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The activation loop tyrosine 823 is essential for the transforming capacity of the c-Kit oncogenic mutant D816V

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Abstract

Oncogenic c-Kit mutations have been shown to display ligand-independent receptor activation and cell proliferation. A substitution of aspartate to valine at amino acid 816 (D816V) is one of the most commonly found oncogenic c-Kit mutation and is found in more than 90% of cases of mastocytosis and less commonly in germ cell tumors, core-binding factor acute myeloid leukemia and mucosal melanomas. The mechanisms by which this mutation leads to constitutive activation and transformation are not fully understood. Previous studies have shown that the D816V mutation causes a structural change in the activation loop resulting in weaker binding of the activation loop to the juxtamembrane domain. In this paper we have investigated the role of Y823, the only tyrosine residue in the activation loop, and its role in oncogenic transformation by c-Kit/D816V by introducing the Y823F mutation. Although dispensable for the kinase activity of c-Kit/D816V, the presence of Y823 was crucial for cell proliferation and survival. Furthermore, mutation of Y823 selectively down-regulates the Ras/Erk and Akt pathways as well as the phosphorylation of STAT5 and reduces the transforming capacity of the D816V/c-Kit in vitro. We further show that mice injected with cells expressing c-Kit/D816V/Y823F display significantly reduced tumor size as well as tumor weight compared to controls. Finally, microarray array analysis, comparing Y823F/D816V cells with cells expressing c-Kit/D816V, demonstrate that mutation of Y823 causes up-regulation of pro-apoptotic genes whereas genes of survival pathways are down-regulated. Thus, phosphorylation of Y823 is not necessary for kinase activation, but essential for the transforming ability of the c-Kit/D816V mutant.

Key words: c-Kit; D816V, Y823F, activation loop, tyrosine phosphorylation, signaling,
Introduction

c-Kit is a type III receptor tyrosine kinase (RTK) that is expressed on the surface of hematopoietic progenitor cells, mast cells, germ cells, melanocytes and interstitial cells of Cajal.\(^1\)\(^,\)\(^2\) Its physiological ligand stem cell factor (SCF) binds to c-Kit resulting in dimerization of the receptors and a conformational change comprising release of the auto-inhibitory constraint that the juxtamembrane domain (JMD) poses on the kinase domain, outward opening of the activation loop and sequential phosphorylation of tyrosine residues in the cytoplasmic region of the receptor.\(^3\) These events in turn activate the signaling cascades through binding, phosphorylation and activation of various signaling molecules. Oncogenic activating mutations in c-Kit have been described in various tumors in the tissues where c-Kit is normally expressed.\(^2\)\(^,\)\(^4\) The most commonly found mutation in c-Kit is a single point mutation resulting from the substitution of an aspartate to a valine at position 816 (D816V) which is found in almost all cases of systemic mastocytosis and less commonly in so-called core-binding factor leukemia,\(^5\)\(^,\)\(^6\) germ cell tumors and melanomas.\(^4\)\(^,\)\(^7\)\(^,\)\(^8\) This mutation results in ligand-independent autoactivation of c-Kit\(^9\) which is followed by activation of multiple signaling cascades\(^10\)\(^-\)\(^12\) all contributing to aberrant gene expression and tumor progression. This makes D816V a target for small molecule tyrosine kinase inhibitors like dasatinib, PKC412 and SU-5416\(^13\)\(^-\)\(^17\) which either directly inhibit D816V or target the downstream effectors controlling mast cell proliferation or cell survival.\(^18\) Although a number of such molecules have been in clinical trials, problems with low efficacy, target specificity and resistance to inhibitors remains a major limitation of most inhibitors. Imatinib is a well-known inhibitor of wild-type c-Kit. However, it is not an effective inhibitor of the D816V mutant.\(^19\)

The activation loop (A-loop) present at the C-terminus of the kinase domain spans about 25 amino acids of the c-Kit receptor and is a region known for a number of activating mutations.
including the D816V mutation. Upon activation, the A-loop positions itself in the so-called DFG-in state allowing the phosphotransfer from ATP to the tyrosine hydroxyl groups on the receptor. The DFG motif is a conserved tripeptide sequence (DFG) present in the N-terminus of the A-loop. In the active kinase conformation, the A-loop extends over the carboxyterminus of the catalytic pocket and the DFG motif moves away from the ATP binding region (DFG-in) and thereby creates an active conformation of the kinase. Previous studies show that Y823 is crucial for maintaining receptor stability rather than kinase activity. It has been also shown that the network via which JMD and A-loop communicate is disturbed by D816V mutation, however introduction of a D792E mutation in the A-loop restores this interaction pattern.

In this study, we have investigated the effects of mutating Y823 to phenylalanine (Y823F) on oncogenic c-Kit/D816V signaling. We show that Y823F renders c-Kit/D816V expressing cells far more sensitive to apoptosis than the cells having Y823 intact. Cell proliferation was also severely reduced in cells expressing the c-Kit/D816V/Y823F compared to cells expressing c-Kit/D816V. Furthermore, the transforming capability of the c-Kit oncogenic mutant was hampered as the cells containing the c-Kit/D816V/Y823F double mutant were unable to phosphorylate STAT5 and lost the ability to form colonies in semi-solid medium. A reduction in phosphorylation of the adaptor proteins Cbl and Shc was also observed. The PI3-kinase/Akt and the Ras/Erk pathways were further perturbed. Tumors formed in mice by Ba/F3 cells expressing the c-Kit/D816V/Y823F double mutant were severely reduced in volume and weight compared to mice injected with c-Kit/D816V expressing cells. Taken together, our data suggests that cells expressing Y823F mutation can counter balance the uncontrolled proliferation and inhibited apoptosis of c-Kit/D816V expressing cells.
Results

Y823F mutation does not affect total tyrosine phosphorylation but reduces cell proliferation

We have previously demonstrated that the kinase activity of wild-type c-Kit is unaffected by
the Y823F mutation. Therefore, we wanted to assess whether mutation of Y823 affects the
kinase activity of c-Kit/D816V. To this end we generated the Y823F mutant in c-Kit/D816V
background stably transfected into Ba/F3 cells since they lack endogenous c-Kit expression
(Fig. 1A). Cell lines expressing c-Kit/D816V/Y823 and c-Kit/D816V, respectively, were
analyzed for phosphorylation of c-Kit. In addition to stably transfected cells, we used
transiently transfected COS-1 cells (which similar to Ba/F3 cells also lack endogenous c-Kit
expression). The absence of phosphorylation at Y823 was confirmed by Western blotting
using a pY823 specific antibody (Fig. 1B). In agreement with our data on wild-type c-Kit, the
Y823F mutation did not impair c-Kit/D816V autophosphorylation (Fig. 1B). The intensity of
the phosphotyrosine antibody signal was quantitated and normalized for c-Kit expression,
further demonstrating that there was no difference in kinase activity due to the presence of the
Y823F mutation (Fig. 1C). Taking together, this suggests that Y823 is not involved in the
regulation of the kinase activity of c-Kit/D816V.

It has previously been shown that cells expressing the c-Kit/D816V mutant display lower cell
surface expression of the receptor than cells expressing wild-type c-Kit. It was demonstrated
that this was dependent on the kinase activity of c-Kit, since it could be reversed by treatment
with a tyrosine kinase inhibitor. We could by flow cytometry analysis demonstrate that
introduction of the Y823F mutation did not alter cell surface expression of c-Kit (Fig. 1A).

We next wanted to assess whether the Y823F mutation led to any phenotypic changes and
analyzed cell proliferation by flow cytometry following EdU staining. Proliferation was
significantly reduced in cell expressing c-Kit/D816V/Y823F as compared to cells expressing the c-Kit/D816V mutant (Fig. 1D). This suggests that while the Y823 site is dispensable for kinase activity, it is involved in signaling downstream of c-Kit/D816V.

Y823 is required for intact Erk and Akt pathway signaling in c-Kit/D816V expressing cells

The D816V mutation induces ligand-independent activation of c-Kit followed by sequential recruitment of several signaling molecules that initiate signaling cascades leading to proliferation, survival and transformation. Despite being constitutively active, the D816V mutant has been reported to only weakly activate Erk and Akt in the absence of SCF\textsuperscript{24, 25} while, in murine myeloid progenitor cells, the D816V mutation renders the regulatory subunit of PI3K constitutively phosphorylated but not Akt and Erk1/2.\textsuperscript{11} We show that Ba/F3 cells expressing c-Kit/D816V responded to SCF stimulation with strong phosphorylation of Akt, while Erk and p38 phosphorylation was constitutive. In the presence of the Y823F mutation, the phosphorylation of Akt as well as Erk were strongly reduced (Fig. 2A and 2B). In contrast, phosphorylation of p38 was constitutive and unaffected by the Y823F mutation (Fig. 2A and B). These data suggest that Y823 is involved in signaling downstream of c-Kit/D816V in a selective manner.

Both cell survival and proliferation are significantly reduced by Y823F mutation

We wanted to ascertain whether the mutation of Y823 in c-Kit had an effect on cell survival. As a complement to the EdU incorporation method, the effect of the Y823F mutation on cell proliferation and survival was investigated by the trypan blue exclusion method. The number of living cells was significantly reduced in cells expressing the c-Kit/D816V/Y823F double mutant (Fig. 3A). In addition, the effect of the Y823F mutation on D816V-mediated cell survival was examined by staining the cells with Annexin V and 7-Amino Actinomycin D and
analyzed by flow cytometry. Ba/F3 cells expressing the c-Kit/D816V/Y823F mutant showed more than 40% reduction in cell survival compared to cells expressing c-Kit/D816V (Fig. 3B). These findings are in agreement with the lowered activation of Akt and Erk in the cells expressing c-Kit/D816V/Y823F.

**Y823F mutation abolishes the ability of c-Kit/D816V to form colonies in methylcellulose and reduces the phosphorylation of STAT5**

As we observed a marked decrease in both Akt and Erk1/2 phosphorylation in cells expressing c-Kit/D816V/Y823F, we wanted to investigate whether this mutation also affects the growth in semi-solid medium. Ba/F3 cells devoid of growth factors and cytokines were mixed with methylcellulose colony medium and incubated under humidified conditions for 8 days while c-Kit/D816V was able to form colonies, introduction of the Y823F mutation dramatically diminished the ability to form colonies or cell clusters (Fig. 4A). This is in agreement with our data demonstrating an increased apoptosis and reduced proliferation of Ba/F3 cells harboring the c-Kit/D816V/Y823F mutant.

Signal transducer and activator of transcription (STAT) proteins have been described to transduce signals from the membrane-bound receptors to the cell nucleus through the classical JAK-STAT pathway. Activation of STAT proteins has been linked to the expression of genes that are crucial for cell proliferation, differentiation and survival. While STAT1, STAT3 and STAT5 were tyrosine phosphorylated in D816V-transformed cells, only STAT5 was shown to be transcriptionally active in the mast cell line HMG-1.2 that carries the D816V mutation. We, therefore, aimed to investigate if phosphorylation of STAT5 was affected by the Y823F mutation. Serum-starved cells were subjected to immunoprecipitation with an anti-STAT5 antibody and phosphorylation was detected by Western blotting using a phosphotyrosine antibody. We observed a marked reduction in phosphorylation of STAT5 in
cells expressing the c-Kit/D816V/Y823F mutant compared to c-Kit/D816V expressing cells
(Fig. 4B and 4C). This suggests the importance of activated STAT5 in mediating signaling
crucial for cell proliferation, survival and probably in the ability of the oncogenic mutant to
form colonies in semi-solid media.

The Y823F mutation in c-Kit/D816V leads to a reduction in both tumor weight and
volume in athymic mice
To investigate the tumor forming capacity, five athymic mice were injected with Ba/F3 cells
expressing the c-Kit/D816V and c-Kit/D816V/Y823F mutants, respectively. All but one
animal developed solid tumors which were isolated and measured for both weight and
volume. Interestingly, one of the mice carrying cells with the Y823F mutation did not develop
any detectable tumor. The four other mice carrying the c-Kit/D816V/Y823F mutant cells
developed tumors that were significantly smaller as compared with the c-Kit/D816V mutant
controls. (Fig. 5A). Average tumor weight (Fig. 5B) and tumor volume (Fig. 5C) were
reduced by almost 80% in mice injected with cells expressing the c-Kit/D816V/Y823F
mutant.

Mutation of Y823 leads to upregulation of tumor suppressor genes and downregulation
of IL2, IL15, TGFβ1 and Myc responsive genes
Since we observed that the Y823F mutation diminishes c-Kit/D816V-mediated cell
proliferation, survival and colony formation through weaker phosphorylation of Akt, Erk1/2
and STAT5, we hypothesized that this mutation might influence c-Kit/D816V-mediated gene
expression. Therefore, we checked global gene expression using Mouse Gene 2.0 ST Array.
Oncogenic c-Kit/D816V initiates aberrant expression of numerous proto-oncogenes and anti-
apoptotic genes. Cells expressing c-Kit/D816V/Y823F displayed, compared to c-Kit/D816V
expressing cells, an up-regulation of pro-apoptotic genes, while expression of oncogenes and anti-apoptotic genes was suppressed (Fig. 6A, Table S1 and S2). Furthermore, gene set enrichment analysis (GSEA) suggests that deregulated genes (Fig. S2) display enrichment of several signaling pathways (Table S3) and oncogenic signatures (Table S4). For example, Myc (Fig. 6B), IL2 (Fig. 6C and 6E), IL15 (Fig. 6D) and TGFβ1 (Fig. 6F) pathway genes are downregulated in c-Kit/D816V/Y823F expressing cells. Surprisingly we also observed that genes that are downregulated under hypoxic conditions are also downregulated in c-Kit/D816V/Y823F expressing cells (Fig. 6G) Thus, we suggest that the Y823F mutation plays an opposing role to that of the oncogenic mutation c-Kit/D816V, which is partially mediated through transcriptional initiation of pro-apoptotic genes as well as suppression of oncogenes and anti-apoptotic genes probably by controlling STAT5 activation.

Y823F mutation causes accelerated degradation of c-Kit receptor as compared with c-Kit/D816V

To investigate the possible mechanism by which Y823F mutation exerts its growth inhibitory potential, we performed degradation assay on Ba/F3 cells transfected with c-Kit/D816V and c-Kit/D816V/Y823F. Cycloheximide treated cells were withdrawn at various time points, lysed and probed with c-Kit antibody. Degradation of receptor having Y823F mutation occurred faster as compared with c-Kit/D816V (Fig 7A). The half-life of c-Kit/D816V/Y823F was only 42 min. as compared with the half-life of c-Kit/D816V which was calculated as 72 min. (Fig. 7B).

**Discussion**

Gain of function mutations in tyrosine kinases are a major cause of progression towards transformation. The two most commonly found regions of gain of function mutations in c-Kit are the juxtamembrane domain (JMD) and the kinase domain near to the activation loop. Together these two regions, located in exon 11 and exon 17 respectively,
constitute the mutational hotspots in c-Kit. While about 85% of gastrointestinal stromal
tumors result from activating mutation in the JMD, 90% of systemic mastocytosis carry a
D816V mutation in the kinase domain. Normally, the JMD maintains the kinase in an auto-
inhibitory state and the activation process involves two check points: the release of the JMD
from the kinase domain that exposes the catalytic site to the substrate and, secondly, the
activation loop coming to the DFG-in state. Exon 18 of the activation loop of c-Kit is located
in the C-lobe of the kinase domain and is a less frequent site for mutation in tumors. To date
rather little is known about the roles of the activation loop tyrosines in other receptors other
than that they are in many cases involved the regulation of kinase activity. Previously, in vitro
studies with recombinant wild-type c-Kit, have demonstrated that the corresponding site,
Y823, is dispensable for kinase activity. A study from Laine and colleagues suggests that
several factors such as binding of a substrate, inhibitor or a point mutation within a protein
can perturb the signal propagation and corresponding cellular communication. They further
demonstrated that the communication pathway between the JMD and the activation loop is
disturbed by the D816V mutation. In the present study, we wanted to investigate the effect of
the Y823F mutation in the activation loop on downstream signaling of c-Kit/D816V. We
demonstrate that although there is no significant effect on the phosphorylation of c-Kit, the
downstream signaling through the Ras/Erk and PI3K/Akt pathways is decreased. Upon ligand
stimulation, activation of Akt, as well as of Erk and STAT5, was strongly reduced in cells
expressing the c-Kit/D816V/Y823F mutant. In contrast, phosphorylation of p38 remained
unchanged suggesting that the effect on downstream signaling is selective and that the
oncogenic mutant of c-Kit partially transduces survival and proliferative signals through the
Y823 residue.
We further show that cells expressing the c-Kit/D816V/Y823F mutant have almost a 50% reduction in cell survival and have a significantly lower cell proliferation compared to cells expressing c-Kit/D816V. However, the phenotypic outcome could be altered in presence of additional mutations due to a perturbed signaling pathway that maintains communication between distant locations in the c-Kit structure. A recent study demonstrated that the long distance communication between juxtamembrane and activation loop is disturbed by D816V mutation.\(^3\) However, mutating the two major phosphorylation sites in the JMD (Y568, Y570) resulted in the D816V mutant in enhanced proliferation\(^{30}\) suggesting that alterations in either positive or negative signaling pathways affect the transforming capacity of c-Kit/D816V. Y823 in the activation loop might be involved in binding and activation of signaling molecules whose activation is crucial for the expression of genes required for maintaining the transforming capacity of c-Kit/D816V oncogenic mutant. Our results are in concordance with other previous studies where murine Y821, analogous to c-Kit/Y823, was suggested to be important for cell proliferation and survival.\(^{31}\) Tyrosine residues homologous to Y823 in other receptors, such as EGFR and PDGFR, have also been linked to cell survival and proliferation.\(^{32-34}\) Given the fact that the effect on signaling is very selective, it is not unlikely that the phosphorylated Y823 forms a binding site for a signal transduction molecule that mediates the described effects. Although most signal transduction molecules have been demonstrated to bind to phosphorylated tyrosine residues outside the kinase domain, there are some exceptions. The corresponding tyrosine in the EGF receptor, Y845, was demonstrated to associate with the cytochrome c oxidase subunit II in a phosphorylation dependent manner.\(^{32}\) In the oncogenic fusion protein NPM-ALK, phosphorylated Y343 in the activation loop binds to the protein tyrosine phosphatase SHP1 in a phosphorylation dependent manner.\(^{35}\) Finally, the adapter protein Grb10 has been demonstrated to associate with the insulin receptor through tyrosine residues in the activation loop.\(^{36}\) We have made attempts to identify
any possible interaction partners with phosphorylated Y823 by peptide affinity pull-down, but have so far not been able to identify any selective binding partner (data not shown).

Since the Y823F mutation affects cell survival and proliferation, we sought to determine its effect on the transforming capability of c-Kit/D816V. We show that cells expressing the c-Kit/D816V/Y823F mutant lose their ability to form colonies in semi-solid medium. This effect is opposite to the tyrosine mutants of JMD, which instead enhance the transformation potential of D816V.\(^{30}\) We further show that the activation of STAT5 is significantly reduced in cells carrying the c-Kit/D816V/Y823F mutant. Under normal physiological conditions, STAT phosphorylation is tightly regulated but constitutive phosphorylation of STAT proteins has been linked to various human malignancies.\(^{37, 38}\) Studies have shown that c-Kit/D816V can directly phosphorylate several different STAT proteins although in human mastocytoma cell lines only STAT5 is activated as a transcription factor.\(^{27}\) Activated STAT5 has been directly associated with transformation of cells and enhances the aggressiveness of the tumor.\(^{39, 40}\) The exact mechanism of STAT phosphorylation by c-Kit/D816V is not clear at the present time. As STAT5 directly links the receptor to its target genes, the decrease in cell proliferation of cells expressing c-Kit/D816V/Y823F mutation could be causally linked to the decrease in STAT5 activation and thereby downregulate genes that are linked to cell proliferation. The mechanism by which Y823 links to phosphorylation of STAT5 is unclear at present. It could be that phosphorylated Y823 serves to recruit proteins involved in phosphorylation of STAT5, but this remains to be shown. To further verify the influence of the Y823F mutation on tumor formation \textit{in vivo}, Ba/F3 cells expressing c-Kit/D816V or c-Kit/D816V/Y823F, respectively, were injected into mice. Introduction of the Y823F mutation led both to reduced weight and volume of the tumors. Finally, we show the differences in global gene expression of cells expressing Y823F mutation in comparison with c-Kit/D816V oncogenic mutant using microarrays. The genes
up-regulated in c-Kit/D816V/Y823F double mutant were mostly tumor suppressor genes. These include Schip1 (Schwannomin-interacting protein 1) and is associated with tumor suppression.\textsuperscript{41} Annexin 3 is also described as both a tumor suppressor and a tumor activator protein depending on tumor and cell type.\textsuperscript{42} Another upregulated gene is Ly75, lymphocyte antigen 75, which is linked to early metastasis in ovarian cancer.\textsuperscript{43} Inpp5f, which is a polyphosphoinositide phosphatase described in cardiac hypertrophy\textsuperscript{44}, is also up-regulated in cells expressing the Y823F mutant. The down-regulated genes, however, belong mostly to anti-apoptotic pathways or survival pathways. Pim1 and Pim2 are associated with several hematological malignancies and other solid tumors.\textsuperscript{45-47} Leukemogenesis through the related receptor mutant, FLT-3-ITD, has been related to increased expression of oncogenic PIM kinases.\textsuperscript{48} Further, down-regulation of Ubiquitin specific proteases, Usp 7 and Usp 18 would enhance receptor degradation which is in concordance with lower cell survival with Y823F mutation.\textsuperscript{49} Further, the downregulated genes Myc and Bcl2 are well-characterized oncoproteins.\textsuperscript{50, 51} Thus, we conclude that tumor suppressor genes and pro-apoptotic genes are upregulated whereas genes involved in acute myeloid leukemia pathway in c-Kit/D816V/Y823F expressing cells are upregulated which is in concordance with its decreased tumorigenic potential.

We have previously shown that Y823F mutant exhibits accelerated degradation as compared with the wild type c-Kit receptor.\textsuperscript{21} We further investigated if this also holds true for Y823F mutation in c-Kit receptor carrying D816V mutation. We observed that c-Kit/D816V/Y823F degrades much faster than c-Kit/D816V and has a half-life of only 42 min. as compared with 72 min. of c-Kit/D816V receptor. Previous studies have shown that activation loop tyrosines are crucial in maintaining structural stability of the receptor, a mutation of the only potential tyrosine in activation loop of c-Kit receptor therefore might destabilize it and cause accelerated and less sustained signaling through the receptor.\textsuperscript{20, 21}
From previous studies, we know that activation loop tyrosine Y823 is not crucial for kinase activity, and its phosphorylation occurs late during the c-Kit activation process. Our study demonstrates that mutation of Y823 causes aberrant downstream signaling including a reduction in the activation of transcription factor STAT5 which further significantly reduces transforming capacity of the oncogenic D816V mutant. Future studies will aim at identifying the proteins that are likely to bind to phosphorylated Y823 that mediates the effects seen. Given the importance of phosphorylation of Y823 for transformation, it will be of importance to understand the mechanisms by which this phosphorylation is regulated, and compounds that interfere with its phosphorylation could potentially be used as selective anti-tumor drugs.

**Materials and Methods**

**Reagents and antibodies:** Transfection reagents used were Lipofectamine 2000 (Life Technologies Europe BV, Stockholm, Sweden) and jetPEI (Polyplus transfections/BioNordika, Stockholm, Sweden). Human recombinant SCF and murine recombinant IL-3 (Interleukin-3) were obtained from ProSpec Tany Technogene (Rehovot, Israel). Rabbit polyclonal anti-c-Kit serum and anti-Cbl antibodies have been described elsewhere. The phospho-tyrosine antibody 4G10 was bought from Millipore (Solna, Sweden). Antibodies against phospho-p38, p38 and Shc were from BD Transduction Laboratories. Anti-phospho-Akt antibody was purchased from Epitomics (Burlingame, CA). Polyclonal anti-Gab2, anti-Akt, anti-phospho-Erk, anti-Erk, anti-STAT5 and horseradish peroxidase-coupled secondary anti-goat antibodies were purchased from Santa Cruz Biotechnology (Dallas, TX). Secondary Horseradish peroxidase-coupled anti-mouse and anti-rabbit antibodies were from Life Technologies (Stockholm, Sweden).
Cell culture: Ba/F3 cells were cultured in RPMI 1640 medium supplemented with 10% heat-inactivated fetal bovine serum (FBS), 100 μg/ml streptomycin, 100 units/ml penicillin and 10 ng/ml recombinant murine interleukin-3 (IL-3). Dulbecco's modified Eagle's medium comprised 10% FBS, 100 μg/ml streptomycin and 100 units/ml penicillin and was used to culture COS-1 and EcoPack cells.

Expression constructs: pcDNA3-c-Kit/D816V, pMSCV-c-Kit/D816V constructs were described previously. pcDNA3-c-Kit/D816V/Y823F and pMSCV-c-Kit/D816V/Y823F constructs were generated by site-directed mutagenesis using QuikChange mutagenesis XL kit (Agilent Technologies, Stockholm, Sweden). All plasmids were verified by sequencing.

Transient and stable transfection: Transient transfection of COS1 cells was performed using JetPEI according to the manufacturer’s instructions. Transfected cells were incubated for about 24 h before they were serum-starved overnight. Cells were stimulated with 100ng/ml SCF for indicated time periods. Cell lysis and immunoprecipitation was performed as described. Stable transfections were performed as described. Cells expressing c-Kit/D816V or c-Kit/D816V/Y823F were confirmed by flow cytometry.

Immunoprecipitation and Western blotting: Stimulated cells were washed 1x with cold PBS followed by cell lysis, immunoprecipitation and Western blotting as described elsewhere. Immunodetection was performed by enhanced chemiluminescence using horseradish peroxidase substrate (Millipore Corporation, Billerica, MA, USA) and the signals were detected by a CCD camera (LAS-3000, Fujifilm, Tokyo, Japan). Signal intensities were quantified using Multi-Gauge software (Fujifilm).
**Cell proliferation and survival assay:** Ba/F3 cells were washed three times with RPMI-1640 medium and seeded in 24-well plates (70,000 cells/well). Cells were then incubated either with or without 100 ng/ml SCF or with 10 ng/ml IL-3 for 48 hours. Viable cells were counted using trypan blue exclusion method. Cell proliferation was also measured by staining the cells with Click-iT EdU Alexa 647 (Life Technologies Europe BV, Stockholm, Sweden) employing the manufacturer's protocol. Stained cells were then analyzed by flow cytometry (BD FACSCalibur). Apoptosis was measured using an Annexin-V, 7-Amino-actinomycin D (7-AAD) kit (BD Biosciences Pharmingen, Stockholm, Sweden), according to the manufacturer's instructions; double negative (Annexin-V-/7-AAD-) cells represent viable cells.

**Degradation experiment:** c-Kit/D816V and c-Kit/D816V/Y823F expressing Ba/F3 cells were incubated with 100 μg/ml of cycloheximide for 1h and samples were withdrawn at indicated time points. Total Cell lysates were subjected to SDS-PAGE followed by detection of c-Kit by Western blotting. Antibody against β-actin was used as a loading control. Half-life was calculated using Graph Pad prism software.

**Colony formation assay:** Ba/F3 cells expressing c-Kit/D816V and c-Kit/D816V/Y823F mutants were cultured in semi-solid methylcellulose medium (MethoCult M3231, Stem Cell Technologies, Grenoble, France) as described elsewhere.25

**Animal experiments:** Female athymic mice (NMRI-Nu/Nu strain) were used and housed in a controlled environment, and all procedures were approved by the regional ethics committee for animal research (approval no. M69/11). Six million cells in 100 μl Matrigel:PBS (2,3:1) were subcutaneously injected on the right flank. Mice (n=5 for each group) were monitored
daily, and tumors were excised, measured and weighed 5 days after injection. Tumor volume is calculated by \((\pi \times l \times s^2)/6\), where \(l=\) long side and \(s=\) short side.

**Gene expression analysis**

Ba/F3-c-Kit-D816V and Ba/F3-cKit-D816V-Y823F cells were serum- and cytokine- starved for 6 hours before extraction of total RNA using RNeasy Mini Kit (Qiagen, Sollentuna, Sweden). Quality of extracted RNA was checked with Bio-analyzer and then subjected to expression analysis using Affymetrix GeneChip® Mouse Gene 2.0 ST Array. Raw data were processed for RMA normalization followed by Significance Analysis of Microarrays (SAM) analysis. Additionally ANOVA analysis was performed. Gene enrichment in signaling pathways was done by Gene Set Enrichment Analysis software (GSEA- Broad Institute). The Kyoto Encyclopedia of Genes and Genomes (KEGG) pathway dataset was used for GSEA analysis.

**Conflict of interests**

The authors declare no conflict of interest.

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Figure Legends

Fig. 1. Y823F mutation in the c-Kit/D816V oncogenic mutant does not affect phosphorylation of c-Kit receptor but reduces cell proliferation.

(A) Ba/F3 cells stably transfected with c-Kit/D816V or c-Kit/D816V/Y823F plasmids, respectively, were labeled with phycoerythrin-conjugated anti-c-Kit antibodies or an isotype control to be analyzed by flow cytometry for cell surface expression. The black peak indicates cells labeled with the isotype control, and the gray peak corresponds to the cells labeled with anti-c-Kit antibody. (B) Ba/F3 cells expressing Ba/F3-c-Kit/D816V and Ba/F3-c-Kit/D816V/Y823F were serum-starved for 4 h at 37°C. Alternatively, transient transfection was performed in Cos1 cells following overnight starvation at 37°C. Following starvation cells were stimulated with SCF for 5 min. Cell lysates were prepared, immunoprecipitated (IP) with anti-c-Kit antibody and analyzed by Western blotting. Loss of phosphorylation in Y823F mutant was verified by anti-pY823 antibody. Total receptor phosphorylation was detected using phosphotyrosine (pY) antibody and c-Kit was used as a loading control. (C) Quantification of total phosphorylation was performed by measuring signal intensities from three independent experiments using Multi-Gauge software. GraphPad Prism was used to calculate significance. ns, not significant. Error bars indicate SEM (D) Ba/F3-c-Kit/D816V and Ba/F3-c-Kit/D816V/Y823F cells were grown for 48 h in the presence or absence of SCF and with IL-3. To analyze proliferating cells, EdU was added, and cells were incubated for 2 h at 37°C. Cells were fixed, labeled with Alexa Fluor 647 and analyzed by flow cytometry.

Fig. 2. The Y823F mutation in c-Kit/D816V negatively regulates select down-stream signaling pathways.
Ba/F3-c-Kit/D816V and Ba/F3-c-Kit/D816V/Y823F cells were serum-starved and treated with or without 100 ng/ml SCF. Total cell lysates were separated by SDS-PAGE, electrotransferred to Immobilon P membrane and probed with either phospho-Akt antibody or phospho-Erk1/2 or phospho-p-38 antibodies (A). Membranes were stripped and reprobed with respective non-phosphorylated total protein as loading controls. (B) Signal intensities from three independent experiments were quantified using Multi-Gauge software to calculate the difference in band intensities between the phosphorylated and unphosphorylated protein. GraphPad Prism was used to calculate significance. *ns*, not significant, **, *p* < 0.01, ***, *p* < 0.001.

**Fig. 3.** Cells expressing c-Kit/D816V/Y823F display decreased survival and proliferative capacity compared to cells expressing c-Kit/D816V

Ba/F3-c-Kit/D816V and Ba/F3-c-Kit/D816V/Y823F cells were grown for 48 h in the presence or absence of SCF and IL-3. (A). Viable cells were counted by trypan blue exclusion method (B) cells were also labeled with annexin V and 7-aminoactinomycin D and living cells were analyzed by flow cytometry. IL-3 was used as a positive control. Quantification of labeled cells was performed using FloJo software and results from three independent experiments were statistically analysed using GraphPad Prism, *ns*, not significant, **p<0.01, ***, *p* < 0.001.

**Fig. 4.** Introduction of the Y823F mutation in c-Kit/D816V leads to loss of transforming capability

Ba/F3 cells depleted from serum and cytokines were mixed with methylcellulose hematopoietic colony assay medium and incubated at 37 °C in a humidified atmosphere (A) c-Kit/D816V/Y823F mutant cells could not form colonies in semi-solid media whereas c-Kit/D816V oncogenic mutant retained its colony formation capability. (B) Stably transfected
c-Kit/D816V and c-Kit/D816V/Y823F cells were serum and cytokine starved for 4h at 37°C. Cell lysates were prepared, and endogenous STAT-5 was immunoprecipitated (IP) with STAT-5 antibody. Activation of STAT-5 was detected by Western blotting using pY antibody. Total STAT-5 was used as a loading control. (C) STAT-5 phosphorylation versus total STAT-5 was quantified using Multi-Gauge software from three independent experiments. GraphPad Prism was further used to calculate the significance. ns, not significant, ***, p < 0.001.

**Fig. 5.** Introduction of the Y823F mutation in c-Kit/D816V leads to a reduction in both tumor weight and volume in female athymic mice

Five athymic mice (NMRI-Nu/Nu strain) were subcutaneously injected with Ba/F3 cells expressing c-Kit/D816V and c-Kit/D816V/Y823F mutation. (A) Tumors carrying the c-Kit/D816V/Y823F mutant were much smaller in size and volume as compared with tumors developed from cells expressing c-Kit/D816V. Mouse 1 carrying the c-Kit/D816V/Y823F mutant was devoid of any tumor formation. (B, C) Tumors from 5 mice were excised, weighed and measured 5 days post infection. Statistical analysis was performed using GraphPad Prism. *, p < 0.05.

**Fig. 6.** Cells expressing the c-Kit/D816V/Y823F mutant display downregulated expression of proto-oncogenes and up-regulated expression of tumor suppressor genes compared to cells expressing c-Kit/D816V

Total RNA extracted from Ba/F3-c-Kit/D816V and Ba/F3-c-Kit/D816V/Y823F cells were subjected to microarray expression analysis using Affymetrix GeneChip® Mouse Gene 2.0 ST Array. (A) Differential gene expression was analyzed and presented using GraphPad
Prism. Gene set enrichment analysis shows enrichment in different oncogenic signatures (B-D) and signaling pathways (F-G).

**Fig. 7.** The c-Kit/D816V/Y823F mutant has a higher degradation rate compared to c-Kit/D816V

(A) Ba/F3 cells expressing c-Kit c-Kit/D816V and c-Kit/D816V/Y823F were treated with 100 µM of cycloheximide. Equal amount of cells were withdrawn at different time points followed by lysis and western blotting analysis. (B) Quantification of total c-Kit was performed by measuring signal intensities using Multi-Gauge software. GraphPad Prism was used to calculate half-life.
A.

B. [Graph showing band intensity for pAkt, Akt, pErk1/2, Erk1/2, P-p38, and p38 for D816V and D816V/Y823F conditions]
Figure 4

A.

D816V

D816V/Y923F

B.

p-STAT5

STAT5

C.

c-Ki/ D816V  

***

ns

0  50  100  150

pSTAT5  STAT5
Figure 5

A. Athymic mice # 1 2 3 4 5

D816V

D816V/Y823F

B. C. Tumor weight (mg) Tumor volume (mm³)

D816V  D816V/Y823F

D816V  D816V/Y823F

*
Figure 7

A.

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- c-Kit
- β-Actin

B.

Graph showing the relative degradation (%) of c-Kit-D816V and c-Kit-D816V-Y823F over time (min).

- c-Kit-D816V-Y823F
- c-Kit-D816V

Time (Min): 0, 20, 40, 60, 80, 100
Relative degradation (%): 0, 50, 100, 150

- 42 min
- 72 min
The activation loop tyrosine 823 is essential for the transforming capacity of the c-Kit oncogenic mutant D816V

Shruti Agarwal1,2, Julhash U. Kazi1,2, Sofie Mohlin1,3, Sven Pählman1,3 and Lars Rönnstrand1,2*

1Translational Cancer Research, Medicon Village, 2Lund Stem Cell Center and 3CREATE Health, Lund University, Lund, Sweden

Supplementary Materials

List of Content

Page 2-3: Table S1: Deregulated genes in Gene Level Differential Expression Analysis.

Page 5-41: Table S2: Deregulated genes in Exon Level Differential Expression Analysis.

Page 42: Table S3: Pathway enrichment analysis using Gene Set Enrichment Analysis (GSEA) pathway signature C2_all_V4.0.

Page 43: Table S4: Pathway enrichment analysis using Gene Set Enrichment Analysis (GSEA) oncogene signature C6_all_V4.0.

Page 44: Figure S1: Heatmap for deregulated genes.
### Table S1: Deregulated genes in Gene Level Differential Expression Analysis (page 2-3)

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**Supp-P3**
## Table S2: Deregulated genes in Exon Level Differential Expression Analysis (Page 4-41)

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**Supplemental Material:**
- Supp-P9

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Table S4: Pathway enrichment analysis using Gene Set Enrichment Analysis (GSEA) oncogene signature C6_all_V4.0

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<td>IL2_UP.V1_UP</td>
<td>164</td>
<td>0.52</td>
<td>2.13</td>
<td>&lt;0.001</td>
<td>0.001</td>
<td>&lt;0.001</td>
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<td>IL15_UP.V1_UP</td>
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<td>0.001</td>
<td>&lt;0.001</td>
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<td>1.58</td>
<td>0.002</td>
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<td>LTE2_UP.V1_DN</td>
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<td>WNT_UP.V1_DN</td>
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<td>1.24</td>
<td>0.065</td>
<td>0.511</td>
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<td>RB_DN.V1_DN</td>
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<td>1.14</td>
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Figure S2: Heatmap for deregulated genes