1. Phylogeny  
   MAPK4, also referred to as ERK4 or PRKM4, is an atypical member of the mitogen‐activated protein kinase (MAPK) family that belongs to the ERK3/ERK4 subgroup, a lineage restricted to vertebrates and distinct from conventional MAPKs such as ERK1/2, JNK, and p38 (aberg2006regulationofmapkactivated pages 1-2). Sequence comparisons indicate that ERK4 displays approximately 73% amino acid identity within its kinase domain with ERK3, reflecting a shared evolutionary ancestry that likely arose from an ancient gene duplication event; correspondingly, both kinases exhibit a unique activation loop motif (SEG) and a substitution of the canonical APE motif by an SPR motif in subdomain VIII, features that demarcate the atypical subgroup from classical MAP kinases (kant2006characterizationofthe pages 1-2, coulombe2007atypicalmitogenactivatedprotein pages 1-2). Extensive phylogenetic analyses, such as those documented by Manning et al. (2002) and Manning et al. (2002), further place ERK4 within an evolutionary core that emerged early in eukaryotic evolution and has been conserved throughout vertebrate species, with orthologs present in mammals, birds, and fish (krens2006functionsofthe pages 1-3). Moreover, ERK4 and ERK3 share similarities in exon–intron organization and domain architecture, with the former encoding a 587-amino acid protein in humans and having a stable cellular expression pattern, whereas ERK3 is less stable and subjected to proteasomal turnover via its unique N-terminal degradation signals (rousseau2009caractérisationdela pages 55-59, aberg2006regulationofmapkactivated pages 4-6).
2. Reaction Catalyzed  
   The catalytic reaction mediated by MAPK4 is a typical phosphorylation reaction in which ATP is utilized to transfer a phosphate group to serine or threonine residues present on target substrate proteins. In this reaction, ATP + [protein]-(L-serine or L-threonine) are converted into ADP + [protein]-(L-serine/threonine)-phosphate + H⁺, representing the canonical activity observed for serine/threonine kinases (deleris2008activationloopphosphorylation pages 280-285, aberg2006regulationofmapkactivated pages 9-10).
3. Cofactor Requirements  
   MAPK4, like other serine/threonine kinases, requires divalent metal ions—most notably Mg²⁺—as essential cofactors for its catalytic activity during the phosphate group transfer reaction from ATP to its substrates (aberg2006regulationofmapkactivated pages 4-6, jiang2022mitogenactivatedproteinkinase pages 1-2).
4. Substrate Specificity  
   The substrate specificity of MAPK4 is relatively narrow compared to classical MAPKs. It is documented to phosphorylate microtubule-associated protein 2 (MAP2) and, more notably, MAPK-activated protein kinase 5 (MK5) as its primary physiological substrate (aberg2006regulationofmapkactivated pages 7-8, kant2006characterizationofthe pages 1-2). The unique docking interactions between ERK4 and MK5 are mediated by specific regions outside the canonical MAPK docking domain, including a critical FRIEDE motif located within the C-terminal extension that is necessary for the binding and subsequent phosphorylation events (aberg2009dockingofprakmk5 pages 2-3, perander2017regulationofatypical pages 9-10). For serine/threonine kinases, recent high-throughput studies such as the atlas compiled by Johnson et al. (2023) provide insights into consensus substrate motifs, wherein substrate phosphorylation is typically facilitated by recognition of sequence motifs bearing a preference for basic residues upstream and proline enrichment immediately following the phosphoacceptor site; however, specific consensus motifs for MAPK4 have not been explicitly detailed beyond its interaction with MK5 (Johnson2023Nature pages 759-766). In contrast, the substrate specificity of tyrosine kinases is characterized by distinct motifs as shown in the study by Yaron-Barir et al. (2024), but these do not pertain to MAPK4 given its classification as a serine/threonine kinase (Yaron-Barir2024Nature pages 1174-1181).
5. Structure  
   MAPK4 exhibits a central kinase domain that spans the majority of its 587 amino acid sequence as determined by sequence corrections from earlier cloning experiments (aberg2006regulationofmapkactivated pages 4-6). The kinase domain contains all the hallmarks of protein serine/threonine kinases, including an ATP-binding pocket and a catalytic loop, but it is distinguished by an atypical activation loop that contains a single phospho-acceptor residue within a Ser-Glu-Gly (SEG) motif instead of the conventional Thr-Xxx-Tyr (TXY) motif (aberg2006regulationofmapkactivated pages 1-2, kant2006characterizationofthe pages 1-2). Additionally, a significant structural feature of MAPK4 is the substitution of the canonical Ala-Pro-Glu (APE) sequence by a Ser-Pro-Arg (SPR) motif in subdomain VIII, a change that is unique to ERK3/ERK4 and likely important for substrate binding and catalytic regulation (coulombe2007atypicalmitogenactivatedprotein pages 2-4, deleris2008activationloopphosphorylation pages 296-300). The overall three-dimensional organization is consistent with other MAP kinases, comprising a smaller N-terminal lobe largely responsible for ATP binding and a larger C-terminal lobe that contributes to substrate recognition; however, ERK4 contains an extended C-terminal region that is implicated in subcellular targeting and protein–protein interactions (aberg2006regulationofmapkactivated pages 6-7, rousseau2009caractérisationdela pages 144-147). Structural models based on homology and AlphaFold predictions support the presence of conserved features such as a defined C-helix and a hydrophobic spine, which are critical for maintaining catalytic conformation; yet, the extended regions support interactions with regulatory proteins like MK5, distinguishing its regulation from classical MAPKs (lindin2014mitogenactivatedproteinkinaseactivated pages 16-22).
6. Regulation  
   The regulation of MAPK4 is achieved predominantly through phosphorylation events in its activation loop and through its interactions with downstream effectors, particularly MK5. Group I p21-activated kinases (PAKs) have been identified as upstream kinases that facilitate the phosphorylation of the key serine residue (Ser186) located in the activation loop of MAPK4, a modification that is indispensable for its catalytic activation and for the formation of a stable complex with MAPKAPK5 (aberg2009dockingofprakmk5 pages 1-2, deleris2008activationloopphosphorylation pages 296-300). Upon binding to MK5, MAPK4 not only phosphorylates MK5 on its activation loop (specifically at Thr182) to promote its activation, but this interaction also results in a reciprocal phosphorylation of MAPK4 itself by MK5, establishing a loop of phosphorylation events that has been proposed to be critical for cell cycle entry (aberg2006regulationofmapkactivated pages 11-12, rousseau2010targetedinactivationof pages 1-2). In addition to activation loop phosphorylation, MAPK4 regulation may also involve its subcellular localization; it is primarily cytoplasmic under basal conditions and is subject to active nuclear export mechanisms that are CRM1-dependent, ensuring that its activity is compartmentalized (aberg2006regulationofmapkactivated pages 6-7, barbagallo2018exploringtheroles pages 24-27). These post-translational modifications, in combination with protein stability control (with ERK4 being notably more stable than ERK3), fine-tune the overall activity of MAPK4 within the cell (rousseau2009caractérisationdela pages 55-59, deleris2008activationloopphosphorylation pages 318-322).
7. Function  
   MAPK4 functions as an atypical MAP kinase whose primary biological role involves the regulation of MAPK-activated protein kinase 5 (MK5), a kinase implicated in processes such as cytoskeletal organization, cell cycle progression, and stress response signaling (aberg2006regulationofmapkactivated pages 7-8, kant2006characterizationofthe pages 1-2). In the MAPK4–MK5 signaling complex, MAPK4 phosphorylates MK5 on Thr182, which is required for MK5’s full activation and cytoplasmic relocalization; in turn, activated MK5 is capable of phosphorylating MAPK4, thereby establishing a bidirectional regulatory loop (aberg2009dockingofprakmk5 pages 1-2, deleris2008activationloopphosphorylation pages 280-285). These phosphorylation events collectively promote entry into the cell cycle, a function inferred by sequence similarity and corroborated by experimental knockdown studies in cellular models (aberg2006regulationofmapkactivated pages 11-12, al2015identificationofnovel pages 33-38). Expression studies have detected MAPK4 in a number of vertebrate tissues including brain, heart, and other organs, and its stability relative to ERK3 suggests that it may exert a sustained regulatory influence in certain cell types; however, knockout mouse studies indicate that its inactivation does not result in gross developmental abnormalities, although subtle phenotypes, such as alterations in cell proliferation or behavior, have been noted (rousseau2009caractérisationdela pages 90-94, barbagallo2018exploringtheroles pages 19-24). The downstream targets of MAPK4 beyond MK5 remain poorly defined, and while MAP2 has been mentioned as a substrate in biochemical studies, the primary established functional pathway involves the MAPK4–MK5 axis that contributes to cytoskeletal dynamics and cell cycle progression (aberg2006regulationofmapkactivated pages 1-2, aberg2009dockingofprakmk5 pages 1-2).
8. Other Comments  
   Studies have detected recurrent mutations within the kinase domain of MAPK4, such as substitutions at critical residues (e.g., R114C/H), which have been found in various cancers including colorectal carcinomas, gliomas, non-small cell lung carcinomas, and melanomas; these mutations point to a potential role of MAPK4 in tumor progression, although the precise functional impact of these mutations remains to be fully elucidated (barbagallo2018exploringtheroles pages 19-24, kant2006characterizationofthe pages 2-3). Inhibitors specific to MAPK4 are not as well characterized as those for classical MAPKs or other kinases, and while its atypical activation mechanisms suggest that targeting its unique docking interactions with MK5 (for instance, the FRIEDE motif-mediated binding) may represent a potential therapeutic strategy, specific small-molecule inhibitors have not yet been advanced into clinical evaluation (dahm2025atypicalmapksin pages 1-3). Furthermore, the interdependent phosphorylation cycle between MAPK4 and MK5, as well as the regulation via CRM1-dependent nuclear export, are considered potential nodes for pharmacological intervention, though the current literature indicates that the biological implications of these regulatory events require further experimental validation (deleris2008activationloopphosphorylation pages 296-300, perander2017regulationofatypical pages 11-12).
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