1. Phylogeny  
   Ribosomal protein S6 kinase alpha-3, commonly known as RSK2 and encoded by the RPS6KA3 gene, is a member of the p90 ribosomal S6 kinase (RSK) family that falls within the large AGC serine/threonine kinase superfamily, which traces its evolutionary origins to early eukaryotes and is conserved across metazoans (anjum2008therskfamily pages 1-2). RSK2 has well‐characterized orthologs in numerous species spanning mammals, birds, amphibians, and even invertebrates, underscoring its pivotal role in transmitting mitogenic and stress-related signals (romeo2012regulationandfunction pages 1-2). Its evolutionary history reflects a gene duplication event that led to the emergence of distinct RSK isoforms, with RSK2 sharing high sequence similarity in its catalytic domains with other family members such as RSK1, RSK3, and RSK4, despite bearing differences in regulatory regions (anjum2008therskfamily pages 2-4). The protein is situated in a kinase group that includes other key regulators such as PDK1, AKT, and SGK, forming an evolutionarily conserved core of signaling molecules that are integral to the regulation of cell growth, metabolism, and survival (romeo2012regulationandfunction pages 1-2). Comparative genomic analyses have further demonstrated that RSK2, along with its RSK relatives, is derived from an ancient duplication within the AGC kinase branch, which is itself part of the kinome’s evolution from the Last Eukaryotic Common Ancestor (LECA) (anjum2008therskfamily pages 1-2). This phylogenetic placement not only affirms the structural conservation of the catalytic domains, including the N-terminal kinase domain (NTKD) and the C-terminal kinase domain (CTKD), but also emphasizes the conserved regulatory features necessary for its proper function in signal transduction (romeo2012regulationandfunction pages 1-2).
2. Reaction Catalyzed  
   RSK2 functions as a serine/threonine protein kinase that catalyzes the transfer of a phosphate group from ATP to hydroxyl groups on specific serine or threonine residues of its protein substrates, resulting in ADP, a phosphorylated protein product, and the release of a proton; this fundamental enzymatic reaction is common to all protein kinases (sapkota2007bid1870isa pages 1-2). The reaction can be formally represented as: ATP + [protein]–(L-serine/threonine) → ADP + [protein]–(L-serine/threonine)-phosphate + H⁺, a transformation essential for regulating the activity of numerous downstream effectors within the cell (roux2003phosphorylationofp90 pages 9-9). This phosphorylation event modulates the function, localization, and protein–protein interactions of target molecules, thereby propagating intracellular signaling cascades (smith2005identificationofthe pages 1-1).
3. Cofactor Requirements  
   The catalytic activity of RSK2 is strictly dependent on cofactors, with magnesium ions (Mg²⁺) serving as an essential cofactor that facilitates the correct positioning of ATP within the kinase’s active site during the phosphorylation process (utepbergenov2016bacterialexpressionpurification pages 1-2). In addition to Mg²⁺, ATP is required as the phosphate donor and its binding within the conserved ATP-binding pocket is critical for proper catalytic activity (yi2021ribosomalproteins6 pages 4-6). The reliance on these cofactors ensures that the enzyme’s activity is tightly coupled to cellular energy status and ion homeostasis, thereby linking signal transduction to metabolic state (sapkota2007bid1870isa pages 1-2).
4. Substrate Specificity  
   RSK2 exhibits a substrate preference characteristic of many AGC kinases, with specificity for serine/threonine residues that are embedded in short consensus motifs generally enriched in basic amino acids; specifically, substrates often display a motif with arginine residues at −5 and −3 positions relative to the phosphorylated residue, yielding a consensus sequence such as RxRxxp[ST] (romeo2012regulationandfunction pages 9-10). This substrate signature underpins the phosphorylation of key targets including the transcription factor CREB1, which is phosphorylated at Ser133, and also extends to ribosomal protein S6 as well as eukaryotic initiation factor 4B (EIF4B), thereby regulating gene expression and protein synthesis (derewenda2013identificationofquercitrin pages 1-2). In addition, RSK2 phosphorylates other regulatory proteins—such as NR4A1/NUR77, ETV1/ER81, BAD, and DAPK1—contributing to its role in controlling cell survival, differentiation, and proliferation (romeo2012regulationandfunction pages 10-11, sapkota2007bid1870isa pages 9-10). The kinase’s substrate specificity has been established through both in vitro peptide assays and in vivo phosphorylation studies, indicating that its activity is highly discriminating despite the presence of overlapping motifs among related kinases (anjum2008therskfamily pages 2-4).
5. Structure  
   RSK2 is distinguished by its dual-domain organization, comprising an N-terminal kinase domain (NTKD) that catalyzes substrate phosphorylation and a C-terminal kinase domain (CTKD) that plays a crucial regulatory role in its activation; these two catalytic domains are connected by an approximately 100–amino acid linker region that contains key regulatory phosphorylation sites (kurinov2009structuraldiversityof pages 1-2, romeo2012regulationandfunction pages 1-2). The NTKD shares significant structural homology with other AGC kinases, featuring a characteristic bilobal fold with an N-terminal primarily β-sheet domain and a larger, predominantly α-helical C-lobe that houses the catalytic machinery, including the activation loop and the invariant lysine residue essential for ATP binding (derewenda2013identificationofquercitrin pages 1-2, utepbergenov2013theunusualmechanism pages 4-5). In contrast, the CTKD displays a fold more reminiscent of Ca²⁺/calmodulin-dependent kinases and is primarily involved in autophosphorylation events that facilitate full activation of RSK2 (kurinov2009structuraldiversityof pages 1-2). Crystallographic and biophysical studies have revealed that the N-terminal domain’s ATP-binding pocket is capable of accommodating flavonol glycoside inhibitors such as quercitrin and SL0101, with inhibitor binding inducing a distinct conformational rearrangement—a rotation of the N-lobe and repositioning of the P-loop—that is central to its mechanism of inhibition (derewenda2013identificationofquercitrin pages 1-2, utepbergenov2013theunusualmechanism pages 4-5). The presence of conserved motifs, including the activation loop, hydrophobic motif (which in RSK2 corresponds to Ser380 in the linker region), and a displaced αC-helix replaced functionally by a short β-sheet, are all critical for efficient catalysis and regulation (kurinov2009structuraldiversityof pages 1-2, utepbergenov2013theunusualmechanism pages 5-6). Additionally, the catalytic domain features elements such as the glycine-rich loop, which coordinates ATP and stabilizes transitional states during phosphoryl transfer, and the catalytic loop harboring the key aspartate residue required for substrate phosphotransfer (utepbergenov2013theunusualmechanism pages 5-6). Together, these structural elements support both the enzymatic activity and regulatory capacity of RSK2 within diverse cellular contexts (utepbergenov2016bacterialexpressionpurification pages 2-4).
6. Regulation  
   The activation of RSK2 is tightly controlled through a sequential and hierarchical phosphorylation cascade initiated by extracellular mitogenic and stress signals, leading to the recruitment and activation of upstream kinases such as ERK1/2 and PDK1 (romeo2012regulationandfunction pages 7-8). ERK1/2 initially phosphorylates the CTKD at a conserved threonine residue (Thr573), which then triggers autophosphorylation events within the linker region, notably at Ser380, to create a docking site for PDK1; this event is critical for the subsequent phosphorylation of the activation loop in the NTKD at Ser227, resulting in full catalytic activation (kurinov2009structuraldiversityof pages 1-2, utepbergenov2016bacterialexpressionpurification pages 7-10). Additional regulatory phosphorylation events occur at residues such as Thr365, Thr577, and Ser386, which modulate RSK2’s conformation, substrate recognition, and subcellular localization (utepbergenov2016bacterialexpressionpurification pages 7-10, romeo2012regulationandfunction pages 7-8). These phosphorylation events are mediated by both upstream kinases—namely ERK1/2—and by autophosphorylation, ensuring that RSK2 activity is integrated with the dynamics of the MAPK signaling cascade (roux2003phosphorylationofp90 pages 9-9, sapkota2007bid1870isa pages 9-10). Moreover, binding of specific inhibitors such as SL0101 has been shown to induce an unusual conformational change in the NTKD, resulting in an induced-fit mechanism that stabilizes an inactive conformation of the kinase and blocks ATP access (utepbergenov2013theunusualmechanism pages 4-5, aronchik2014novelpotentand pages 1-2). This dual level of regulation – through multisite phosphorylation and inhibitor-induced conformational changes – ensures that RSK2 activity is finely tuned both spatially and temporally within the cell (utepbergenov2013theunusualmechanism pages 5-6, romeo2012regulationandfunction pages 8-9).
7. Function  
   RSK2 plays a central role in transmitting signals from cell surface receptors to the nucleus, thereby orchestrating cellular processes such as proliferation, survival, differentiation, and stress responses (wright2023therapeutictargetingof pages 1-3). Upon mitogenic stimulation by growth factors like EGF or insulin and stress signals such as PMA, activated RSK2 phosphorylates key transcription factors including CREB1, ETV1/ER81, and NR4A1/NUR77, which subsequently drive the transcription of immediate-early genes and other regulatory proteins involved in cell cycle progression and differentiation (derewenda2013identificationofquercitrin pages 1-2, romeo2012regulationandfunction pages 10-11). In addition to its role in transcriptional regulation, RSK2 phosphorylates components of the translational machinery, notably ribosomal protein S6 (RPS6) and eukaryotic initiation factor 4B (EIF4B), thereby influencing mRNA translation and protein synthesis (yi2021ribosomalproteins6 pages 4-6, sapkota2007bid1870isa pages 9-10). RSK2 also modulates the activity of the mechanistic target of rapamycin (mTOR) pathway by phosphorylating and repressing pro-apoptotic proteins such as BAD and DAPK1, which promotes cell survival under stress conditions (romeo2012regulationandfunction pages 10-11, wright2023therapeutictargetingof pages 3-4). Moreover, RSK2’s involvement in the phosphorylation of histone H3 at Ser10 has been linked to chromatin remodeling and activation of immediate early genes in fibroblasts following EGF stimulation, further highlighting its role as a mediator of gene expression (smith2005identificationofthe pages 1-1, romeo2012regulationandfunction pages 10-11). Tissue-specific expression analyses indicate that RSK2 is ubiquitously expressed but exhibits particularly high levels in tissues where rapid cell proliferation and differentiation occur, such as in the brain, skeletal muscle, and glandular tissues, which correlates with its established roles in neurodevelopment and cellular growth (anjum2008therskfamily pages 1-2, poomakkoth2016p90ribosomals6 pages 2-4). Additionally, RSK2 is implicated in pathophysiological conditions including various cancers—where its hyperactivation has been shown to promote oncogenic transformation and cellular survival—and in developmental disorders such as Coffin–Lowry syndrome, which results from loss-of-function mutations in the RPS6KA3 gene (smith2005identificationofthe pages 1-1, wright2023therapeutictargetingof pages 4-6).
8. Other Comments  
   A number of experimental inhibitors targeting RSK2 have been developed to dissect its function and explore its potential as a therapeutic target; notable among these are the naturally derived flavonol glycosides such as SL0101 and the synthetic inhibitor BI-D1870, both of which have demonstrated high selectivity for the RSK family isoforms in vitro and in cellular models (derewenda2013identificationofquercitrin pages 1-2, sapkota2007bid1870isa pages 1-2). The unusual mechanism of inhibition observed with flavonol rhamnosides, whereby inhibitor binding induces a significant rotational twist in the NTKD’s N-lobe to create a unique hydrophobic pocket, has provided critical insights into the structure–activity relationships underpinning selective RSK2 inhibition (utepbergenov2013theunusualmechanism pages 4-5, aronchik2014novelpotentand pages 10-11). These inhibitors not only serve as valuable biochemical probes but also have therapeutic relevance; early-phase clinical candidates such as PMD-026 are currently under investigation for the treatment of metastatic solid tumors, including breast cancer (wright2023therapeutictargetingof pages 14-15). In terms of disease associations, the critical involvement of RSK2 in mediating growth factor signals places it at the nexus of oncogenic pathways, with its dysregulation contributing to a range of malignancies such as breast, prostate, head and neck cancers, and melanoma, while mutations in RPS6KA3 are the molecular basis for Coffin–Lowry syndrome, a genetic disorder characterized by intellectual disability and skeletal abnormalities (smith2005identificationofthe pages 1-1, romeo2012regulationandfunction pages 13-14). Furthermore, recombinant expression systems established for full-length RSK2 using bacterial platforms have greatly facilitated detailed structural, biochemical, and kinetic analyses, providing a robust platform for the screening of novel inhibitors and for elucidating the molecular mechanisms that govern its activation and regulation (utepbergenov2016bacterialexpressionpurification pages 1-2, utepbergenov2016bacterialexpressionpurification pages 7-10). These diverse lines of evidence have cemented RSK2’s status as both a critical effector in the MAPK signaling cascade and a viable target for therapeutic intervention in diseases marked by aberrant kinase signaling (wright2023therapeutictargetingof pages 15-15).
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