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Author Index

COVER:

Discovery in Japan

Dr. Hidenori Ichijo and his colleagues identified the MAP kinase kinase kinase ASK1 that is preferentially activated by various cytotoxic stressors. ASK1 plays pivotal roles in a wide variety of physico-chemical and biological stress responses such as oxidative stress and ER stress responses (*1*, *2*). In non-stimulated cells, ASK1 forms an inactive homo-oligomer complexed with thioredoxin, which is a redox-sensitive protein with inhibitory activity on ASK1. Oxidative stress such as reactive oxygen species dissociates thioredoxin from ASK1 and subsequently induces binding of TNF receptor-associated factor (TRAF) 2 and TRAF6 to ASK1, leading to ASK1 activation by inducing auto-phosphorylation of ASK1 (*3*, *4*). This system provides a prototypical model in which the redox signal is converted to signalling through protein phosphorylation, and the accumulating evidence suggests the involvement of aberrant ASK1 signalling in a variety of human diseases (*2*).

References

1. Ichijo, H., Nishida, E., Irie, K., ten Dijke, P., Saitoh, M., Moriguchi, T., Takagi, M., Matsumoto, K., Miyazono, K., and Gotoh, Y. (1997) Induction of apoptosis by ASK1, a mammalian MAPKKK that activates SAPK/JNK and p38 signaling pathways. *Science* **275**, 90–94.
2. Takeda, K., Noguchi, T., Naguro, I., and Ichijo, H. (2008) Apoptosis signal-regulating kinase 1 in stress and immune response. *Annu. Rev. Pharmacol. Toxicol.* **48**, 199–225.
3. Saitoh, M., Nishitoh, H., Fujii, M., Takeda, K., Tobiume, K., Sawada, Y., Kawabata, M., Miyazono, K., and Ichijo, H. (1998) Mammalian thioredoxin is a direct inhibitor of apoptosis signal-regulating kinase (ASK) 1. *EMBO J.* **17**, 2596–2606.
4. Fujino, G., Noguchi, T., Matsuzawa, A., Yamauchi, S., Saitoh, M., Takeda, K. and Ichijo, H. (2007) Thioredoxin and TRAF family proteins regulate ROS-dependent activation of ASK1 through reciprocal modulation of the N-terminal homophilic interaction of ASK1. *Mol. Cell. Biol.* **27**, 8152–8163.