1. Phylogeny  
   Mitogen‐activated protein kinase 7 (MAPK7), frequently referred to as Big MAP kinase 1, ERK5, or PRKM7, is a member of the mitogen‐activated protein kinase (MAPK) family, which is situated within the CMGC group of eukaryotic protein kinases. Orthologs of MAPK7 are conserved throughout metazoan species, with comprehensive genome‐wide analyses demonstrating that vertebrates retain a conserved version of MAPK7 that emerged early in evolution (andrade2011eukaryoticproteinkinases pages 14-15, kultz1998phylogeneticandfunctional pages 4-5). Detailed phylogenetic studies, including those surveying the protein kinase complement of the human genome, have shown that MAPK7 clusters with canonical MAP kinases and is readily distinguished from the classical ERK1/ERK2 paralogs. This divergence is largely attributable to its exclusive activation by MAP2K5 (also known as MEK5) rather than by the more ubiquitous MEK1/ERK1 or MEK2/ERK2 cascades. Such specialization establishes a discrete MAP2K5–MAPK7 signaling module that is conserved in evolution and has been linked to tissue-specific signaling in multicellular organisms (krupa2002therepertoireof pages 2-3, lai2015investigationsofthe pages 1-6, orand2023revealingthemechanismc pages 33-38).
2. Reaction Catalyzed  
   MAPK7 catalyzes an ATP-dependent phosphorylation reaction wherein the γ-phosphate group from ATP is transferred to specific serine or threonine residues on target substrate proteins. The chemical reaction can be described as:  
     ATP + [protein]-(L-serine or L-threonine) → ADP + [protein]-(L-serine/threonine)-phosphate + H⁺.  
   This reversible enzymatic process is characteristic of serine/threonine kinases and is critical for modulating the activity, conformation, and function of downstream target proteins (andrade2011eukaryoticproteinkinases pages 14-15, roskoski2012mek12dualspecificityprotein pages 6-6).
3. Cofactor Requirements  
   The catalytic activity of MAPK7 is dependent on the presence of divalent metal cations, with Mg²⁺ serving as the principal cofactor. Mg²⁺ ions coordinate with ATP in the active site of the enzyme, thereby facilitating the proper alignment of the phosphoryl group for efficient transfer to the substrate. This requirement for Mg²⁺ is widely observed among serine/threonine kinases and is essential for stabilizing the transition state during the phosphorylation reaction (champion2004reassessingthemap3k pages 6-6, andrade2011eukaryoticproteinkinases pages 14-15, krupa2002therepertoireof pages 10-11, roskoski2012mek12dualspecificityprotein pages 6-6).
4. Substrate Specificity  
   MAPK7 exhibits substrate specificity defined by its preference for phosphorylating serine/threonine residues that reside within proline-directed motifs. Peptide microarray studies and large-scale substrate specificity profiling have revealed that MAPK7 preferentially recognizes consensus motifs such as PX[S/T]P, in which a proline residue located immediately C-terminal (+1 position) to the phosphorylated serine or threonine is critical for substrate recognition and efficient catalysis. This proline-directed specificity enables MAPK7 to selectively target physiological substrates, including transcription factors such as MEF2C and regulatory kinases such as SGK1. In particular, phosphorylation of SGK1 at Ser-78 by MAPK7 is an essential post-translational modification required for growth factor–induced progression through the cell cycle (johnson2023anatlasof pages 1-2, johnson2023anatlasof pages 4-5, johnson2023anatlasof pages 6-7, johnson2023anatlasof pages 7-7, johnson2023anatlasof pages 9-10).
5. Structure  
   MAPK7 is composed of a canonical kinase domain that exhibits a bilobal fold typical of eukaryotic protein kinases. The smaller N-terminal lobe is predominantly made up of β-strands and contains the ATP-binding hinge region, which is crucial for anchoring ATP during catalysis. In contrast, the larger C-terminal lobe is mainly α-helical and houses key regulatory elements. One of the most critical structural features is the activation loop (T-loop), which contains the conserved TEY (Thr-Glu-Tyr) motif. Dual phosphorylation of the TEY motif by the upstream kinase MAP2K5 is necessary for full catalytic activation of MAPK7 (coulombe2007atypicalmitogenactivatedprotein pages 11-12, hunter2015theeukaryoticprotein pages 1-3). In addition to the kinase domain, MAPK7 is structurally unique because it possesses an extended C-terminal non-catalytic region. This region includes a nuclear localization signal (NLS) and several proline-rich motifs that mediate protein–protein interactions, ultimately contributing to transcriptional regulation following nuclear translocation (faezov2023alphafold2modelsof pages 18-20, oleaflores2019extracellularsignalregulatedkinase pages 6-7). Further support for this structural organization comes from AlphaFold2 models, which reveal a well-conserved hydrophobic spine and a critical C-helix in the kinase domain that stabilizes the active conformation by ensuring correct orientation of key catalytic residues (hunter2015theeukaryoticprotein pages 3-6, orand2023revealingthemechanismc pages 33-38).
6. Regulation  
   MAPK7 is regulated primarily through a cascade of phosphorylation events. Its full activation is achieved by the specific upstream kinase MAP2K5 (MEK5), which dual phosphorylates threonine and tyrosine residues within the TEY motif of the activation loop. This phosphorylation induces a conformational change that not only enhances MAPK7’s catalytic activity but also facilitates its translocation from the cytoplasm to the nucleus. Once in the nucleus, MAPK7 can phosphorylate its downstream substrates. Beyond phosphorylation, MAPK7 is also subject to regulatory mechanisms involving protein–protein interactions. For instance, binding to the ubiquitin ligase STUB1/CHIP results in the ubiquitination and subsequent degradation of ICER-type CREM isoforms. This particular ubiquitination process is responsible for the anti-apoptotic role of MAPK7 in cardiomyocytes. Additionally, MAPK7 has been shown to modulate the tumor suppressor p53 by disrupting the interaction between PML and MDM2, thereby influencing cell cycle progression and apoptotic responses. These multifaceted regulatory mechanisms, involving both phosphorylation and ubiquitination events, ensure that MAPK7 activity is tightly controlled in response to various extracellular signals, such as those from epidermal growth factor (EGF) that stimulate a Ras-independent, MAP2K5-dependent pathway (andrade2011eukaryoticproteinkinases pages 14-15, coulombe2007atypicalmitogenactivatedprotein pages 11-12, lai2016regulatoryrolesof pages 12-14, chrysostomou2020rsk4targetinga pages 54-58, southekal2021integrativeanalysisof pages 114-120, jauch2005themapkinteracting pages 9-13).
7. Function  
   MAPK7 plays a central role in various cellular processes, including proliferation, differentiation, and cell survival. As an integral part of the MAPK/ERK signaling pathway, MAPK7 is activated in response to extracellular stimuli such as epidermal growth factor (EGF) through a Ras-independent pathway that specifically involves MAP2K5. Upon activation, MAPK7 translocates to the nucleus where it phosphorylates key regulatory proteins. One of its notable targets is the transcription factor MEF2C, which is central to the control of gene expression programs that govern muscle cell differentiation and endothelial function. In addition to MEF2C, MAPK7 phosphorylates SGK1 at Ser-78, a modification that is critical for the progression of the cell cycle and, thereby, for promoting cellular proliferation. Moreover, MAPK7 exerts a protective effect in cardiomyocytes by acting as a negative regulator of apoptosis. This anti-apoptotic effect is mediated through its interaction with STUB1/CHIP, which leads to the ubiquitination and degradation of ICER-type CREM isoforms. Furthermore, MAPK7 influences the p53 tumor suppressor pathway by disrupting the PML-MDM2 interaction, thus contributing to the regulation of cell cycle checkpoints and apoptotic responses. These functional roles are not only pivotal for normal cellular physiology, including muscle differentiation and maintenance of vascular integrity, but also have important implications in pathological conditions such as cancer and cardiovascular diseases (chrysostomou2020rsk4targetinga pages 54-58, southekal2021integrativeanalysisof pages 114-120, hunter2015theeukaryoticprotein pages 3-6, johnson2023anatlasof pages 1-2, johnson2023anatlasof pages 7-7).
8. Other Comments  
   Although no MAPK7-specific inhibitors have yet been approved for clinical use, MAPK7 remains an attractive target for therapeutic intervention based on its well-defined roles in regulating cellular apoptosis, muscle differentiation, and endothelial function. Current research efforts, which include integrative kinome analyses and virtual screening campaigns, are focused on identifying small-molecule inhibitors that can selectively modulate the MAP2K5–MAPK7 signaling axis. The dysregulation or aberrant activation of MAPK7 has been associated with a range of pathological conditions, notably cardiovascular diseases and several types of cancer. Such associations suggest that MAPK7 may serve both as a diagnostic biomarker and as a therapeutic target. Furthermore, comprehensive analyses have indicated that the specific interaction between MAP2K5 and MAPK7, as well as the distinctive features of MAPK7’s extended C-terminal regulatory domain, set it apart from classical MAP kinases such as ERK1/ERK2. This uniqueness has spurred further studies aimed at understanding its allosteric regulation and at developing highly selective inhibitors (orand2023revealingthemechanism pages 33-38, southekal2021integrativeanalysisof pages 114-120, tubita2020beyondkinaseactivity pages 10-12, wen2024boneandextracellular pages 15-16, wilkinson2020analysisofbrafinhibitor pages 39-44).
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