). Melanopsin-expressing ganglion cells in primate retina signal colour and irradiance and project to the LGN. *Nature* 433, 749-754.
- Dardente,H. and Cermakian,N. (2007). Molecular circadian rhythms in central and peripheral clocks in mammals. *Chronobiol. Int.* 24, 195-213.
- Dardente,H., Poirel,V.J., Klosen,P., Pevet,P., and Masson-Pevet,M. (2002). Per and neuropeptide expression in the rat suprachiasmatic nuclei: compartmentalization and differential cellular induction by light. *Brain Res.* 958, 261-271.

- Davidson,A.J., Yamazaki,S., and Menaker,M. (2003). SCN: ringmaster of the circadian circus or conductor of the circadian orchestra? *Novartis Found. Symp.* 253, 110-121.
- De Jeu,M. and Pennartz,C. (2002). Circadian modulation of GABA function in the rat suprachiasmatic nucleus: excitatory effects during the night phase. *J. Neurophysiol.* 87, 834-844.
- de la Iglesia,H.O., Meyer,J., Carpino,A., Jr., and Schwartz,W.J. (2000). Antiphase oscillation of the left and right suprachiasmatic nuclei. *Science* 290, 799-801.
- de la Iglesia,H.O., Meyer,J., and Schwartz,W.J. (2004). Using *Per* gene expression to search for photoperiodic oscillators in the hamster suprachiasmatic nucleus. *Brain Res. Mol. Brain Res.* 127, 121-127.
- de Vries,M.J., Treep,J.A., de Pauw,E.S., and Meijer,J.H. (1994). The effects of electrical stimulation of the optic nerves and anterior optic chiasm on the circadian activity rhythm of the Syrian hamster: involvement of excitatory amino acids. *Brain Res.* 642, 206-212.
- Deboer,T., Vansteensel,M.J., Detari,L., and Meijer,J.H. (2003). Sleep states alter activity of suprachiasmatic nucleus neurons. *Nat. Neurosci.* 6, 1086-1090.
- DeCoursey,P.J. (1964). Function of a light response rhythm in hamsters. *J Cell Physiol* 63, 189-196.
- DeCoursey,P.J. and Krulas,J.R. (1998). Behavior of SCN-lesioned chipmunks in natural habitat: a pilot study. *J. Biol. Rhythms* 13, 229-244.
- DeCoursey,P.J., Krulas,J.R., Mele,G., and Holley,D.C. (1997). Circadian performance of suprachiasmatic nuclei (SCN)-lesioned antelope ground squirrels in a desert enclosure. *Physiol. Behav.* 62, 1099-1108.
- DeCoursey,P.J., Walker,J.K., and Smith,S.A. (2000). A circadian pacemaker in free-living chipmunks: essential for survival? *J. Comp. Physiol. [A].* 186, 169-180.
- Ding,J.M., Chen,D., Weber,E.T., Faiman,L.E., Rea,M.A., and Gillette,M.U. (1994). Resetting the biological clock: mediation of nocturnal circadian shifts by glutamate and NO. *Science* 266, 1713-1717.
- Doyle,S.E., Castrucci,A.M., McCall,M., Provencio,I., and Menaker,M. (2006). Nonvisual light responses in the *Rpe65* knockout mouse: rod loss restores

- sensitivity to the melanopsin system. *Proc Natl Acad Sci U. S. A* *103*, 10432-10437.
- Drouyer,E., Rieux,C., Hut,R.A., and Cooper,H.M. (2007). Responses of suprachiasmatic nucleus neurons to light and dark adaptation: relative contributions of melanopsin and rod-cone inputs. *J. Neurosci.* *27*, 9623-9631.
- Dudek,F.E., Kim,Y.I., and Bouskila,Y. (1993). Electrophysiology of the suprachiasmatic nucleus: synaptic transmission, membrane properties, and neuronal synchronization. *J. Biol. Rhythms* *8 Suppl*, S33-S37.
- Duncan,M.J. (2006). Aging of the Mammalian Circadian Timing System: Changes in the Central Pacemaker and Its Regulation by Photic and Nonphotic Signals. *Neuroembryology and Aging* *4*, 85-101.
- Eilers,P.H.C. (2003). A perfect smoother. *Anal. Chem.* *75*, 3631-3636.
- Eskes,G.A. and Rusak,B. (1985). Horizontal knife cuts in the suprachiasmatic area prevent hamster gonadal responses to photoperiod. *Neurosci. Lett.* *61*, 261-266.
- Evans,J.A., Elliott,J.A., and Gorman,M.R. (2004). Photoperiod differentially modulates photic and nonphotic phase response curves of hamsters. *Am J Physiol Regul Integr. Comp Physiol* *286*, R539-R546.
- Fee,M.S., Mitra,P.P., and Kleinfeld,D. (1996). Automatic sorting of multiple unit neuronal signals in the presence of anisotropic and non-Gaussian variability. *J. Neurosci. Methods* *69*, 175-188.
- Foster,R.G., Provencio,I., Hudson,D., Fiske,S., De,G.W., and Menaker,M. (1991). Circadian photoreception in the retinally degenerate mouse (rd/rd). *J Comp Physiol A* *169*, 39-50.
- Gekakis,N., Staknis,D., Nguyen,H.B., Davis,F.C., Wilsbacher,L.D., King,D.P., Takahashi,J.S., and Weitz,C.J. (1998). Role of the CLOCK protein in the mammalian circadian mechanism. *Science* *280*, 1564-1569.
- Gillette,M.U. (1986). The suprachiasmatic nuclei: circadian phase-shifts induced at the time of hypothalamic slice preparation are preserved in vitro. *Brain Res.* *379*, 176-181.
- Gillette,M.U., DeMarco,S.J., Ding,J.M., Gallman,E.A., Faiman,L.E., Liu,C., McArthur,A.J., Medanic,M., Richard,D., and Tchong,T.K. (1993). The organization of the suprachiasmatic circadian pacemaker of the rat and its

- regulation by neurotransmitters and modulators. *J. Biol. Rhythms* 8 *Suppl*, S53-S58.
- Gillette, M.U., Medanic, M., McArthur, A.J., Liu, C., Ding, J.M., Faiman, L.E., Weber, E.T., Tchong, T.K., and Gallman, E.A. (1995). Intrinsic neuronal rhythms in the suprachiasmatic nuclei and their adjustment. *Ciba Found. Symp.* 183, 134-144.
- Gillette, M.U. and Prosser, R.A. (1988). Circadian rhythm of the rat suprachiasmatic brain slice is rapidly reset by daytime application of cAMP analogs. *Brain Res.* 474, 348-352.
- Goldman, B.D. (2001). Mammalian photoperiodic system: formal properties and neuroendocrine mechanisms of photoperiodic time measurement. *J. Biol. Rhythms* 16, 283-301.
- Gorman, M.R., Goldman, B.D., and Zucker, I. (2001). Mammalian Photoperiodism. In *Circadian Clocks*, J.S. Takahashi, F.W. Turek, and R.Y. Moore, eds. (New York: Kluwer Academic / Plenum Publishers), pp. 481-510.
- Green, D.J. and Gillette, R. (1982). Circadian Rhythm of Firing Rate Recorded from Single Cells in the Rat Suprachiasmatic Brain Slice. *Brain Res.* 245, 198-200.
- Gribkoff, V.K., Pieschl, R.L., Wisialowski, T.A., van den Pol, A.N., and Yocca, F.D. (1998). Phase shifting of circadian rhythms and depression of neuronal activity in the rat suprachiasmatic nucleus by neuropeptide Y: mediation by different receptor subtypes. *J. Neurosci.* 18, 3014-3022.
- Groos, G. and Hendriks, J. (1982). Circadian rhythms in electrical discharge of rat suprachiasmatic neurones recorded in vitro. *Neurosci. Lett.* 34, 283-288.
- Groos, G.A. and Meijer, J.H. (1985). Effects of illumination on suprachiasmatic nucleus electrical discharge. *Ann. N. Y. Acad. Sci.* 453, 134-146.
- Güler, A.D., Ecker, J.L., Lall, G.S., Haq, S., Altimus, C.M., Liao, H.W., Barnard, A.R., Cahill, H., Badea, T.C., Zhao, H., Hankins, M.W., Berson, D.M., Lucas, R.J., Yau, K.W., and Hattar, S. (2008). Melanopsin cells are the principal conduits for rod-cone input to non-image-forming vision. *Nature* 453, 102-105.
- Hannibal, J. (2002). Neurotransmitters of the retino-hypothalamic tract. *Cell Tissue Res.* 309, 73-88.

- Hannibal,J. (2006). Roles of PACAP-containing retinal ganglion cells in circadian timing. *Int. Rev. Cytol.* *251*, 1-39.
- Hannibal,J. and Fahrenkrug,J. (2002). Melanopsin: a novel photopigment involved in the photoentrainment of the brain's biological clock? *Ann. Med.* *34*, 401-407.
- Härmä,M.I., Hakola,T., Akerstedt,T., and Laitinen,J.T. (1994). Age and adjustment to night work. *Occup. Environ. Med.* *51*, 568-573.
- Harmar,A.J., Marston,H.M., Shen,S., Spratt,C., West,K.M., Sheward,W.J., Morrison,C.F., Dorin,J.R., Piggins,H.D., Reubi,J.C., Kelly,J.S., Maywood,E.S., and Hastings,M.H. (2002). The VPAC(2) receptor is essential for circadian function in the mouse suprachiasmatic nuclei. *Cell* *109*, 497-508.
- Harrington,M.E., Hoque,S., Hall,A., Golombek,D., and Biello,S. (1999). Pituitary adenylate cyclase activating peptide phase shifts circadian rhythms in a manner similar to light. *J. Neurosci.* *19*, 6637-6642.
- Harrington,M.E. and Rusak,B. (1986). Lesions of the thalamic intergeniculate leaflet alter hamster circadian rhythms. *J Biol Rhythms* *1*, 309-325.
- Harrington,M.E. and Rusak,B. (1988). Ablation of the geniculo-hypothalamic tract alters circadian activity rhythms of hamsters housed under constant light. *Physiol. Behav.* *42*, 183-189.
- Hastings,M.H., Field,M.D., Maywood,E.S., Weaver,D.R., and Reppert,S.M. (1999). Differential regulation of mPER1 and mTIM proteins in the mouse suprachiasmatic nuclei: new insights into a core clock mechanism. *J. Neurosci.* *19*, RC11.
- Hastings,M.H. and Herzog,E.D. (2004). Clock genes, oscillators, and cellular networks in the suprachiasmatic nuclei. *J. Biol. Rhythms* *19*, 400-413.
- Hazlerigg,D.G., Ebling,F.J., and Johnston,J.D. (2005). Photoperiod differentially regulates gene expression rhythms in the rostral and caudal SCN. *Curr. Biol.* *15*, R449-R450.
- Herzog,E.D., Aton,S.J., Numano,R., Sakaki,Y., and Tei,H. (2004). Temporal precision in the mammalian circadian system: a reliable clock from less reliable neurons. *J. Biol. Rhythms* *19*, 35-46.

- Herzog,E.D., Geusz,M.E., Khalsa,S.B., Straume,M., and Block,G.D. (1997). Circadian rhythms in mouse suprachiasmatic nucleus explants on multimicroelectrode plates. *Brain Res.* 757, 285-290.
- Herzog,E.D., Takahashi,J.S., and Block,G.D. (1998). Clock controls circadian period in isolated suprachiasmatic nucleus neurons. *Nat. Neurosci.* 1, 708-713.
- Hong,H.K., Chong,J.L., Song,W., Song,E.J., Jyawook,A.A., Schook,A.C., Ko,C.H., and Takahashi,J.S. (2007). Inducible and reversible Clock gene expression in brain using the tTA system for the study of circadian behavior. *PLoS Genet.* 3, e33.
- Honma,S., Honma,K., and Hiroshige,T. (1984). Dissociation of circadian rhythms in rats with a hypothalamic island. *Am J Physiol* 246, R949-R954.
- Honma,S., Shirakawa,T., Katsuno,Y., Namihira,M., and Honma,K. (1998). Circadian periods of single suprachiasmatic neurons in rats. *Neurosci. Lett.* 250, 157-160.
- Inagaki,N., Honma,S., Ono,D., Tanahashi,Y., and Honma,K. (2007). Separate oscillating cell groups in mouse suprachiasmatic nucleus couple photoperiodically to the onset and end of daily activity. *Proc. Natl. Acad. Sci. U. S. A.* 104, 7664-7669.
- Indic,P., Schwartz,W.J., Herzog,E.D., Foley,N.C., and Antle,M.C. (2007). Modeling the behavior of coupled cellular circadian oscillators in the suprachiasmatic nucleus. *J. Biol. Rhythms* 22, 211-219.
- Inouye,S. and Kawamura,H. (1982). Characteristics of a circadian pacemaker in the suprachiasmatic nucleus. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology* 146, 153-160.
- Inouye,S.T. and Kawamura,H. (1979). Persistence of circadian rhythmicity in a mammalian hypothalamic "island" containing the suprachiasmatic nucleus. *Proc. Natl. Acad. Sci. U. S. A.* 76, 5962-5966.
- Itri,J.N., Michel,S., Vansteensel,M.J., Meijer,J.H., and Colwell,C.S. (2005). Fast delayed rectifier potassium current is required for circadian neural activity. *Nat. Neurosci.* 8, 650-656.
- Jac,M., Sumova,A., and Illnerova,H. (2000). c-Fos rhythm in subdivisions of the rat suprachiasmatic nucleus under artificial and natural photoperiods. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 279, R2270-R2276.

- Jagota,A., de la Iglesia,H.O., and Schwartz,W.J. (2000). Morning and evening circadian oscillations in the suprachiasmatic nucleus in vitro. *Nat. Neurosci.* *3*, 372-376.
- Jiang,Z.G., Yang,Y.Q., and Allen,C.N. (1997). Tracer and electrical coupling of rat suprachiasmatic nucleus neurons. *Neuroscience* *77*, 1059-1066.
- Johnson,C.H. (1999). Forty years of PRCs--what have we learned? *Chronobiol. Int.* *16*, 711-743.
- Johnson,C.H., Mori,T., and Xu,Y. (2008). A cyanobacterial circadian clockwork. *Curr Biol* *18*, R816-R825.
- Johnson,M.S. (1926). Activity and distribution of certain wild mice in relation to biotic communities. *J. Mammal.* *7*, 245-277.
- Johnson,M.S. (1939). Effects of continuous light on periodic spontaneous activity of white-footed mice (*Peromyscus*). *J. Exp. Zool.* *82*, 315-328.
- Johnston,J.D. (2005). Measuring seasonal time within the circadian system: regulation of the suprachiasmatic nuclei by photoperiod. *J. Neuroendocrinol.* *17*, 459-465.
- Johnston,J.D., Ebling,F.J., and Hazlerigg,D.G. (2005). Photoperiod regulates multiple gene expression in the suprachiasmatic nuclei and pars tuberalis of the Siberian hamster (*Phodopus sungorus*). *Eur. J. Neurosci.* *21*, 2967-2974.
- Kalsbeek,A., Foppen,E., Scholij,I., Van,H.C., van,d., V, Fliers,E., and Buijs,R.M. (2008). Circadian control of the daily plasma glucose rhythm: an interplay of GABA and glutamate. *PLoS One.* *3*, e3194.
- Kalsbeek,A., Palm,I.F., La Fleur,S.E., Scheer,F.A., Perreau-Lenz,S., Ruiter,M., Kreier,F., Cailotto,C., and Buijs,R.M. (2006). SCN outputs and the hypothalamic balance of life. *J. Biol. Rhythms* *21*, 458-469.
- Kim,D.Y., Kang,H.C., Shin,H.C., Lee,K.J., Yoon,Y.W., Han,H.C., Na,H.S., Hong,S.K., and Kim,Y.I. (2001). Substance p plays a critical role in photic resetting of the circadian pacemaker in the rat hypothalamus. *J. Neurosci.* *21*, 4026-4031.
- King,V.M., Chahad-Ehlers,S., Shen,S., Harmar,A.J., Maywood,E.S., and Hastings,M.H. (2003). A hVIPR transgene as a novel tool for the analysis of circadian function in the mouse suprachiasmatic nucleus. *Eur. J. Neurosci.* *17*, 822-832.

- Klein,D.C. and Moore,R.Y. (1979). Pineal N-acetyltransferase and hydroxyindole-O-methyltransferase: control by the retinohypothalamic tract and the suprachiasmatic nucleus. *Brain Res.* 174, 245-262.
- Ko,C.H. and Takahashi,J.S. (2006). Molecular components of the mammalian circadian clock. *Hum. Mol. Genet.* 15 *Spec No 2*, R271-R277.
- Kopp,M.D., Meissl,H., Dehghani,F., and Korf,H.W. (2001). The pituitary adenylate cyclase-activating polypeptide modulates glutamatergic calcium signalling: investigations on rat suprachiasmatic nucleus neurons. *J. Neurochem.* 79, 161-171.
- Kramer,A., Yang,F.C., Snodgrass,P., Li,X., Scammell,T.E., Davis,F.C., and Weitz,C.J. (2001). Regulation of daily locomotor activity and sleep by hypothalamic EGF receptor signaling. *Science* 294, 2511-2515.
- Kuhlman,S.J. and McMahon,D.G. (2004). Rhythmic regulation of membrane potential and potassium current persists in SCN neurons in the absence of environmental input. *Eur. J. Neurosci.* 20, 1113-1117.
- Kuhlman,S.J. and McMahon,D.G. (2006). Encoding the ins and outs of circadian pacemaking. *J. Biol. Rhythms* 21, 470-481.
- Kuhlman,S.J., Silver,R., Le Sauter,J., Bult-Ito,A., and McMahon,D.G. (2003). Phase resetting light pulses induce *Per1* and persistent spike activity in a subpopulation of biological clock neurons. *J. Neurosci.* 23, 1441-1450.
- Kume,K., Zylka,M.J., Sriram,S., Shearman,L.P., Weaver,D.R., Jin,X., Maywood,E.S., Hastings,M.H., and Reppert,S.M. (1999). *mCRY1* and *mCRY2* are essential components of the negative limb of the circadian clock feedback loop. *Cell* 98, 193-205.
- Lee,C., Etchegaray,J.P., Cagampang,F.R., Loudon,A.S., and Reppert,S.M. (2001). Posttranslational mechanisms regulate the mammalian circadian clock. *Cell* 107, 855-867.
- Lewicki,M.S. (1998). A review of methods for spike sorting: the detection and classification of neural action potentials. *Network.* 9, R53-R78.
- Lincoln,G., Messenger,S., Andersson,H., and Hazlerigg,D. (2002). Temporal expression of seven clock genes in the suprachiasmatic nucleus and the pars tuberalis of the sheep: evidence for an internal coincidence timer. *Proc. Natl. Acad. Sci. U. S. A.* 99, 13890-13895.

- Linden,A.M., Sandu,C., Aller,M.I., Vekovischeva,O.Y., Rosenberg,P.H., Wisden,W., and Korpi,E.R. (2007). TASK-3 Knockout Mice Exhibit Exaggerated Nocturnal Activity, Impairments in Cognitive Functions, and Reduced Sensitivity to Inhalation Anesthetics. *J. Pharmacol. Exp. Ther.* 323, 924-934.
- Liu,A.C., Welsh,D.K., Ko,C.H., Tran,H.G., Zhang,E.E., Priest,A.A., Buhr,E.D., Singer,O., Meeker,K., Verma,I.M., Doyle,F.J., III, Takahashi,J.S., and Kay,S.A. (2007). Intercellular Coupling Confers Robustness against Mutations in the SCN Circadian Clock Network. *Cell* 129, 605-616.
- Liu,C. and Gillette,M.U. (1996). Cholinergic regulation of the suprachiasmatic nucleus circadian rhythm via a muscarinic mechanism at night. *J. Neurosci.* 16, 744-751.
- Liu,C. and Reppert,S.M. (2000). GABA synchronizes clock cells within the suprachiasmatic circadian clock. *Neuron* 25, 123-128.
- Liu,C., Weaver,D.R., Jin,X., Shearman,L.P., Pieschl,R.L., Gribkoff,V.K., and Reppert,S.M. (1997a). Molecular dissection of two distinct actions of melatonin on the suprachiasmatic circadian clock. *Neuron* 19, 91-102.
- Liu,C., Weaver,D.R., Strogatz,S.H., and Reppert,S.M. (1997b). Cellular construction of a circadian clock: period determination in the suprachiasmatic nuclei. *Cell* 91, 855-860.
- Long,M.A., Jutras,M.J., Connors,B.W., and Burwell,R.D. (2005). Electrical synapses coordinate activity in the suprachiasmatic nucleus. *Nat. Neurosci.* 8, 61-66.
- Low-Zeddies,S.S. and Takahashi,J.S. (2001). Chimera analysis of the Clock mutation in mice shows that complex cellular integration determines circadian behavior. *Cell* 105, 25-42.
- Lowrey,P.L., Shimomura,K., Antoch,M.P., Yamazaki,S., Zemenides,P.D., Ralph,M.R., Menaker,M., and Takahashi,J.S. (2000). Positional syntenic cloning and functional characterization of the mammalian circadian mutation tau. *Science* 288, 483-492.
- Lowrey,P.L. and Takahashi,J.S. (2000). Genetics of the mammalian circadian system: Photic entrainment, circadian pacemaker mechanisms, and posttranslational regulation. *Annu. Rev. Genet.* 34, 533-562.

- Lucas,R.J., Freedman,M.S., Lupi,D., Munoz,M., vid-Gray,Z.K., and Foster,R.G. (2001). Identifying the photoreceptive inputs to the mammalian circadian system using transgenic and retinally degenerate mice. *Behav. Brain Res.* 125, 97-102.
- Lucas,R.J., Hattar,S., Takao,M., Berson,D.M., Foster,R.G., and Yau,K.W. (2003). Diminished pupillary light reflex at high irradiances in melanopsin-knockout mice. *Science* 299, 245-247.
- Lucassen,P.J., Hofman,M.A., and Swaab,D.F. (1995). Increased light intensity prevents the age related loss of vasopressin-expressing neurons in the rat suprachiasmatic nucleus. *Brain Res.* 693, 261-266.
- Lucassen,P.J., Tilders,F.J., Salehi,A., and Swaab,D.F. (1997). Neuropeptides vasopressin (AVP), oxytocin (OXT) and corticotropin-releasing hormone (CRH) in the human hypothalamus: activity changes in aging, Alzheimer's disease and depression. *Aging (Milano.)* 9, 48-50.
- Lundkvist,G.B. and Block,G.D. (2005). Role of neuronal membrane events in circadian rhythm generation. *Methods Enzymol.* 393, 623-642.
- Lundkvist,G.B., Kwak,Y., Davis,E.K., Tei,H., and Block,G.D. (2005). A calcium flux is required for circadian rhythm generation in mammalian pacemaker neurons. *J. Neurosci.* 25, 7682-7686.
- Mason,R. and Rusak,B. (1990). Neurophysiological responses to melatonin in the SCN of short-day sensitive and refractory hamsters. *Brain Res.* 533, 15-19.
- Maywood,E.S., Reddy,A.B., Wong,G.K., O'Neill,J.S., O'Brien,J.A., McMahon,D.G., Hattar,A.J., Okamura,H., and Hastings,M.H. (2006). Synchronization and maintenance of timekeeping in suprachiasmatic circadian clock cells by neuropeptidergic signaling. *Curr. Biol.* 16, 599-605.
- McArthur,A.J., Coogan,A.N., Ajpru,S., Sugden,D., Biello,S.M., and Piggins,H.D. (2000). Gastrin-releasing peptide phase-shifts suprachiasmatic nuclei neuronal rhythms in vitro. *J. Neurosci.* 20, 5496-5502.
- McArthur,A.J., Gillette,M.U., and Prosser,R.A. (1991). Melatonin directly resets the rat suprachiasmatic circadian clock in vitro. *Brain Res.* 565, 158-161.
- Meijer,J.H. (2001). Photic Entrainment in Mammals. In *Circadian Clocks*, J.S.Takahashi, F.W.Turek, and R.Y.Moore, eds. (New York: Kluwer Academic / Plenum Publishers), pp. 183-222.

- Meijer, J.H., Groos, G.A., and Rusak, B. (1986). Luminance coding in a circadian pacemaker: the suprachiasmatic nucleus of the rat and the hamster. *Brain Res.* 382, 109-118.
- Meijer, J.H. and Rietveld, W.J. (1989). Neurophysiology of the suprachiasmatic circadian pacemaker in rodents. *Physiol. Rev.* 69, 671-707.
- Meijer, J.H., Schaap, J., Watanabe, K., and Albus, H. (1997). Multiunit activity recordings in the suprachiasmatic nuclei: in vivo versus in vitro models. *Brain Res.* 753, 322-327.
- Meijer, J.H., Thio, B., Albus, H., Schaap, J., and Ruijs, A.C. (1999). Functional absence of extraocular photoreception in hamster circadian rhythm entrainment. *Brain Res.* 831, 337-339.
- Meijer, J.H., Watanabe, K., Detari, L., and Schaap, J. (1996). Circadian rhythm in light response in suprachiasmatic nucleus neurons of freely moving rats. *Brain Res.* 741, 352-355.
- Meijer, J.H., Watanabe, K., Schaap, J., Albus, H., and Detari, L. (1998). Light responsiveness of the suprachiasmatic nucleus: long-term multiunit and single-unit recordings in freely moving rats. *J. Neurosci.* 18, 9078-9087.
- Menaker, M. (1971). Rhythms, reproduction, and photoreception. *Biol Reprod* 4, 295-308.
- Meng, Q.J., Logunova, L., Maywood, E.S., Gallego, M., Lebiecki, J., Brown, T.M., Sladek, M., Semikhodskii, A.S., Glossop, N.R., Piggins, H.D., Chesham, J.E., Bechtold, D.A., Yoo, S.H., Takahashi, J.S., Virshup, D.M., Boot-Handford, R.P., Hastings, M.H., and Loudon, A.S. (2008). Setting clock speed in mammals: the CK1 epsilon tau mutation in mice accelerates circadian pacemakers by selectively destabilizing PERIOD proteins. *Neuron* 58, 78-88.
- Meredith, A.L., Wiler, S.W., Miller, B.H., Takahashi, J.S., Fodor, A.A., Ruby, N.F., and Aldrich, R.W. (2006). BK calcium-activated potassium channels regulate circadian behavioral rhythms and pacemaker output. *Nat. Neurosci.* 9, 1041-1049.
- Messenger, S., Hazlerigg, D.G., Mercer, J.G., and Morgan, P.J. (2000). Photoperiod differentially regulates the expression of *Per1* and *ICER* in the pars tuberalis and the suprachiasmatic nucleus of the Siberian hamster. *Eur. J. Neurosci.* 12, 2865-2870.

- Messenger,S., Ross,A.W., Barrett,P., and Morgan,P.J. (1999). Decoding photoperiodic time through Per1 and ICER gene amplitude. *Proc. Natl. Acad. Sci. U. S. A.* *96*, 9938-9943.
- Michel,S., Clark,J.P., Ding,J.M., and Colwell,C.S. (2006). Brain-derived neurotrophic factor and neurotrophin receptors modulate glutamate-induced phase shifts of the suprachiasmatic nucleus. *Eur. J. Neurosci.* *24*, 1109-1116.
- Michel,S., Geusz,M.E., Zaritsky,J.J., and Block,G.D. (1993). Circadian rhythm in membrane conductance expressed in isolated neurons. *Science* *259*, 239-241.
- Michel,S., Manivannan,K., Zaritsky,J.J., and Block,G.D. (1999). A delayed rectifier current is modulated by the circadian pacemaker in Bulla. *J. Biol. Rhythms* *14*, 141-150.
- Miller,J.D., Morin,L.P., Schwartz,W.J., and Moore,R.Y. (1996). New insights into the mammalian circadian clock. *Sleep* *19*, 641-667.
- Moore,R.Y. and Eichler,V.B. (1972). Loss of a circadian adrenal corticosterone rhythm following suprachiasmatic lesions in the rat. *Brain Res.* *42*, 201-206.
- Moore,R.Y. and Klein,D.C. (1974). Visual pathways and the central neural control of a circadian rhythm in pineal serotonin N-acetyltransferase activity. *Brain Res.* *71*, 17-33.
- Moore,R.Y. and Lenn,N.J. (1972). A retinohypothalamic projection in the rat. *J. Comp. Neurol.* *146*, 1-14.
- Morin,L.P. (1994). The circadian visual system. *Brain Res. Brain Res. Rev.* *19*, 102-127.
- Morin,L.P. and Allen,C.N. (2006). The circadian visual system, 2005. *Brain Res. Rev.* *51*, 1-60.
- Mrosovsky,N., Edelstein,K., Hastings,M.H., and Maywood,E.S. (2001). Cycle of period gene expression in a diurnal mammal (*Spermophilus tridecemlineatus*): implications for nonphotic phase shifting. *J. Biol. Rhythms* *16*, 471-478.
- Mrugala,M., Zlomanczuk,P., Jagota,A., and Schwartz,W.J. (2000). Rhythmic multiunit neural activity in slices of hamster suprachiasmatic nucleus reflect prior photoperiod. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* *278*, R987-R994.

- Nagano,M., Adachi,A., Nakahama,K., Nakamura,T., Tamada,M., Meyer-Bernstein,E., Sehgal,A., and Shigeyoshi,Y. (2003). An abrupt shift in the day/night cycle causes desynchrony in the mammalian circadian center. *J. Neurosci.* 23, 6141-6151.
- Naito,E., Watanabe,T., Tei,H., Yoshimura,T., and Ebihara,S. (2008). Reorganization of the suprachiasmatic nucleus coding for day length. *J. Biol. Rhythms* 23, 140-149.
- Nakamura,W., Honma,S., Shirakawa,T., and Honma,K. (2001). Regional pacemakers composed of multiple oscillator neurons in the rat suprachiasmatic nucleus. *Eur. J. Neurosci.* 14, 666-674.
- Nakamura,W., Yamazaki,S., Takasu,N.N., Mishima,K., and Block,G.D. (2005). Differential response of Period 1 expression within the suprachiasmatic nucleus. *J. Neurosci.* 25, 5481-5487.
- Nelson,R.J. and Zucker,I. (1981). Photoperiodic control of reproduction in olfactory-bulbectomized rats. *Neuroendocrinology* 32, 266-271.
- Nitabach,M.N., Blau,J., and Holmes,T.C. (2002). Electrical silencing of *Drosophila* pacemaker neurons stops the free-running circadian clock. *Cell* 109, 485-495.
- Nuesslein-Hildesheim,B., O'Brien,J.A., Ebling,F.J., Maywood,E.S., and Hastings,M.H. (2000). The circadian cycle of mPER clock gene products in the suprachiasmatic nucleus of the siberian hamster encodes both daily and seasonal time. *Eur. J. Neurosci.* 12, 2856-2864.
- Nygård,M. and Palomba,M. (2006). The GABAergic network in the suprachiasmatic nucleus as a key regulator of the biological clock: does it change during senescence? *Chronobiol. Int.* 23, 427-435.
- Ohta,H., Yamazaki,S., and McMahon,D.G. (2005). Constant light desynchronizes mammalian clock neurons. *Nat. Neurosci.* 8, 267-269.
- Okamura,H., Miyake,S., Sumi,Y., Yamaguchi,S., Yasui,A., Muijtjens,M., Hoeijmakers,J.H., and van der Horst,G.T. (1999). Photic induction of mPer1 and mPer2 in cry-deficient mice lacking a biological clock. *Science* 286, 2531-2534.
- Panda,S. and Hogenesch,J.B. (2004). It's all in the timing: many clocks, many outputs. *J. Biol. Rhythms* 19, 374-387.

- Panda,S., Provencio,I., Tu,D.C., Pires,S.S., Rollag,M.D., Castrucci,A.M., Pletcher,M.T., Sato,T.K., Wiltshire,T., Andahazy,M., Kay,S.A., Van Gelder,R.N., and Hogenesch,J.B. (2003). Melanopsin is required for non-image-forming photic responses in blind mice. *Science* 301, 525-527.
- Paxinos,G. and Franklin,K.B.J. (2001). *The Mouse Brain in Stereotaxic Coordinates*, Second Edition. (San Diego: Academic Press).
- Pennartz,C.M., de Jeu,M.T., Bos,N.P., Schaap,J., and Geurtsen,A.M. (2002). Diurnal modulation of pacemaker potentials and calcium current in the mammalian circadian clock. *Nature* 416, 286-290.
- Pickard,G.E., Ralph,M.R., and Menaker,M. (1987). The intergeniculate leaflet partially mediates effects of light on circadian rhythms. *J. Biol. Rhythms* 2, 35-56.
- Piggins,H.D. and Rusak,B. (1997). Effects of microinjections of substance P into the suprachiasmatic nucleus region on hamster wheel-running rhythms. *Brain Res. Bull.* 42, 451-455.
- Pittendrigh,C.S. and Daan,S. (1976a). A functional analysis of circadian pacemakers in nocturnal rodents. IV. Entrainment: Pacemaker as Clock. *Journal of Comparative Physiology ? A* 106, 291-331.
- Pittendrigh,C.S. and Daan,S. (1976b). A functional analysis of circadian pacemakers in nocturnal rodents: V. Pacemaker structure: a clock for all seasons. *J. Comp. Physiol. [A]*. 333-355.
- Pittendrigh,C.S., Elliott,J., and Takamura,T. (1984). The Circadian Component in Photoperiodic induction. In *Photoperiodic Regulation of Insect and Molluscan Hormones*, R.Porter and J.M.Collins, eds. (London: Pitman), pp. 26-47.
- Pittendrigh,C.S., Kyner,W.T., and Takamura,T. (1991). The amplitude of circadian oscillations: temperature dependence, latitudinal clines, and the photoperiodic time measurement. *J. Biol. Rhythms* 6, 299-313.
- Pitts,G.R., Ohta,H., and McMahon,D.G. (2006). Daily rhythmicity of large-conductance Ca²⁺ -activated K⁺ currents in suprachiasmatic nucleus neurons. *Brain Res.* 1071, 54-62.
- Portaluppi,F., Touitou,Y., and Smolensky,M.H. (2008). Ethical and methodological standards for laboratory and medical biological rhythm research. *Chronobiol Int* 25, 999-1016.

- Preitner,N., Damiola,F., Lopez-Molina,L., Zakany,J., Duboule,D., Albrecht,U., and Schibler,U. (2002). The orphan nuclear receptor REV-ERB α controls circadian transcription within the positive limb of the mammalian circadian oscillator. *Cell* 110, 251-260.
- Prosser,R.A. (1998). In vitro circadian rhythms of the mammalian suprachiasmatic nuclei: comparison of multi-unit and single-unit neuronal activity recordings. *J. Biol. Rhythms* 13, 30-38.
- Provencio,I. and Foster,R.G. (1995). Circadian rhythms in mice can be regulated by photoreceptors with cone-like characteristics. *Brain Res* 694, 183-190.
- Provencio,I., Rodriguez,I.R., Jiang,G., Hayes,W.P., Moreira,E.F., and Rollag,M.D. (2000). A novel human opsin in the inner retina. *J Neurosci* 20, 600-605.
- Pulivarthy,S.R., Tanaka,N., Welsh,D.K., De,H.L., Verma,I.M., and Panda,S. (2007). Reciprocity between phase shifts and amplitude changes in the mammalian circadian clock. *Proc Natl Acad Sci U. S. A* 104, 20356-20361.
- Quintero,J.E., Kuhlman,S.J., and McMahon,D.G. (2003). The biological clock nucleus: a multiphasic oscillator network regulated by light. *J. Neurosci.* 23, 8070-8076.
- Ralph,M.R., Foster,R.G., Davis,F.C., and Menaker,M. (1990). Transplanted suprachiasmatic nucleus determines circadian period. *Science* 247, 975-978.
- Ralph,M.R. and Menaker,M. (1988). A mutation of the circadian system in golden hamsters. *Science* 241, 1225-1227.
- Rangarajan,R., Heller,H.C., and Miller,J.D. (1994). Chloride channel block phase advances the single-unit activity rhythm in the SCN. *Brain Res. Bull.* 34, 69-72.
- Reddy,A.B., Field,M.D., Maywood,E.S., and Hastings,M.H. (2002). Differential resynchronisation of circadian clock gene expression within the suprachiasmatic nuclei of mice subjected to experimental jet lag. *J. Neurosci.* 22, 7326-7330.
- Reed,H.E., Cutler,D.J., Brown,T.M., Brown,J., Coen,C.W., and Piggins,H.D. (2002). Effects of vasoactive intestinal polypeptide on neurones of the rat suprachiasmatic nuclei in vitro. *J. Neuroendocrinol.* 14, 639-646.

- Reed,H.E., Meyer-Spasche,A., Cutler,D.J., Coen,C.W., and Piggins,H.D. (2001). Vasoactive intestinal polypeptide (VIP) phase-shifts the rat suprachiasmatic nucleus clock in vitro. *Eur. J. Neurosci.* *13*, 839-843.
- Refinetti,R. (2001). Dark adaptation in the circadian system of the mouse. *Physiol. Behav.* *74*, 101-107.
- Refinetti,R. (2002). Compression and expansion of circadian rhythm in mice under long and short photoperiods. *Integr. Physiol. Behav. Sci.* *37*, 114-127.
- Reppert,S.M. and Weaver,D.R. (2001). Molecular analysis of mammalian circadian rhythms. *Annu. Rev. Physiol.* *63*, 647-676.
- Reppert,S.M. and Weaver,D.R. (2002). Coordination of circadian timing in mammals. *Nature* *418*, 935-941.
- Rohling,J., Meijer,J.H., VanderLeest,H.T., and Admiraal,J. (2006a). Phase differences between SCN neurons and their role in photoperiodic encoding; a simulation of ensemble patterns using recorded single unit electrical activity patterns. *J. Physiol Paris* *100*, 261-270.
- Rohling,J., Wolters,L., and Meijer,J.H. (2006b). Simulation of day-length encoding in the SCN: from single-cell to tissue-level organization. *J. Biol. Rhythms* *21*, 301-313.
- Ruby,N.F., Hwang,C.E., Wessells,C., Fernandez,F., Zhang,P., Sapolsky,R., and Heller,H.C. (2008). Hippocampal-dependent learning requires a functional circadian system. *Proc. Natl. Acad. Sci. U. S. A* *105*, 15593-15598.
- Rusak,B. (1977). The role of the Suprachiasmatic Nuclei in the Generation of Circadian-Rhythms in the Golden-Hamster, *Mesocricetus-auratus*. *Journal of Comparative Physiology* *118*, 145-164.
- Rusak,B. and Boulos,Z. (1981). Pathways for photic entrainment of mammalian circadian rhythms. *Photochem Photobiol* *34*, 267-273.
- Saeb-Parsy,K. and Dyball,R.E. (2003). Defined cell groups in the rat suprachiasmatic nucleus have different day/night rhythms of single-unit activity in vivo. *J. Biol. Rhythms* *18*, 26-42.
- Sato,T.K., Panda,S., Miraglia,L.J., Reyes,T.M., Rudic,R.D., McNamara,P., Naik,K.A., FitzGerald,G.A., Kay,S.A., and Hogenesch,J.B. (2004). A functional genomics strategy reveals Rora as a component of the mammalian circadian clock. *Neuron* *43*, 527-537.

- Schaap,J., Albus,H., Eilers,P.H., Detari,L., and Meijer,J.H. (2001). Phase differences in electrical discharge rhythms between neuronal populations of the left and right suprachiasmatic nuclei. *Neuroscience* 108, 359-363.
- Schaap,J., Albus,H., VanderLeest,H.T., Eilers,P.H., Detari,L., and Meijer,J.H. (2003). Heterogeneity of rhythmic suprachiasmatic nucleus neurons: Implications for circadian waveform and photoperiodic encoding. *Proc. Natl. Acad. Sci. U. S. A.* 100, 15994-15999.
- Schaap,J. and Meijer,J.H. (2001). Opposing effects of behavioural activity and light on neurons of the suprachiasmatic nucleus. *Eur. J. Neurosci.* 13, 1955-1962.
- Schak,K.M. and Harrington,M.E. (1999). Protein kinase C inhibition and activation phase advances the hamster circadian clock. *Brain Res.* 840, 158-161.
- Schibler,U. and Sassone-Corsi,P. (2002). A web of circadian pacemakers. *Cell* 111, 919-922.
- Schwartz,W.J., Carpino,A., Jr., de la Iglesia,H.O., Baler,R., Klein,D.C., Nakabeppu,Y., and Aronin,N. (2000). Differential regulation of fos family genes in the ventrolateral and dorsomedial subdivisions of the rat suprachiasmatic nucleus. *Neuroscience* 98, 535-547.
- Schwartz,W.J., Gross,R.A., and Morton,M.T. (1987). The suprachiasmatic nuclei contain a tetrodotoxin-resistant circadian pacemaker. *Proc. Natl. Acad. Sci. U. S. A.* 84, 1694-1698.
- Shearman,L.P., Sriram,S., Weaver,D.R., Maywood,E.S., Chaves,I., Zheng,B., Kume,K., Lee,C.C., van der Horst,G.T., Hastings,M.H., and Reppert,S.M. (2000). Interacting molecular loops in the mammalian circadian clock. *Science* 288, 1013-1019.
- Shearman,L.P., Zylka,M.J., Weaver,D.R., Kolakowski,L.F., Jr., and Reppert,S.M. (1997). Two period homologs: circadian expression and photic regulation in the suprachiasmatic nuclei. *Neuron* 19, 1261-1269.
- Shibata,S. and Moore,R.Y. (1993). Neuropeptide Y and optic chiasm stimulation affect suprachiasmatic nucleus circadian function in vitro. *Brain Res.* 615, 95-100.
- Shibata,S., Oomura,Y., Kita,H., and Hattori,K. (1982). Circadian rhythmic changes of neuronal activity in the suprachiasmatic nucleus of the rat hypothalamic slice. *Brain Res.* 247, 154-158.

- Shibata,S., Tsuneyoshi,A., Hamada,T., Tominaga,K., and Watanabe,S. (1992). Effect of substance P on circadian rhythms of firing activity and the 2-deoxyglucose uptake in the rat suprachiasmatic nucleus in vitro. *Brain Res.* 597, 257-263.
- Shibata,S., Watanabe,A., Hamada,T., Ono,M., and Watanabe,S. (1994). N-methyl-D-aspartate induces phase shifts in circadian rhythm of neuronal activity of rat SCN in vitro. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 267, R360-R364.
- Shimomura,K., Low-Zeddies,S.S., King,D.P., Steeves,T.D., Whiteley,A., Kushla,J., Zemenides,P.D., Lin,A., Vitaterna,M.H., Churchill,G.A., and Takahashi,J.S. (2001). Genome-wide epistatic interaction analysis reveals complex genetic determinants of circadian behavior in mice. *Genome Res.* 11, 959-980.
- Shinohara,K., Funabashi,T., Mitushima,D., and Kimura,F. (2000a). Effects of gap junction blocker on vasopressin and vasoactive intestinal polypeptide rhythms in the rat suprachiasmatic nucleus in vitro. *Neurosci. Res.* 38, 43-47.
- Shinohara,K., Honma,S., Katsuno,Y., Abe,H., and Honma,K. (1995). Two distinct oscillators in the rat suprachiasmatic nucleus in vitro. *Proc. Natl. Acad. Sci. U. S. A.* 92, 7396-7400.
- Shinohara,K., Honma,S., Katsuno,Y., and Honma,K. (2000b). Circadian release of excitatory amino acids in the suprachiasmatic nucleus culture is Ca^{2+} -independent. *Neurosci. Res.* 36, 245-250.
- Shirakawa,T., Honma,S., Katsuno,Y., Oguchi,H., and Honma,K.I. (2000). Synchronization of circadian firing rhythms in cultured rat suprachiasmatic neurons. *Eur. J. Neurosci.* 12, 2833-2838.
- Silver,R., LeSauter,J., Tresco,P.A., and Lehman,M.N. (1996). A diffusible coupling signal from the transplanted suprachiasmatic nucleus controlling circadian locomotor rhythms. *Nature* 382, 810-813.
- Silver,R. and Schwartz,W.J. (2005). The Suprachiasmatic Nucleus is a Functionally Heterogeneous Timekeeping Organ. *Methods Enzymol.* 393, 451-465.
- Soscia,S.J. and Harrington,M.E. (2004). Neuropeptide Y attenuates NMDA-induced phase shifts in the SCN of NPY Y1 receptor knockout mice in vitro. *Brain Res.* 1023, 148-153.

- Stephan,F.K. and Zucker,I. (1972). Circadian rhythms in drinking behavior and locomotor activity of rats are eliminated by hypothalamic lesions. *Proc. Natl. Acad. Sci. U. S. A.* 69, 1583-1586.
- Sumova,A., Jac,M., Sladek,M., Sauman,I., and Illnerova,H. (2003). Clock gene daily profiles and their phase relationship in the rat suprachiasmatic nucleus are affected by photoperiod. *J. Biol. Rhythms* 18, 134-144.
- Sumova,A., Sladek,M., Jac,M., and Illnerova,H. (2002). The circadian rhythm of *Per1* gene product in the rat suprachiasmatic nucleus and its modulation by seasonal changes in daylength. *Brain Res.* 947, 260-270.
- Sumova,A., Travnickova,Z., and Illnerova,H. (2000). Spontaneous c-Fos rhythm in the rat suprachiasmatic nucleus: location and effect of photoperiod. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* 279, R2262-R2269.
- Sumova,A., Travnickova,Z., Peters,R., Schwartz,W.J., and Illnerova,H. (1995). The rat suprachiasmatic nucleus is a clock for all seasons. *Proc. Natl. Acad. Sci. U. S. A.* 92, 7754-7758.
- Takahashi,J.S. (1993). Circadian-clock regulation of gene expression. *Curr. Opin. Genet. Dev.* 3, 301-309.
- Takahashi,J.S., DeCoursey,P.J., Bauman,L., and Menaker,M. (1984). Spectral sensitivity of a novel photoreceptive system mediating entrainment of mammalian circadian rhythms. *Nature* 308, 186-188.
- Takahashi,J.S., Hong,H.K., Ko,C.H., and McDearmon,E.L. (2008). The genetics of mammalian circadian order and disorder: implications for physiology and disease. *Nat Rev Genet* 9, 764-775.
- Takahashi,J.S., Turek,F.W., and Moore,R.Y. (2001). *Circadian Clocks*. (New York: Kluwer Academic / Plenum Publishers).
- Tournier,B.B., Menet,J.S., Dardente,H., Poirel,V.J., Malan,A., Masson-Pevet,M., Pevet,P., and Vuilleuz,P. (2003). Photoperiod differentially regulates clock genes' expression in the suprachiasmatic nucleus of Syrian hamster. *Neuroscience* 118, 317-322.
- Ukai,H., Kobayashi,T.J., Nagano,M., Masumoto,K.H., Sujino,M., Kondo,T., Yagita,K., Shigeyoshi,Y., and Ueda,H.R. (2007). Melanopsin-dependent photoperturbation reveals desynchronization underlying the singularity of mammalian circadian clocks. *Nat. Cell Biol.* 9, 1327-1334.

- van den Pol,A.N. (1980). The hypothalamic suprachiasmatic nucleus of rat: intrinsic anatomy. *J. Comp. Neurol.* *191*, 661-702.
- van den Pol,A.N. and Dudek,F.E. (1993). Cellular communication in the circadian clock, the suprachiasmatic nucleus. *Neuroscience* *56*, 793-811.
- van der Horst,G.T., Muijtjens,M., Kobayashi,K., Takano,R., Kanno,S., Takao,M., de,W.J., Verkerk,A., Eker,A.P., Van,L.D., Buijs,R., Bootsma,D., Hoeijmakers,J.H., and Yasui,A. (1999). Mammalian Cry1 and Cry2 are essential for maintenance of circadian rhythms. *Nature* *398*, 627-630.
- van Oosterhout,F., Michel,S., Deboer,T., Houben,T., van de Ven,R.C., Albus,H., Westerhout,J., Vansteensel,M.J., Ferrari,M.D., van den Maagdenberg,A.M., and Meijer,J.H. (2008). Enhanced circadian phase resetting in R192Q Cav2.1 calcium channel migraine mice. *Ann. Neurol.* *64*, 315-324.
- Van Someren,E.J., Riemersma,R.F., and Swaab,D.F. (2002). Functional plasticity of the circadian timing system in old age: light exposure. *Prog. Brain Res.* *138*, 205-231.
- Van Someren,E.J. and Riemersma-van der Lek RF (2007). Live to the rhythm, slave to the rhythm. *Sleep Med. Rev.* *11*, 465-484.
- VanderLeest,H.T., Houben,T., Michel,S., Deboer,T., Albus,H., Vansteensel,M.J., Block,G.D., and Meijer,J.H. (2007). Seasonal encoding by the circadian pacemaker of the SCN. *Curr. Biol.* *17*, 468-473.
- VanderLeest,H.T., Rohling,J.H., Michel,S., and Meijer,J.H. (2009a). Phase shifting capacity of the circadian pacemaker determined by the SCN neuronal network organization. *PLoS One.* *4*, e4976.
- VanderLeest,H.T., Vansteensel,M.J., Duindam,H., Michel,S., and Meijer,J.H. (2009b). Phase of the electrical activity rhythm in the SCN in vitro not influenced by preparation time. *Chronobiol. Int.* *26*, 1075-1089.
- Vansteensel,M.J., Deboer,T., Dahan,A., and Meijer,J.H. (2003a). Differential responses of circadian activity onset and offset following GABA-ergic and opioid receptor activation. *J. Biol. Rhythms* *18*, 297-306.
- Vansteensel,M.J., Michel,S., and Meijer,J.H. (2008). Organization of cell and tissue circadian pacemakers: a comparison among species. *Brain Res. Rev.* *58*, 18-47.

- Vansteensel,M.J., Yamazaki,S., Albus,H., Deboer,T., Block,G.D., and Meijer,J.H. (2003b). Dissociation between circadian *Per1* and neuronal and behavioral rhythms following a shifted environmental cycle. *Curr. Biol.* *13*, 1538-1542.
- Vitaterna,M.H., King,D.P., Chang,A.M., Kornhauser,J.M., Lowrey,P.L., Mcdonald,J.D., Dove,W.F., Pinto,L.H., Turek,F.W., and Takahashi,J.S. (1994). Mutagenesis and Mapping of A Mouse Gene Clock, Essential for Circadian Behavior. *Science* *264*, 719-725.
- Vitaterna,M.H., Selby,C.P., Todo,T., Niwa,H., Thompson,C., Fruechte,E.M., Hitomi,K., Thresher,R.J., Ishikawa,T., Miyazaki,J., Takahashi,J.S., and Sancar,A. (1999). Differential regulation of mammalian period genes and circadian rhythmicity by cryptochromes 1 and 2. *Proc. Natl. Acad. Sci. U. S. A.* *96*, 12114-12119.
- Vosko,A.M., Schroeder,A., Loh,D.H., and Colwell,C.S. (2007). Vasoactive intestinal peptide and the mammalian circadian system. *Gen. Comp Endocrinol.* *152*, 165-175.
- Warren,E.J., Allen,C.N., Brown,R.L., and Robinson,D.W. (2003). Intrinsic light responses of retinal ganglion cells projecting to the circadian system. *Eur. J. Neurosci.* *17*, 1727-1735.
- Watanabe,K., Deboer,T., and Meijer,J.H. (2001). Light-Induced resetting of the circadian pacemaker: quantitative analysis of transient versus steady-state phase shifts. *J. Biol. Rhythms* *16*, 564-573.
- Webb,A.B., Angelo,N., Huettnner,J.E., and Herzog,E.D. (2009). Intrinsic, nondeterministic circadian rhythm generation in identified mammalian neurons. *Proc. Natl. Acad. Sci. U. S. A* *106*, 16493-16498.
- Welsh,D.K. (2007). VIP activates and couples clock cells. Focus on "Disrupted neuronal activity rhythms in the suprachiasmatic nucleus of vasoactive intestinal polypeptide-deficient mice". *J. Neurophysiol.* *97*, 1885-1886.
- Welsh,D.K., Logothetis,D.E., Meister,M., and Reppert,S.M. (1995). Individual neurons dissociated from rat suprachiasmatic nucleus express independently phased circadian firing rhythms. *Neuron* *14*, 697-706.
- Westermarck,P.O., Welsh,D.K., Okamura,H., and Herzel,H. (2009). Quantification of circadian rhythms in single cells. *PLoS. Comput. Biol.* *5*, e1000580.

- Winfree,A.T. (2000). The Geometry of Biological Time. (New York: Springer).
- Witting,W., Boerma,D., Hoffen,G.C.K., Swaab,D.F., and Mirmiran,M. (1995). Light suppresses frequency and endogenous amplitude of the circadian system in nocturnal animals. *Biological Rhythm Research* 26, 477-485.
- Woelfle,M.A., Ouyang,Y., Phanvijhitsiri,K., and Johnson,C.H. (2004). The adaptive value of circadian clocks: an experimental assessment in cyanobacteria. *Curr Biol* 14, 1481-1486.
- Yamaguchi,S., Isejima,H., Matsuo,T., Okura,R., Yagita,K., Kobayashi,M., and Okamura,H. (2003). Synchronization of cellular clocks in the suprachiasmatic nucleus. *Science* 302, 1408-1412.
- Yamaguchi,S., Kobayashi,M., Mitsui,S., Ishida,Y., van der Horst,G.T., Suzuki,M., Shibata,S., and Okamura,H. (2001). View of a mouse clock gene ticking. *Nature* 409, 684.
- Yamazaki,S., Alones,V., Irelan,W., and Menaker,M. (1999). Serotonin-containing cell bodies in novel brain locations: effects of light input. *Neuroreport* 10, 431-435.
- Yamazaki,S., Kerbeshian,M.C., Hocker,C.G., Block,G.D., and Menaker,M. (1998). Rhythmic properties of the hamster suprachiasmatic nucleus in vivo. *J. Neurosci.* 18, 10709-10723.
- Yamazaki,S., Numano,R., Abe,M., Hida,A., Takahashi,R., Ueda,M., Block,G.D., Sakaki,Y., Menaker,M., and Tei,H. (2000). Resetting central and peripheral circadian oscillators in transgenic rats. *Science* 288, 682-685.
- Yannielli,P.C. and Harrington,M.E. (2000). Neuropeptide Y applied in vitro can block the phase shifts induced by light in vivo. *Neuroreport* 11, 1587-1591.
- Yannielli,P.C., Kinley Brewer,J., and Harrington,M.E. (2002). Is novel wheel inhibition of per1 and per2 expression linked to phase shift occurrence? *Neuroscience* 112, 677-685.
- Yoo,S.H., Yamazaki,S., Lowrey,P.L., Shimomura,K., Ko,C.H., Buhr,E.D., Siepka,S.M., Hong,H.K., Oh,W.J., Yoo,O.J., Menaker,M., and Takahashi,J.S. (2004). PERIOD2::LUCIFERASE real-time reporting of circadian dynamics reveals persistent circadian oscillations in mouse peripheral tissues. *Proc. Natl. Acad. Sci. U. S. A.* 101, 5339-5346.

- Yoshikawa,T., Yamazaki,S., and Menaker,M. (2005). Effects of preparation time on phase of cultured tissues reveal complexity of circadian organization. *J. Biol. Rhythms* 20, 500-512.
- Zhou,Q.Y. and Cheng,M.Y. (2005). Prokineticin 2 and circadian clock output. *Febs J.* 272, 5703-5709.
- Zlomanczuk,P., Margraf,R.R., and Lynch,G.R. (1991). In vitro electrical activity in the suprachiasmatic nucleus following splitting and masking of wheel-running behavior. *Brain Res.* 559, 94-99.

