1. Phylogeny  
   Tyrosine‐protein kinase Lck (gene LCK) is a member of the Src family of non‐receptor protein tyrosine kinases that are largely restricted to lymphoid cells. Lck shares conserved sequence motifs and domain architectures with its paralogs such as Src, Fyn, Lyn, and others, in which the common precursor of these kinases is traceable to early metazoan evolution as proposed in the kinase complement studies (korademirnics2000srckinasemediatedsignaling pages 2-3, kwon2019tracingtheevolution pages 15-19). Orthologs of Lck have been described from invertebrate chordates to mammals, and its identification in amphioxus (Branchiostoma belcheri) further supports the evolutionary conservation of this kinase in regulating immune‐like responses (zhou2021identificationandcharacterization pages 12-13). Lck is thus placed within the Src module subgroup of the tyrosine kinome, with its phylogenetic relationships defined by its characteristic SH3 and SH2 domains followed by a catalytic kinase domain (kwon2019tracingtheevolution pages 28-32, korademirnics2000srckinasemediatedsignaling pages 9-10).
2. Reaction Catalyzed  
   Lck catalyzes the transfer of a γ‐phosphate from ATP to tyrosine residues on substrate proteins. The enzymatic reaction can be summarized as:  
     ATP + [protein]–tyrosine → ADP + [protein]–phosphotyrosine + H⁺  
   This reaction is characteristic of tyrosine kinases and underlies the mechanism by which Lck initiates phosphorylation cascades following T‑cell receptor (TCR) engagement (chylek2014phosphorylationsitedynamics pages 14-15).
3. Cofactor Requirements  
   The catalytic activity of Lck, similar to most protein kinases, requires divalent cations as cofactors. In particular, magnesium ions (Mg²⁺) are essential to coordinate ATP in the kinase active site and facilitate the phosphoryl transfer reaction (chylek2014phosphorylationsitedynamics pages 14-15, loris2007exploringstructureand pages 43-46).
4. Substrate Specificity  
   Lck displays substrate specificity for tyrosine residues, phosphorylating immunoreceptor tyrosine-based activation motifs (ITAMs) located on the cytoplasmic tails of CD3 subunits and TCR‐associated proteins. Its intrinsic substrate recognition is defined by the modular context provided by its SH2 and SH3 domains, which aid in docking to phosphorylated partners and proline‐rich motifs, respectively. For example, during TCR activation, Lck selectively phosphorylates tyrosine residues within ITAMs that have a conserved motif arrangement, thereby creating binding sites for downstream effectors such as the ZAP-70 tyrosine kinase (samraj2005rolefortyrosine pages 33-36, chylek2014phosphorylationsitedynamics pages 15-16). This substrate specificity, while influenced by direct recognition of the target sequence, is also dictated by the recruitment of Lck to plasma membrane microdomains via its interactions with CD4, CD8 and other receptor-associated proteins (korademirnics2000srckinasemediatedsignaling pages 4-5).
5. Structure  
   Lck exhibits the canonical domain organization typical of Src family kinases. At its N-terminus, a unique domain undergoes myristoylation which is critical for its membrane association; frequently, palmitoylation further strengthens its localization to lipid rafts. Following the unique domain, Lck contains an SH3 domain that binds proline-rich sequences, and an SH2 domain that binds phosphotyrosine-containing motifs, thereby enabling precise substrate targeting and regulation. The central catalytic kinase (SH1) domain is responsible for the phosphoryl transfer reaction. A short C-terminal tail harbors a regulatory tyrosine (Y505) whose phosphorylation by C-terminal Src kinase (Csk) enforces an intramolecular interaction with the SH2 domain, stabilizing an autoinhibited conformation. In contrast, phosphorylation of Y394 within the activation loop facilitates full activation of the kinase (majeti2000negativeregulationof pages 19-25, posevitz2007functionalelucidationof pages 34-37). High-resolution structural studies and homology models reveal that the assembly of a hydrophobic regulatory spine and positioning of the C-helix in the kinase domain are critical for the switch between inactive and active states (kwon2019tracingtheevolution pages 28-32, loris2007exploringstructureand pages 49-52).
6. Regulation  
   Lck activity is tightly regulated by reversible phosphorylation events. Autophosphorylation at Y394 in the activation loop leads to kinase activation, whereas phosphorylation at Y505 creates an intramolecular association with its SH2 domain that results in an inactive conformation (majeti2000negativeregulationof pages 19-25, samraj2005rolefortyrosine pages 93-96). Regulation is further modulated by opposing enzymes: the kinase Csk phosphorylates Y505 which suppresses Lck activity, while the receptor-like phosphatase CD45 dephosphorylates Y505, thereby maintaining Lck in a “primed” state ready for activation upon TCR stimulation (majeti2000negativeregulationof pages 245-251, okada2012regulationofthe pages 1-3). Additional regulatory layers include reversible lipid modifications such as myristoylation and palmitoylation, which ensure proper plasma membrane localization and targeting to specialized microdomains (posevitz2007functionalelucidationof pages 43-46, korademirnics2000srckinasemediatedsignaling pages 1-2). The dynamic interplay among these post-translational modifications orchestrates the balance between Lck’s active and inactive forms, thereby controlling the threshold for T-cell activation (samraj2005rolefortyrosine pages 8-13, korademirnics2000srckinasemediatedsignaling pages 5-6).
7. Function  
   Lck plays a central role in T-cell development and activation. It is expressed at all stages of thymocyte maturation and is essential for T-cell receptor (TCR) signaling. Upon engagement of the TCR by a peptide antigen bound to MHC molecules, Lck associated with the cytoplasmic tails of CD4 and CD8 is recruited to the TCR complex. In this localized environment, Lck phosphorylates ITAMs on CD3 and ζ-chain subunits initiating a signaling cascade that recruits and activates ZAP-70. This cascade culminates in the activation of multiple downstream effectors, ultimately leading to lymphokine production and full T-cell activation (chylek2014phosphorylationsitedynamics pages 14-15, samraj2005rolefortyrosine pages 1-8). In addition to its role in TCR signaling, Lck is involved in signaling pathways of other receptors, such as CD2 and the IL2 receptor, contributing to the regulation of T-cell proliferation (chylek2014phosphorylationsitedynamics pages 12-13, posevitz2007functionalelucidationof pages 34-37). Lck also phosphorylates a variety of substrates including transcription factors and signaling proteins like RUNX3, PTK2B/PYK2, MAPT, RHOH, and TYROBP, linking it to broader functions in cell adhesion, migration, and apoptosis (samraj2005rolefortyrosine pages 36-41, majeti2000negativeregulationof pages 245-251).
8. Other Comments  
   Aberrant regulation of Lck has been associated with immune dysfunction and oncogenic transformation. Overactivation of Lck due to impaired phosphorylation control has been implicated in T-cell leukemias and thymic tumors, while its absence or misregulation contributes to defective T-cell development, resulting in immunodeficiency disorders (samraj2005rolefortyrosine pages 93-96, majeti2000negativeregulationof pages 245-251). Several experimental inhibitors targeting Src family kinases are in various stages of investigation for their therapeutic potential in modulating immune responses and treating malignancies; however, their specificity for Lck requires careful evaluation (posevitz2007functionalelucidationof pages 95-97, okada2012regulationofthe pages 11-12). Additionally, the evolutionary conservation of Lck, as documented in non-mammalian species like amphioxus, underscores its fundamental role in immune signaling, making Lck a target of interest in both basic and clinical immunology research (zhou2021identificationandcharacterization pages 12-13, kwon2019tracingtheevolution pages 65-69).
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