



Pathway Analysis Report

This report contains the pathway analysis results for the submitted sample ". Analysis was performed against Reactome version 89 on 26/09/2024. The web link to these results is:

<https://reactome.org/PathwayBrowser/#/ANALYSIS=MjAyNDA4MjQyMzM4NDJfMTU4MTA%3D>

Please keep in mind that analysis results are temporarily stored on our server. The storage period depends on usage of the service but is at least 7 days. As a result, please note that this URL is only valid for a limited time period and it might have expired.

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1. Introduction

Reactome is a curated database of pathways and reactions in human biology. Reactions can be considered as pathway 'steps'. Reactome defines a 'reaction' as any event in biology that changes the state of a biological molecule. Binding, activation, translocation, degradation and classical biochemical events involving a catalyst are all reactions. Information in the database is authored by expert biologists, entered and maintained by Reactome's team of curators and editorial staff. Reactome content frequently cross-references other resources e.g. NCBI, Ensembl, UniProt, KEGG (Gene and Compound), ChEBI, PubMed and GO. Orthologous reactions inferred from annotation for *Homo sapiens* are available for 14 non-human species including mouse, rat, chicken, puffer fish, worm, fly and yeast. Pathways are represented by simple diagrams following an SBGN-like format.

Reactome's annotated data describe reactions possible if all annotated proteins and small molecules were present and active simultaneously in a cell. By overlaying an experimental dataset on these annotations, a user can perform a pathway over-representation analysis. By overlaying quantitative expression data or time series, a user can visualize the extent of change in affected pathways and its progression. A binomial test is used to calculate the probability shown for each result, and the p-values are corrected for the multiple testing (Benjamini–Hochberg procedure) that arises from evaluating the submitted list of identifiers against every pathway.

To learn more about our Pathway Analysis, please have a look at our relevant publications:

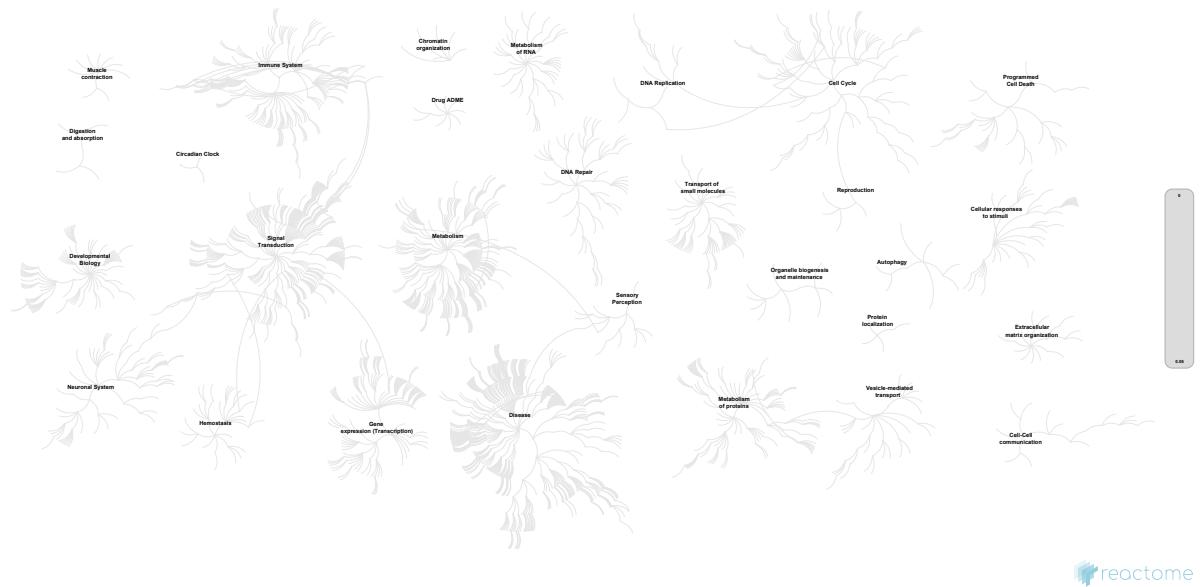
Fabregat A, Sidiropoulos K, Garapati P, Gillespie M, Hausmann K, Haw R, ... D'Eustachio P (2016). The reactome pathway knowledgebase. *Nucleic Acids Research*, 44(D1), D481–D487. <https://doi.org/10.1093/nar/gkv1351>. 

Fabregat A, Sidiropoulos K, Viteri G, Forner O, Marin-Garcia P, Arnau V, ... Hermjakob H (2017). Reactome pathway analysis: a high-performance in-memory approach. *BMC Bioinformatics*, 18. 

2. Properties

- This is an **overrepresentation** analysis: A statistical (hypergeometric distribution) test that determines whether certain Reactome pathways are over-represented (enriched) in the submitted data. It answers the question 'Does my list contain more proteins for pathway X than would be expected by chance?' This test produces a probability score, which is corrected for false discovery rate using the Benjamani-Hochberg method. ↗
- 6189 out of 10999 identifiers in the sample were found in Reactome, where 2484 pathways were hit by at least one of them.
- All non-human identifiers have been converted to their human equivalent. ↗
- This report is filtered to show only results for species 'Homo sapiens' and resource 'all resources'.
- The unique ID for this analysis (token) is MjAyNDA4MjQyMzM4NDJfMTU4MTA%3D. This ID is valid for at least 7 days in Reactome's server. Use it to access Reactome services with your data.

3. Genome-wide overview



This figure shows a genome-wide overview of the results of your pathway analysis. Reactome pathways are arranged in a hierarchy. The center of each of the circular "bursts" is the root of one top-level pathway, for example "DNA Repair". Each step away from the center represents the next level lower in the pathway hierarchy. The color code denotes over-representation of that pathway in your input dataset. Light grey signifies pathways which are not significantly over-represented.

4. Most significant pathways

The following table shows the 25 most relevant pathways sorted by p-value.

Pathway name	Entities				Reactions	
	found	ratio	p-value	FDR*	found	ratio
Unwinding of DNA	12 / 12	7.68e-04	0.192	0.943	4 / 4	2.67e-04
BH3-only proteins associate with and inactivate anti-apoptotic BCL-2 members	11 / 11	7.04e-04	0.204	0.943	5 / 5	3.33e-04
Recruitment of mitotic centrosome proteins and complexes	67 / 81	0.005	0.213	0.943	3 / 3	2.00e-04
Displacement of DNA glycosylase by APEX1	10 / 10	6.40e-04	0.218	0.943	8 / 8	5.33e-04
Inactivation of CSF3 (G-CSF) signaling	24 / 27	0.002	0.221	0.943	9 / 9	6.00e-04
Regulation of NFE2L2 gene expression	9 / 9	5.76e-04	0.234	0.943	7 / 7	4.67e-04
Diseases of DNA repair	45 / 54	0.003	0.247	0.943	34 / 34	0.002
Activation of ATR in response to replication stress	33 / 39	0.002	0.256	0.943	9 / 9	6.00e-04
Recognition and association of DNA glycosylase with site containing an affected purine	32 / 38	0.002	0.269	0.943	10 / 10	6.67e-04
DEx/H-box helicases activate type I IFN and inflammatory cytokines production	7 / 7	4.48e-04	0.27	0.943	5 / 5	3.33e-04
TNFR1-induced NF-kappa-B signaling pathway	28 / 33	0.002	0.272	0.943	5 / 5	3.33e-04
Centrosome maturation	67 / 83	0.005	0.273	0.943	6 / 6	4.00e-04
TP53 regulates transcription of additional cell cycle genes whose exact role in the p53 pathway remain uncertain	24 / 28	0.002	0.274	0.943	14 / 14	9.33e-04
AURKA Activation by TPX2	60 / 74	0.005	0.274	0.943	2 / 2	1.33e-04
TP53 Regulates Transcription of Death Receptors and Ligands	16 / 18	0.001	0.274	0.943	7 / 7	4.67e-04
TP53 Regulates Transcription of Cell Cycle Genes	53 / 65	0.004	0.275	0.943	41 / 42	0.003
Negative regulators of DDX58/IFIH1 signaling	31 / 37	0.002	0.282	0.943	13 / 13	8.67e-04
Diseases of DNA Double-Strand Break Repair	34 / 41	0.003	0.29	0.943	9 / 9	6.00e-04
Defective homologous recombination repair (HRR) due to BRCA2 loss of function	34 / 41	0.003	0.29	0.943	4 / 4	2.67e-04

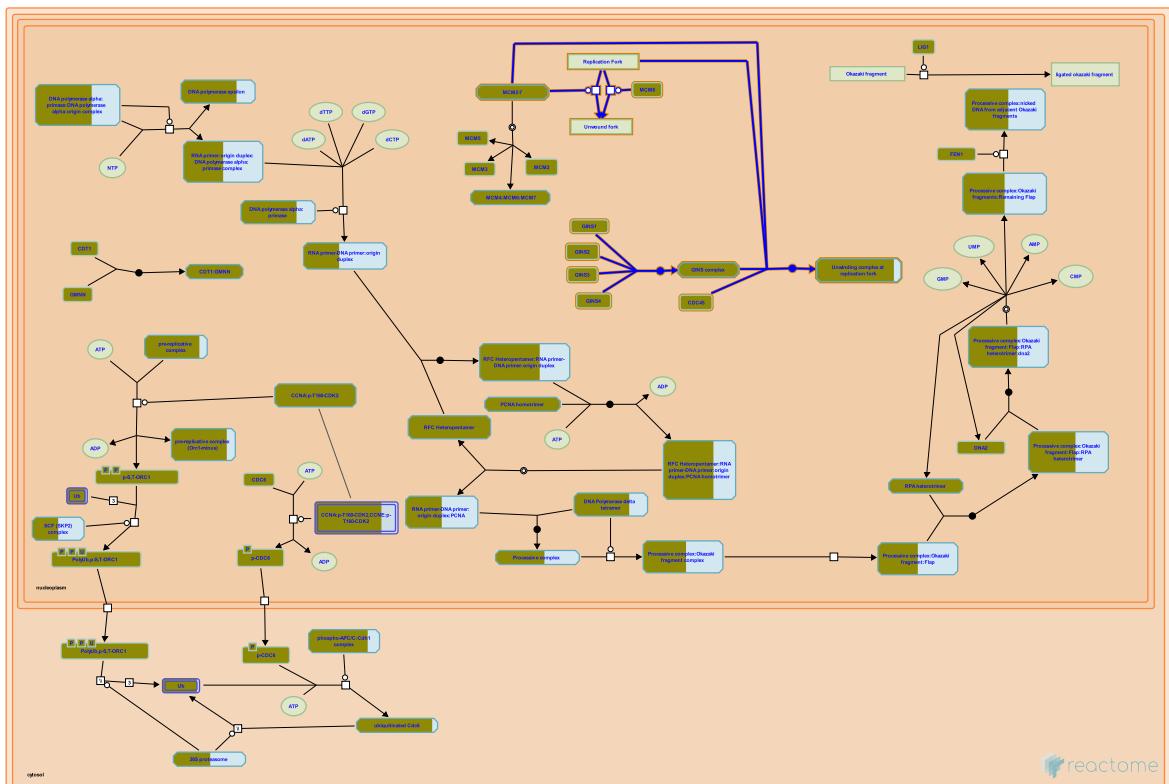
Pathway name	Entities				Reactions	
	found	ratio	p-value	FDR*	found	ratio
Recognition and association of DNA glycosylase with site containing an affected pyrimidine	34 / 41	0.003	0.29	0.943	20 / 21	0.001
TNF receptor superfamily (TNFSF) members mediating non-canonical NF- κ B pathway	15 / 17	0.001	0.292	0.943	12 / 12	8.00e-04
Regulation of HMOX1 expression and activity	6 / 6	3.84e-04	0.292	0.943	4 / 4	2.67e-04
NADE modulates death signalling	6 / 6	3.84e-04	0.292	0.943	3 / 3	2.00e-04
NFE2L2 regulating ER-stress associated genes	6 / 6	3.84e-04	0.292	0.943	2 / 2	1.33e-04
APC-Cdc20 mediated degradation of Nek2A	22 / 26	0.002	0.305	0.943	3 / 3	2.00e-04

* False Discovery Rate

5. Pathways details

For every pathway of the most significant pathways, we present its diagram, as well as a short summary, its bibliography and the list of inputs found in it.

1. Unwinding of DNA (R-HSA-176974)



Cellular compartments: nucleoplasm.

DNA Replication is regulated accurately and precisely by various protein complexes. Many members of the MCM protein family are assembled into the pre-Replication Complexes (pre-RC) at the end of M phase of the cell cycle. DNA helicase activity of some of the MCM family proteins are important for the unwinding of DNA and initiation of replication processes. This section contains four events which have been proved in different eukaryotic experimental systems to involve various proteins for this essential step during DNA Replication.

References

- Danis E, Maiorano D, Cuvier O & Mechali M (2005). MCM8 is an MCM2-7-related protein that functions as a DNA helicase during replication elongation and not initiation. *Cell*, 120, 315-28. [🔗](#)
- Diffley JF, Labib K & Tercero JA (2000). Uninterrupted MCM2-7 function required for DNA replication fork progression. *Science*, 288, 1643-7. [🔗](#)

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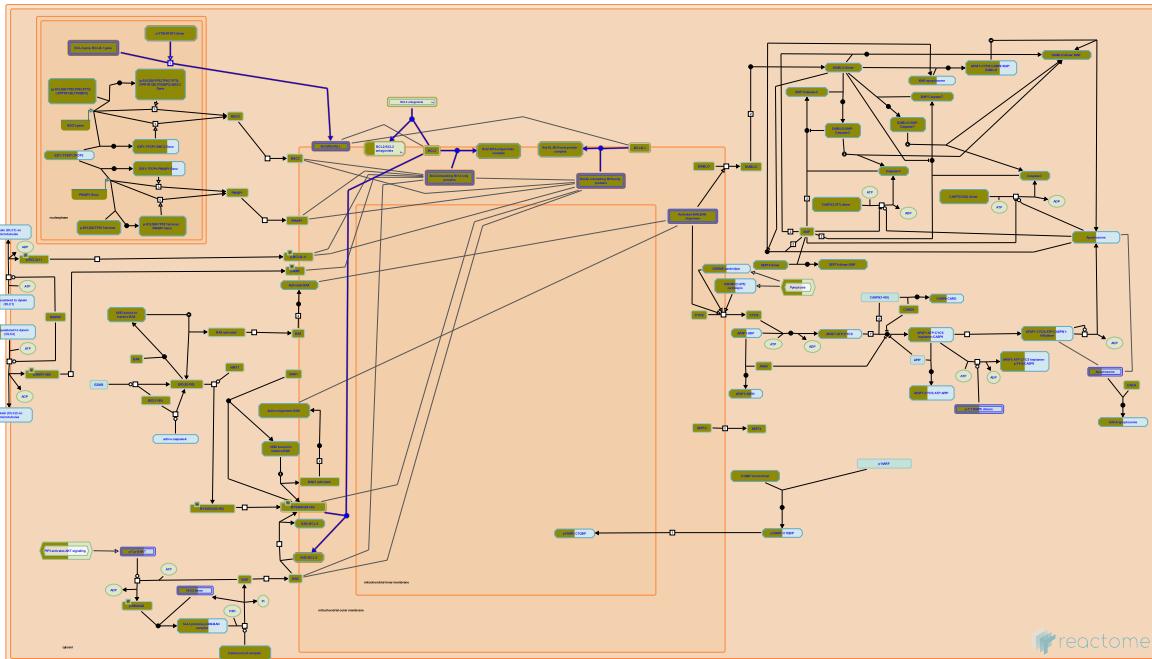
Date	Action	Author
2006-03-17	Edited	Gopinathrao G
2006-03-17	Authored	Tye BK

Date	Action	Author
2006-03-18	Created	Gopinathrao G
2024-05-25	Modified	Weiser JD

12 submitted entities found in this pathway, mapping to 12 Reactome entities

Input	UniProt Id	Input	UniProt Id	Input	UniProt Id
ENSG0000073111	P49736	ENSG0000076003	Q14566	ENSG0000093009	O75419
ENSG0000100297	P33992	ENSG0000101003	Q14691	ENSG0000104738	P33991
ENSG0000112118	P25205	ENSG0000125885	Q9UJA3	ENSG0000131153	Q9Y248
ENSG0000147536	Q9BRT9	ENSG0000166508	P33993	ENSG0000181938	Q9BRX5

2. BH3-only proteins associate with and inactivate anti-apoptotic BCL-2 members (R-HSA-111453)



Cellular compartments: mitochondrial outer membrane.

Bcl-2 interacts with tBid (Yi et al. 2003), BIM (Puthalakath et al. 1999), PUMA (Nakano and Vousden 2001), NOXA (Oda et al. 2000), BAD (Yang et al. 2005), BMF (Puthalakath et al. 2001), resulting in inactivation of BCL2. Binding of BCL2 to tBID inhibits BID-induced cytochrome C release and apoptosis (Yi et al. 2003). BH3 only proteins associate with and inactivate anti-apoptotic BCL-XL.

References

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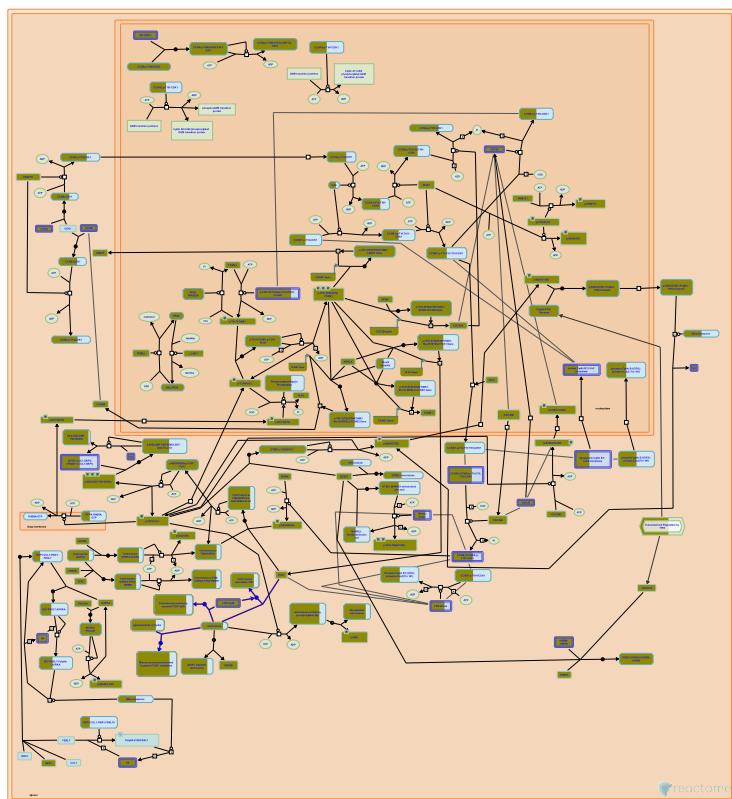
Date	Action	Author
2004-08-09	Created	Tsujimoto Y, Hardwick JM

9 submitted entities found in this pathway, mapping to 11 Reactome entities

Input	UniProt Id	Input	UniProt Id	Input	UniProt Id
ENSG00000002330	Q92934	ENSG00000015475	P55957	ENSG00000104081	Q96LC9
ENSG00000105327	Q9BXH1	ENSG00000141682	Q13794	ENSG00000153094	O43521
ENSG00000168610	P40763	ENSG00000171552	Q07817	ENSG00000171791	P10415

Input	Ensembl Id	Input	Ensembl Id
ENSG00000171552	ENSG00000171552	ENSG00000171791	ENSG00000171791

3. Recruitment of mitotic centrosome proteins and complexes (R-HSA-380270)



Cellular compartments: cytosol.

The mitotic spindle becomes established once centrosomes have migrated to opposite poles and the nuclear envelope has broken down. During this stage, interphase centrosomes mature into mitotic centrosomes recruiting additional gamma TuRC complexes and acquiring mitosis-associated centrosomal proteins including NuMA, Plk1 and CDK11p58 (reviewed in Schatten 2008; Raynaud-Messina and Merdes 2007).

References

Schatten H (2008). The mammalian centrosome and its functional significance. *Histochem Cell Biol*, 129, 667-86. [🔗](#)

Raynaud-Messina B & Merdes A (2007). Gamma-tubulin complexes and microtubule organization. *Curr Opin Cell Biol*, 19, 24-30. [🔗](#)

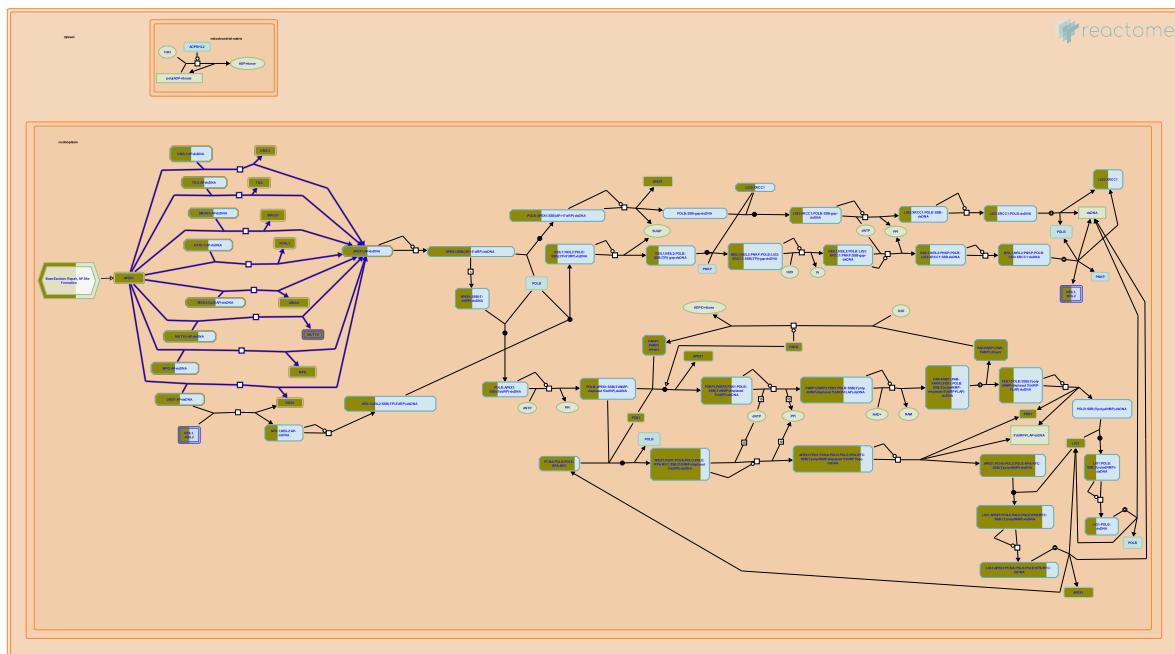
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Date	Action	Author
2008-11-09	Edited	Matthews L
2008-11-11	Authored	Matthews L
2008-11-11	Created	Matthews L
2008-11-17	Reviewed	Merdes A
2024-05-25	Modified	Weiser JD

67 submitted entities found in this pathway, mapping to 68 Reactome entities

Input	UniProt Id	Input	UniProt Id	Input	UniProt Id
ENSG0000005249	P31323	ENSG00000007168	P43034	ENSG00000008128	Q9UQ88
ENSG00000037042	Q9NRH3	ENSG00000054282	Q86SQ7	ENSG00000072864	Q9NXR1
ENSG00000074054	Q7Z460	ENSG00000077380	Q13409	ENSG00000078674	Q15154
ENSG00000080824	P07900	ENSG00000092036	Q9H6D7	ENSG00000101004	Q9Y2I6
ENSG00000101367	Q15691	ENSG00000101639	Q8TEP8	ENSG00000103540	O43303
ENSG00000104833	P04350	ENSG00000105568	P30153	ENSG00000106477	Q9BYV8
ENSG00000108953	P62258	ENSG00000110274	Q9UPV0	ENSG00000112877	Q9P209
ENSG00000114107	Q8NHQ1	ENSG00000116127	Q8TCU4	ENSG00000117650	P51955
ENSG00000126001	Q9BV73	ENSG00000126216	Q96CW5	ENSG00000127824	P68366
ENSG00000127914	Q99996	ENSG00000128159	Q96RT7	ENSG00000131351	Q9BT25
ENSG00000131462	P23258, Q9NRH3	ENSG00000136861	Q96SN8	ENSG00000137100	O75935
ENSG00000137814	Q9NVX0	ENSG00000137822	Q9UGJ1	ENSG00000138107	P61163
ENSG00000141551	P48730	ENSG00000141577	Q9UPN4	ENSG00000142731	O00444
ENSG00000147400	P41208	ENSG00000148019	Q5JTW2	ENSG00000151849	Q9HC77
ENSG00000152082	Q6NZ67	ENSG00000152240	Q96CS2	ENSG00000160299	O95613
ENSG00000166037	Q86XR8	ENSG00000166851	P53350	ENSG00000170027	P61981
ENSG00000173272	Q6P582	ENSG00000174799	Q66GS9	ENSG00000175203	Q13561
ENSG00000175216	Q14008	ENSG00000176101	O43805	ENSG00000182923	Q96MT8
ENSG00000188229	P68371	ENSG00000197102	Q14204	ENSG00000198089	A8K8P3
ENSG00000204843	Q14203-2	ENSG00000204899	Q08AG7	ENSG00000213066	O95684
ENSG00000213397	Q99871	ENSG00000213923	P49674	ENSG00000214367	Q68CZ6
ENSG00000227739	P07437	ENSG00000248333	P21127	ENSG00000249115	O94927
ENSG00000275835	Q96RT8				

4. Displacement of DNA glycosylase by APEX1 (R-HSA-110357)



Cellular compartments: nucleoplasm.

Following cleavage of the damaged base, DNA glycosylase is displaced by APEX1, an AP endonuclease (Parikh et al. 1998).

References

Tainer JA, Bharati S, Krokan HE, Mol CD, Slupphaug G & Parikh SS (1998). Base excision repair initiation revealed by crystal structures and binding kinetics of human uracil-DNA glycosylase with DNA. EMBO J, 17, 5214-26. [View](#)

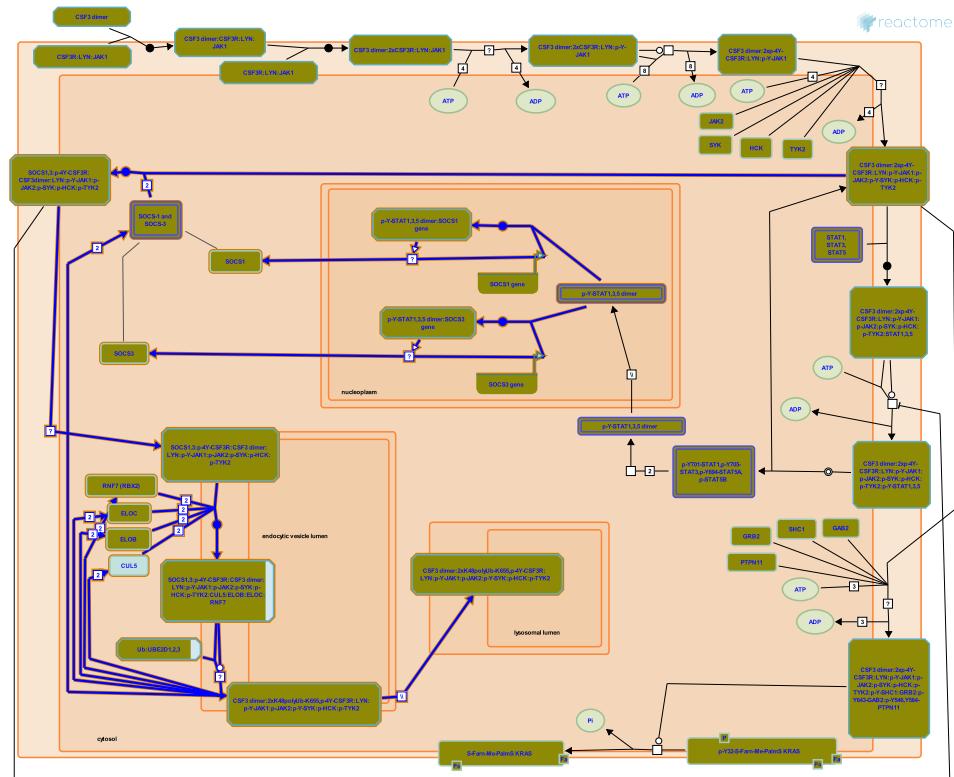
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Date	Action	Author
2004-01-29	Created	Matthews L
2004-02-03	Edited	Matthews L
2004-02-03	Authored	Matthews L
2014-12-04	Revised	Orlic-Milacic M
2014-12-04	Edited	Orlic-Milacic M
2014-12-22	Reviewed	Borowiec JA
2024-05-25	Modified	Weiser JD

9 submitted entities found in this pathway, mapping to 10 Reactome entities

Input	UniProt Id	Input	UniProt Id	Input	UniProt Id
ENSG00000065057	P78549	ENSG00000076248	P13051-1	ENSG00000100823	P27695
ENSG00000103152	P29372	ENSG00000114026	O15527	ENSG00000123415	Q53HV7
ENSG00000129071	O95243	ENSG00000132781	Q9UIF7-3, Q9UIF7-6	ENSG00000139372	Q13569

5. Inactivation of CSF3 (G-CSF) signaling (R-HSA-9705462)



Signaling by CSF3 causes its own inactivation, thereby preventing overproliferation of neutrophils (reviewed in Beekman and Touw 2010, Palande et al. 2013). Activated CSF3R recruits and activates JAK2, which phosphorylates STAT1, STAT3, and STAT5. The phosphorylated STATs transit to the nucleus and enhance the expression of SOCS1 and SOCS3, inhibitors of CSF3R signaling (inferred from mouse homologs). SOCS3, the principle negative regulator, binds the phosphorylated C-terminal region of CSF3R (Hörtner et al. 2002, van de Geijn et al. 2004, and inferred from mouse homologs) and acts in two ways: direct inhibition of the phosphorylation activity of JAK2 (van de Geijn et al. 2004) and promotion of endocytosis (Ward et al. 1999, Aarts et al. 2004, Irandoost et al. 2007) and ubiquitination (Irandoost et al. 2007, Wölfle et al. 2009) of CSF3R.

References

- Roovers O, Aarts LH, Ward AC & Touw IP (2004). Receptor activation and 2 distinct COOH-terminal motifs control G-CSF receptor distribution and internalization kinetics. *Blood*, 103, 571-9. [🔗](#)
- Meenhuys A, Palande K, Jevdjovic T & Touw IP (2013). Scratching the surface: signaling and routing dynamics of the CSF3 receptor. *Front Biosci (Landmark Ed)*, 18, 91-105. [🔗](#)
- Johnston JA, Nielsch U, Haan S, Hörtner M, Mayr LM & Heinrich PC (2002). Suppressor of cytokine signaling-3 is recruited to the activated granulocyte-colony stimulating factor receptor and modulates its signal transduction. *J Immunol*, 169, 1219-27. [🔗](#)
- Touw IP & Beekman R (2010). G-CSF and its receptor in myeloid malignancy. *Blood*, 115, 5131-6. [🔗](#)
- Irandoost M, Roovers O, Meenhuys A, Gits J, Touw IP & Wölfle A (2009). Site-specific ubiquitination determines lysosomal sorting and signal attenuation of the granulocyte colony-stimulating factor receptor. *Traffic*, 10, 1168-79. [🔗](#)

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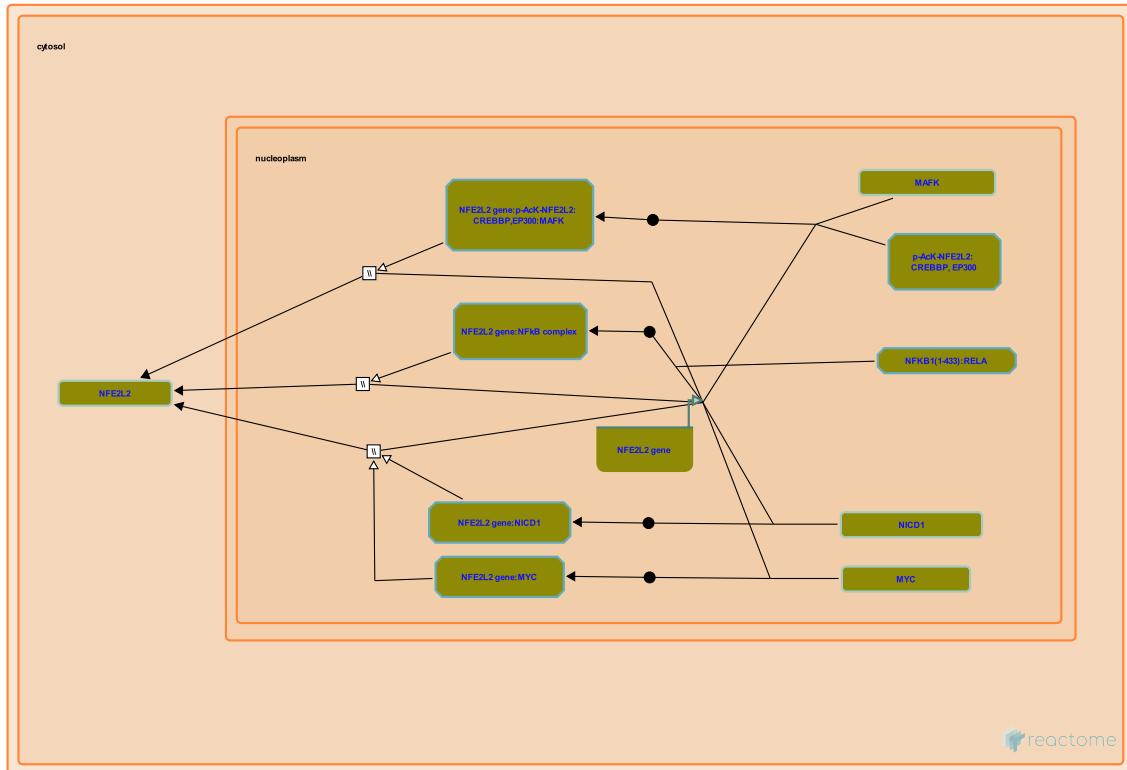
Date	Action	Author
2020-10-18	Edited	May B
2020-10-18	Authored	May B
2020-10-24	Created	May B
2020-12-12	Reviewed	Touw IP

21 submitted entities found in this pathway, mapping to 24 Reactome entities

Input	UniProt Id	Input	UniProt Id	Input	UniProt Id
ENSG0000072401	P51668	ENSG0000096968	O60674	ENSG0000101336	P08631
ENSG0000103363	Q15370	ENSG0000105397	P29597	ENSG0000108342	P09919
ENSG0000109332	P61077	ENSG0000114125	Q9UBF6	ENSG0000115415	P42224
ENSG0000119535	Q99062	ENSG0000126561	P42229	ENSG0000150991	P0CG48
ENSG0000154582	Q15369	ENSG0000162434	P23458	ENSG0000165025	P43405
ENSG0000168610	P40763	ENSG0000170315	P0CG47, P62987	ENSG0000173757	P51692
ENSG0000184557	O14543	ENSG0000185338	O15524	ENSG0000254087	P07948

Input	Ensembl Id	Input	Ensembl Id
ENSG0000184557	ENSG0000184557	ENSG0000185338	ENSG0000185338

6. Regulation of NFE2L2 gene expression (R-HSA-9818749)



Sub-pathway represents a collection of events involved in the expression of the NFE2L2 gene. The NFE2L2 gene is transcriptionally regulated by multiple transcription factors like Myc, NFKB, NFE2L2 itself and many more. This diverse regulation of NFE2L2 connects its regulation with other signalling pathways (He et al, 2020)

References

Edit history

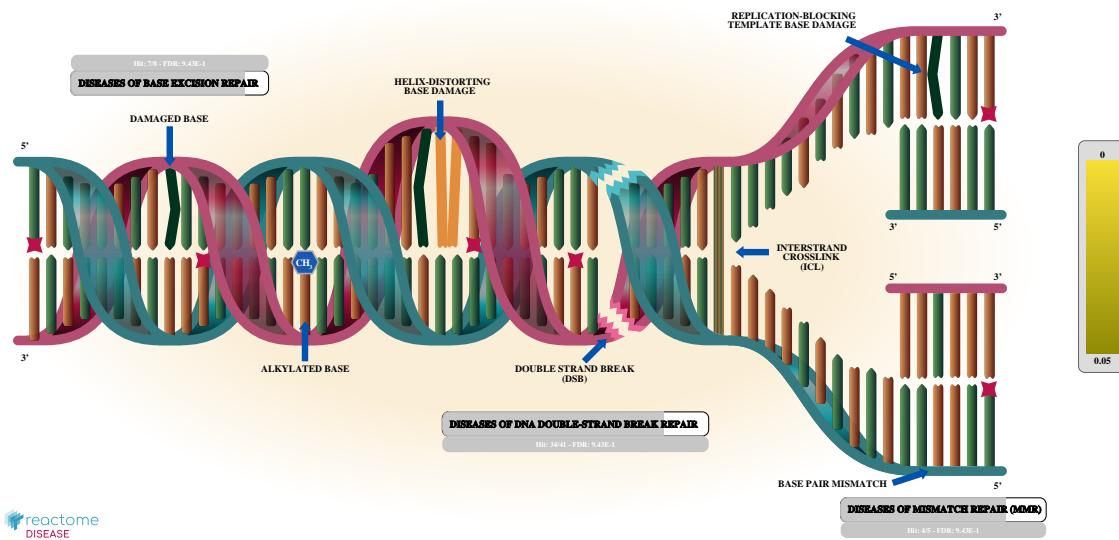
Date	Action	Author
2022-10-10	Edited	Tiwari K
2022-10-10	Authored	Tiwari K
2022-10-20	Created	Tiwari K
2023-10-12	Modified	Weiser JD

8 submitted entities found in this pathway, mapping to 9 Reactome entities

Input	UniProt Id	Input	UniProt Id	Input	UniProt Id
ENSG0000005339	Q92793	ENSG0000100393	Q09472	ENSG0000109320	P19838
ENSG0000116044	Q16236	ENSG0000136997	P01106	ENSG0000148400	P46531
ENSG0000173039	Q04206	ENSG0000198517	O60675		

Input	Ensembl Id
ENSG0000116044	ENSG0000116044

7. Diseases of DNA repair (R-HSA-9675135)



Diseases: genetic disease.

Germline and somatic defects in genes that encode proteins that participate in DNA repair give rise to genetic instability that can lead to malignant transformation or trigger cellular senescence or apoptosis. Germline defects in DNA repair genes are an underlying cause of familial cancer syndromes and premature ageing syndromes. Somatic defects in DNA repair genes are frequently found in tumors. For review, please refer to Tiwari and Wilson 2019.

We have so far annotated diseases of mismatch repair, diseases of base excision repair and diseases of DNA double-strand break repair.

Defects in mammalian DNA mismatch repair (MMR) genes (MLH1, PMS2, MSH2, and MSH6) result in microsatellite instability (MSI) and reduced fidelity during replication and repair steps. Defective variants of MMR genes are associated with sporadic cancers with hypermutation phenotypes as well as hereditary cancer syndromes such as Lynch syndrome (hereditary non-polyposis colorectal cancer) and constitutional mismatch repair deficiency syndrome (CMMRD). MSI is an important predictor of sensitivity to cancer immunotherapy as the high mutational burden renders MSI tumors immunogenic and sensitive to programmed cell death-1 (PD-1) immune checkpoint inhibitors (Mandal et al. 2019). For review, please refer to Pena-Diaz and Rasmussen 2016, Sijmons and Hofstra 2016, Tabori et al. 2017, Baretti and Le 2018.

Germline mutations, single nucleotide polymorphisms (SNPs) and somatic mutations in several genes involved in base excision repair (BER), a DNA repair pathway where a damaged DNA base is excised and replaced with a correct base, are involved in the development of cancer and several oxidative stress-related diseases. For review, please refer to Fu et al. 2012, Fletcher and Houlston 2010, Brenerman et al. 2014, Patrono et al. 2014, and D'Errico et al. 2017.

Germline mutations in genes involved in repair of DNA double-strand breaks (DSBs) are the underlying cause of several cancer predisposition syndromes, some of which also encompass developmental disorders associated with immune dysfunction, radiosensitivity and neurodegeneration. Somatic mutations in genes involved in DSB repair also occur in sporadic cancers. For review, please refer to McKinnon and Caldecott 2007, Keijzers et al. 2017, and Jachimowicz et al. 2019.

References

- Houlston RS & Fletcher O (2010). Architecture of inherited susceptibility to common cancer. *Nat. Rev. Cancer*, 10, 353-61. [🔗](#)
- Wilson DM & Tiwari V (2019). DNA Damage and Associated DNA Repair Defects in Disease and Premature Aging. *Am. J. Hum. Genet.*, 105, 237-257. [🔗](#)
- Fu D, Samson LD & Calvo JA (2012). Balancing repair and tolerance of DNA damage caused by alkylating agents. *Nat. Rev. Cancer*, 12, 104-20. [🔗](#)
- Wilson DM, Brenerman BM & Illuzzi JL (2014). Base excision repair capacity in informing health-span. *Carcinogenesis*, 35, 2643-52. [🔗](#)
- Peña-Díaz J & Rasmussen LJ (2016). Approaches to diagnose DNA mismatch repair gene defects in cancer. *DNA Repair (Amst.)*, 38, 147-154. [🔗](#)

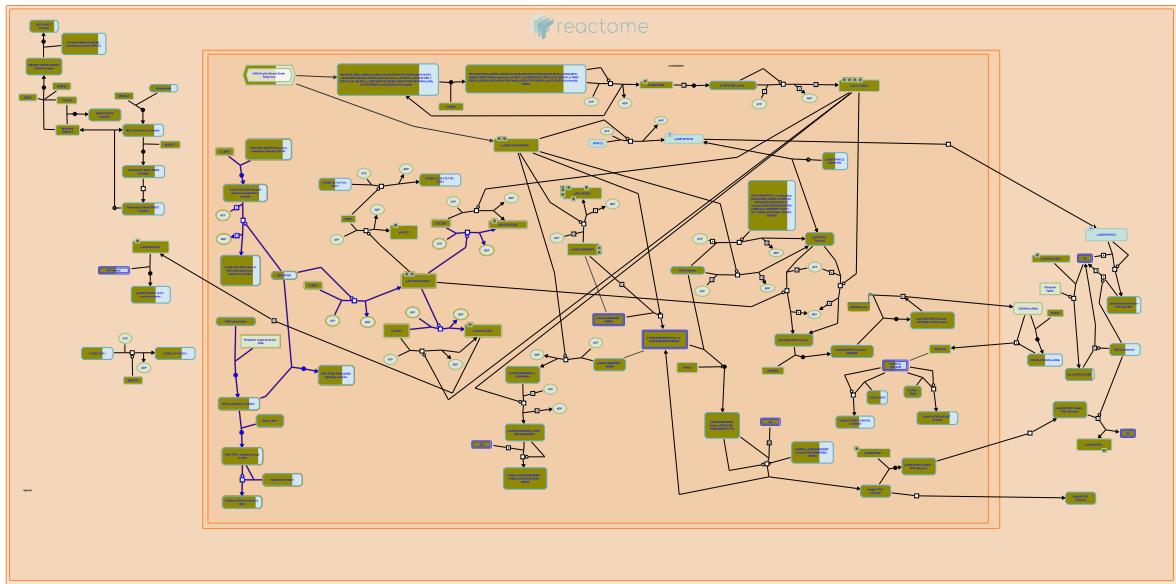
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2020-01-31	Created	Orlic-Milacic M
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2020-02-24	Edited	Orlic-Milacic M
2020-02-24	Reviewed	D'Eustachio P
2020-11-11	Reviewed	D'Eustachio P
2020-11-12	Edited	Orlic-Milacic M
2023-10-12	Modified	Weiser JD

45 submitted entities found in this pathway, mapping to 48 Reactome entities

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ENSG00000012048	P38398	ENSG00000020922	P49959	ENSG00000049541	P35250
ENSG00000051180	Q06609	ENSG00000064933	P54278	ENSG00000065057	P78549
ENSG00000083093	Q86YC2	ENSG00000092871	O75771	ENSG00000095002	P43246
ENSG00000104320	O60934	ENSG00000106399	P35244	ENSG00000108384	O43502
ENSG00000109674	Q8TAT5	ENSG00000111247	Q96B01	ENSG00000111445	P40937
ENSG00000113318	P20585	ENSG00000113522	Q92878	ENSG00000114026	O15527, O15527-4
ENSG00000116062	P52701	ENSG00000117748	P15927	ENSG00000122512	P54278
ENSG00000127922	P60896	ENSG00000132383	P27694	ENSG00000132781	Q9UIF7-3, Q9UIF7-6
ENSG00000133119	P40938	ENSG00000136273	O60921	ENSG00000136492	Q9BX63
ENSG00000138346	P51530	ENSG00000138376	Q99728	ENSG00000140398	Q96FI4
ENSG00000149311	Q13315	ENSG00000152942	O60671, O75943	ENSG00000163781	Q92547
ENSG00000163918	P35249	ENSG00000171792	Q9BSD3	ENSG00000172613	Q99638
ENSG00000172977	Q92993	ENSG00000174371	Q9UQ84	ENSG00000175054	Q13535
ENSG00000175643	Q96E14	ENSG00000178966	Q9H9A7	ENSG00000185379	O75771
ENSG00000196584	O43543	ENSG00000197299	P54132	ENSG00000276618	O75943

8. Activation of ATR in response to replication stress (R-HSA-176187)



Cellular compartments: nucleoplasm.

Genotoxic stress caused by DNA damage or stalled replication forks can lead to genomic instability. To guard against such instability, genotoxically-stressed cells activate checkpoint factors that halt or slow cell cycle progression. Among the pathways affected are DNA replication by reduction of replication origin firing, and mitosis by inhibiting activation of cyclin-dependent kinases (Cdks). A key factor involved in the response to stalled replication forks is the ATM- and rad3-related (ATR) kinase, a member of the phosphoinositide-3-kinase-related kinase (PIKK) family. Rather than responding to particular lesions in DNA, ATR and its binding partner ATRIP (ATR-interacting protein) sense replication fork stalling indirectly by associating with persistent ssDNA bound by RPA. These structures would be formed, for example, by dissociation of the replicative helicase from the leading or lagging strand DNA polymerase when the polymerase encounters a DNA lesion that blocks DNA synthesis. Along with phosphorylating the downstream transducer kinase Chk1 and the tumor suppressor p53, activated ATR modifies numerous factors that regulate cell cycle progression or the repair of DNA damage. The persistent ssDNA also stimulates recruitment of the RFC-like Rad17-Rfc2-5 alternative clamp-loading complex, which subsequently loads the Rad9-Hus1-Rad1 complex onto the DNA. The latter '9-1-1' complex serves to facilitate Chk1 binding to the stalled replication fork, where Chk1 is phosphorylated by ATR and thereby activated. Upon activation, Chk1 can phosphorylate additional substrates including the Cdc25 family of phosphatases (Cdc25A, Cdc25B, and Cdc25C). These enzymes catalyze the removal of inhibitory phosphate residues from cyclin-dependent kinases (Cdks), allowing their activation. In particular, Cdc25A primarily functions at the G1/S transition to dephosphorylate Cdk2 at Thr 14 and Tyr 15, thus positively regulating the Cdk2-cyclin E complex for S-phase entry. Cdc25A also has mitotic functions. Phosphorylation of Cdc25A at Ser125 by Chk1 leads to Cdc25A ubiquitination and degradation, thus inhibiting DNA replication origin firing. In contrast, Cdc25B and Cdc25C regulate the onset of mitosis through dephosphorylation and activation of Cdk1-cyclin B complexes. In response to replication stress, Chk1 phosphorylates Cdc25B and Cdc25C leading to Cdc25B/C complex formation with 14-3-3 proteins. As these complexes are sequestered in the cytoplasm, they are unable to activate the nuclear Cdk1-cyclin B complex for mitotic entry.

These events are outlined in the figure. Persistent single-stranded DNA associated with RPA binds claspin (A) and ATR:ATRIP (B), leading to claspin phosphorylation (C). In parallel, the same single-stranded DNA:RPA complex binds RAD17:RFC (D), enabling the loading of RAD9:HUS1:RAD1 (9-1-1) complex onto the DNA (E). The resulting complex of proteins can then repeatedly bind (F) and phosphorylate (G) CHK1, activating multiple copies of CHK1.

References

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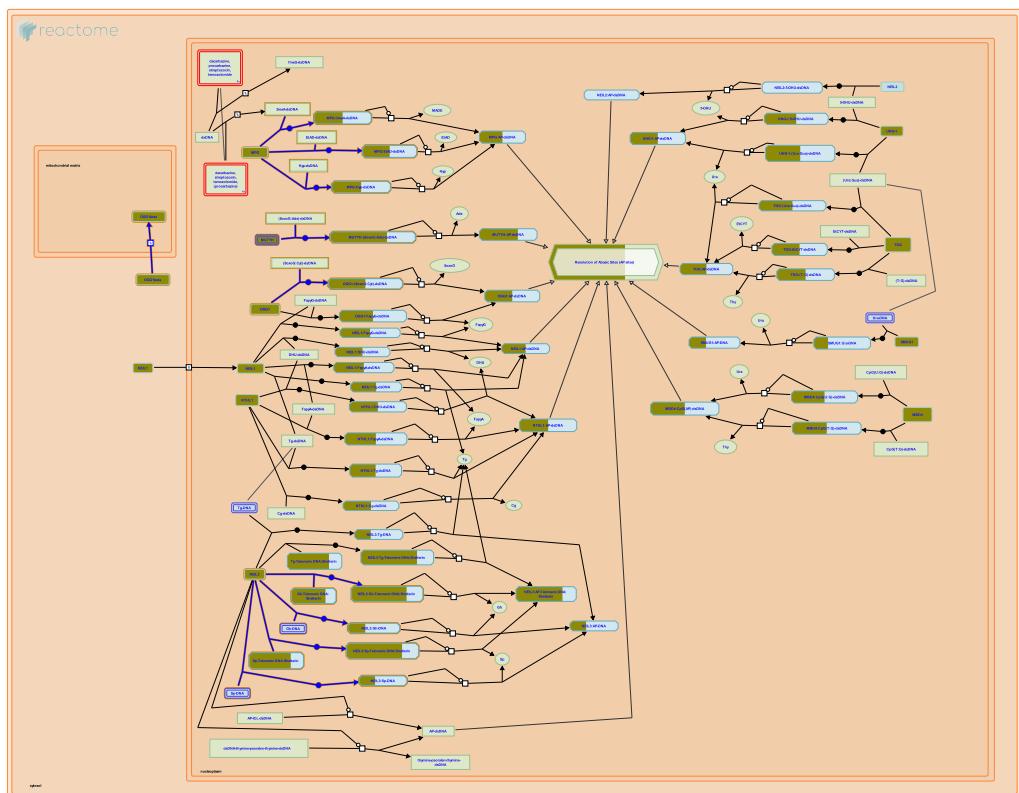
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Date	Action	Author
2006-02-25	Edited	D'Eustachio P
2006-02-25	Authored	Borowiec JA
2006-03-03	Created	D'Eustachio P

33 submitted entities found in this pathway, mapping to 34 Reactome entities

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ENSG0000097046	O00311	ENSG0000100297	P33992	ENSG0000104738	P33991
ENSG0000106399	P35244	ENSG0000111445	P40937	ENSG0000112118	P25205
ENSG0000115942	Q13416	ENSG0000117748	P15927	ENSG0000123374	P24941
ENSG0000125885	Q9UJA3	ENSG0000132383	P27694	ENSG0000133119	P40938
ENSG0000135336	Q9UBD5	ENSG0000136273	O60921	ENSG0000149554	O14757
ENSG0000152942	O60671, O75943	ENSG0000158402	P30307	ENSG0000163918	P35249
ENSG0000164045	P30304	ENSG0000164815	O43913	ENSG0000166508	P33993
ENSG0000172613	Q99638	ENSG0000175054	Q13535	ENSG0000276618	O75943

9. Recognition and association of DNA glycosylase with site containing an affected purine ([R-HSA-110330](#))



Cellular compartments: nucleoplasm.

The recognition and removal of an altered base by a DNA glycosylase is thought to involve the diffusion of the enzyme along the minor groove of the DNA molecule. The enzyme presumably compresses the backbone of the affected DNA strand at the site of damage. This compression is thought to result in an outward rotation of the damaged residue into a "pocket" of the enzyme that recognizes and cleaves the altered base from the backbone (Slupphaug et al. 1996, Parikh et al. 1998).

References

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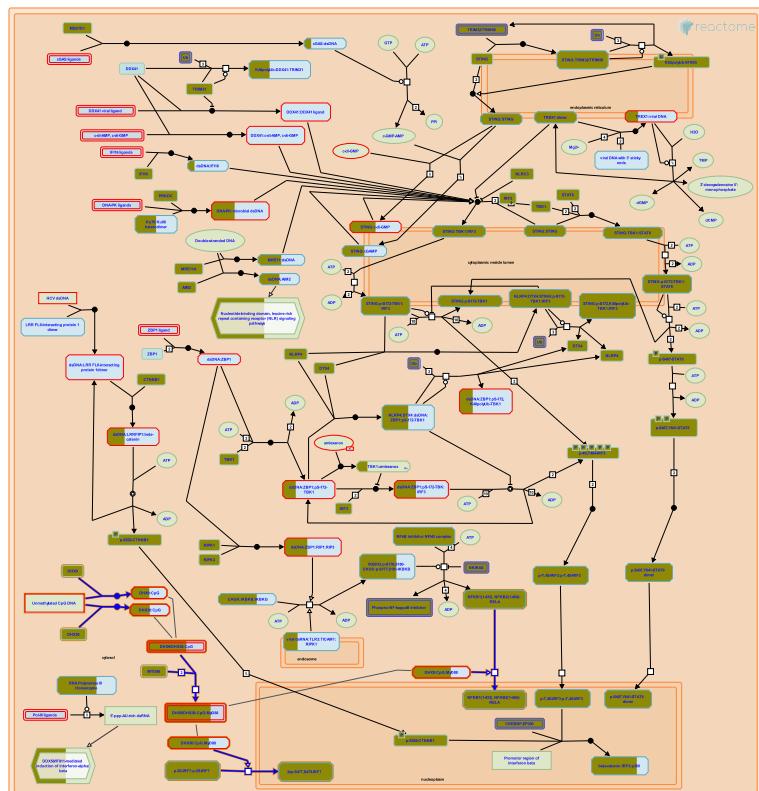
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2004-02-09	Authored	Matthews L
2014-12-04	Revised	Orlic-Milacic M
2014-12-04	Edited	Orlic-Milacic M

Date	Action	Author
2014-12-22	Reviewed	Borowiec JA
2024-05-25	Modified	Weiser JD

34 submitted entities found in this pathway, mapping to 39 Reactome entities

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ENSG00000124635	P06899	ENSG00000128513	Q9NUX5	ENSG00000132604	Q15554
ENSG00000132781	Q9UIF7-3, Q9UIF7-6	ENSG00000147601	P54274	ENSG00000158373	P58876, Q93079, Q99879
ENSG00000158406	P62805	ENSG00000166848	Q9NYB0	ENSG00000180573	Q93077
ENSG00000180596	P62807	ENSG00000184260	Q16777	ENSG00000184678	Q16778
ENSG00000187837	Q99880	ENSG00000188486	P16104	ENSG00000196787	Q99878
ENSG00000196890	Q8N257	ENSG00000197061	P62805	ENSG00000197238	P62805
ENSG00000197903	O60814	ENSG00000203812	Q6FI13	ENSG00000233822	Q99877, Q99879
ENSG00000234289	P57053	ENSG00000270276	P62805	ENSG00000270882	P62805
ENSG00000273802	P62807	ENSG00000274183	P0C5Y9	ENSG00000274290	P62807
ENSG00000277075	P04908				

10. DEx/H-box helicases activate type I IFN and inflammatory cytokines production (R-HSA-3134963)



DHX36 and DHX9 are aspartate-glutamate-any amino acid aspartate/histidine (DExD/H) box helicase (DHX) proteins that localize in the cytosol. The DHX RNA helicases family includes a large number of proteins that are implicated in RNA metabolism. Members of this family, RIG-1 and MDA5, have been shown to sense a non-self RNA leading to type I IFN production. RNA helicases DHX36 and DHX9 were found to trigger host responses to non-self DNA in MyD88-dependent manner. DHX36 sensed CpG class A, while DHX9 sensed CpG class B. Both DHX36 and DHX9 were critical for antiviral immune responses in viral DNA-stimulated human plasmacytoid dendritic cells (pDC) (Kim T et al. 2010).

References

Hanabuchi S, Plumas J, Pazhoor S, Bover L, Kim T, Facchinetti V, ... Qin J (2010). Aspartate-glutamate-alanine-histidine box motif (DEAH)/RNA helicase A helicases sense microbial DNA in human plasmacytoid dendritic cells. Proc. Natl. Acad. Sci. U.S.A., 107, 15181-6. [\[PubMed\]](#)

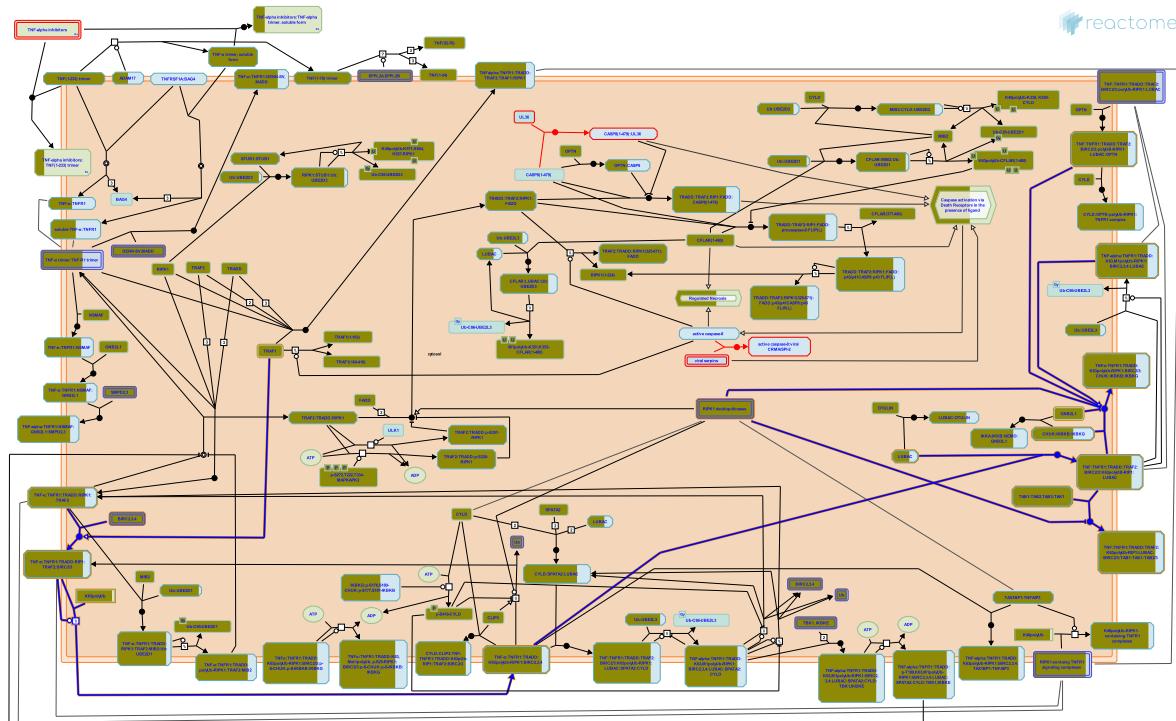
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2013-02-06	Authored	Shamovsky V
2013-02-11	Reviewed	D'Eustachio P
2013-02-13	Created	Shamovsky V
2013-05-17	Edited	Shamovsky V
2013-05-22	Reviewed	Wu J, Jin L

8 submitted entities found in this pathway, mapping to 8 Reactome entities

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ENSG0000172936	Q99836	ENSG0000173039	Q04206	ENSG0000174953	Q9H2U1
ENSG0000185507	Q92985	ENSG0000276561	Q92985		

11. TNFR1-induced NF-kappa-B signaling pathway (R-HSA-5357956)



Activation of tumor necrosis factor receptor 1 (TNFR1) can trigger multiple signal transduction pathways to induce inflammation, cell proliferation, survival or cell death (Ward C et al. 1999; Micheau O and Tschopp J 2003; Widera D et al. 2006). Whether a TNF- α -stimulated cell will survive or die is dependent on the cellular context. TNF- α -induced signals lead to the activation of transcriptional factors such as nuclear factor-kappa B (NFkappaB) and activator protein-1 (AP1) (Ward C et al. 1999; Widera D et al. 2006; Tsou HK et al. 2012).

The binding of TNF- α to TNFR1 leads to recruitment of the adapter protein TNFR1-associated death domain (TRADD) and of receptor- α -interacting protein 1 (RIPK1). TRADD subsequently recruits also TNF receptor-associated factor 2 (TRAF2). RIPK1 is promptly K63-polyubiquitinated which results in the recruitment of the TAB2:TAK1 complex and the I κ B kinase (IKK) complex to TNFR1. The activated IKK complex mediates phosphorylation of the inhibitor of NFkappaB (I κ B), which targets I κ B for ubiquitination and subsequent degradation. Released NFkappaB induces the expression of a variety of genes including inflammation-related genes and anti-apoptotic genes encoding proteins such as inhibitor of apoptosis proteins cIAP1/2, Bcl-2, Bcl-xL or cellular FLICE-like inhibitory protein (FLIP) (Blonska M et al. 2005; Ea CK et al. 2006; Wu CJ et al. 2006; Chen C et al. 2000; Manna SK et al. 2000; Kreuz S et al. 2001; Micheau O et al. 2001). NFkB-mediated inhibition of cell death also involves attenuating TNF-induced activation of c-Jun activating kinase (JNK). Whereas transient activation of JNK upon TNF treatment is associated with cellular survival, prolonged JNK activation contributes to cell death. However, as caspases activate JNK quite efficiently, JNKs are also regularly stimulated in course of apoptosis without being essential for cell death (Wicovsky A et al. 2007). AP1-mediated gene induction results from activation of JNK via TRAF2 (not shown here) (Tsou HK et al. 2012). While pro-survival signaling is initiated and regulated via the activated TNFR1 receptor complex at the cell membrane, cell death signals are induced by internalization-associated fashion upon the release of RIPK1 from the membrane complex (Micheau O and Tschopp J 2003; Schneider-Brachert W et al. 2004; Tchikov V et al. 2011).

TNFR1-mediated transcriptional activity of NFkB is both antiapoptotic and highly proinflammatory and thus must be tightly regulated to prevent constitutive activation that leads to persistent inflammation and cancer (Ward C et al. 1999; Fujihara S et al. 2002; Pekalski J et al. 2013; Kankaanranta H et al. 2014; Shukla S and Gupta S 2004; Jackson-Bernitsas DG et al. 2007; Zhang JY et al. 2007). Multiple mechanisms normally ensure the proper control of NFkappaB activation including two negative feedback loops mediated by NFkappaB inducible inhibitors, I kB-alpha (NFKBIA) and ubiquitin-editing protein A20 (He KL & Ting AT 2002; Wertz IE et al. 2004; Vereecke L et al. 2009; Pekalski J et al. 2013).

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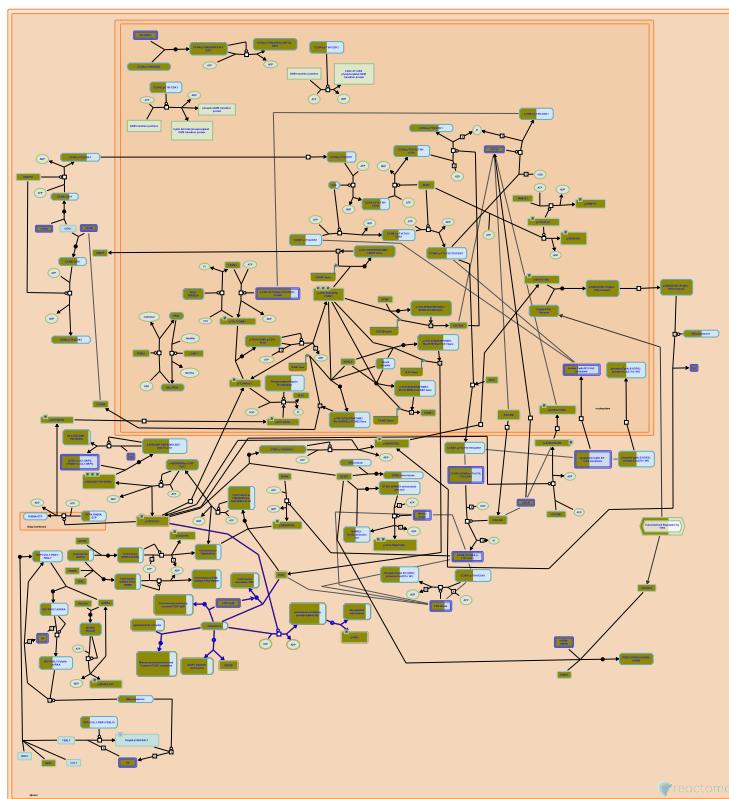
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2014-03-26	Created	Shamovsky V
2015-02-15	Edited	Shamovsky V
2015-03-12	Reviewed	Gillespie ME
2015-05-12	Authored	Shamovsky V
2015-08-25	Reviewed	Wajant H

28 submitted entities found in this pathway, mapping to 28 Reactome entities

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ENSG00000101966	P98170	ENSG00000102871	Q15628	ENSG00000104365	O14920
ENSG00000110330	Q13490	ENSG00000114316	Q13107	ENSG00000118503	P21580
ENSG00000123240	Q96CV9	ENSG00000127191	Q12933	ENSG00000135341	O43318
ENSG00000137275	Q13546	ENSG00000143258	Q9UK80	ENSG00000150991	P0CG48
ENSG00000157625	Q8N5C8	ENSG00000158480	Q9UM82	ENSG00000165312	Q5VV17
ENSG00000170315	P0CG47	ENSG00000179526	Q9H0F6	ENSG00000204628	P63244
ENSG00000213341	O15111	ENSG00000213928	Q96EP0	ENSG00000230108	P01375
ENSG00000264522	Q6GQQ9				

12. Centrosome maturation (R-HSA-380287)



The centrosome is the primary microtubule organizing center (MTOC) in vertebrate cells and plays an important role in orchestrating the formation of the mitotic spindle. Centrosome maturation is an early event in this process and involves a major reorganization of centrosomal material at the G2/M transition. During maturation, centrosomes undergo a dramatic increase in size and microtubule nucleating capacity. As part of this process, a number of proteins and complexes, including some that are required for microtubule nucleation and anchoring, are recruited to the centrosome while others that are required for organization of interphase microtubules and centrosome cohesion are lost (reviewed in Schatten, 2008; Raynaud-Messina and Merdes 2007).

References

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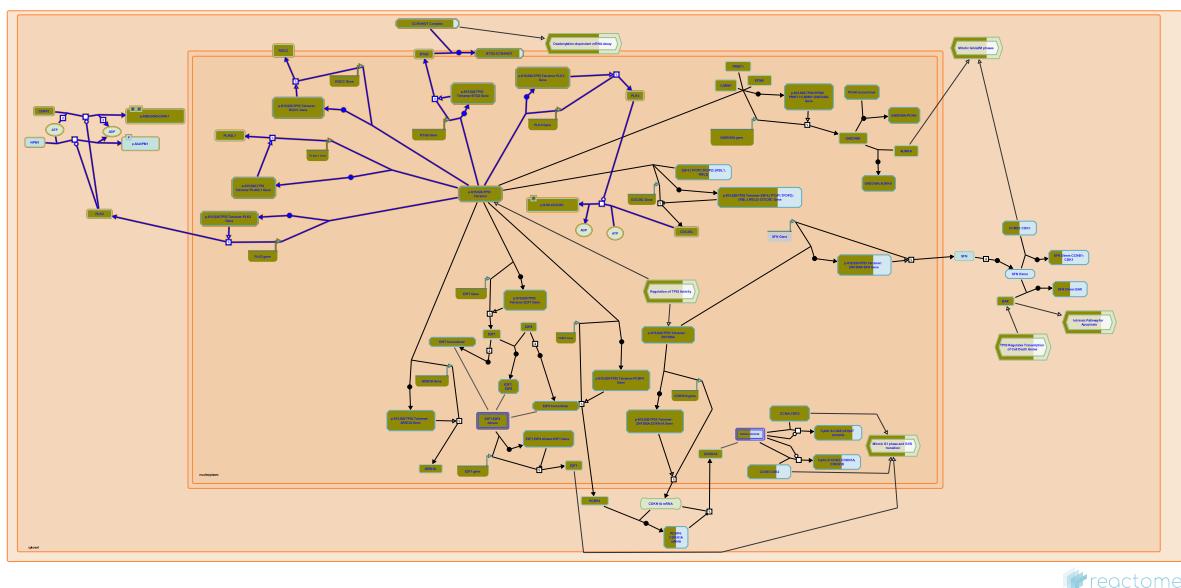
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2008-11-11	Authored	Matthews L
2008-11-11	Created	Matthews L
2008-11-17	Reviewed	Merdes A
2008-11-24	Edited	Matthews L
2024-05-25	Modified	Weiser JD

67 submitted entities found in this pathway, mapping to 68 Reactome entities

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ENSG00000080824	P07900	ENSG00000092036	Q9H6D7	ENSG00000101004	Q9Y2I6
ENSG00000101367	Q15691	ENSG00000101639	Q8TEP8	ENSG00000103540	O43303
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ENSG00000126001	Q9BV73	ENSG00000126216	Q96CW5	ENSG00000127824	P68366
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ENSG00000147400	P41208	ENSG00000148019	Q5JTW2	ENSG00000151849	Q9HC77
ENSG00000152082	Q6NZ67	ENSG00000152240	Q96CS2	ENSG00000160299	O95613
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ENSG00000173272	Q6P582	ENSG00000174799	Q66GS9	ENSG00000175203	Q13561
ENSG00000175216	Q14008	ENSG00000176101	O43805	ENSG00000182923	Q96MT8
ENSG00000188229	P68371	ENSG00000197102	Q14204	ENSG00000198089	A8K8P3
ENSG00000204843	Q14203-2	ENSG00000204899	Q08AG7	ENSG00000213066	O95684
ENSG00000213397	Q99871	ENSG00000213923	P49674	ENSG00000214367	Q68CZ6
ENSG00000227739	P07437	ENSG00000248333	P21127	ENSG00000249115	O94927
ENSG00000275835	Q96RT8				

13. TP53 regulates transcription of additional cell cycle genes whose exact role in the p53 pathway remain uncertain (R-HSA-6804115)



reactome

BTG2 is induced by TP53, leading to cessation of cellular proliferation (Rouault et al. 1996, Duriez et al. 2002). BTG2 binds to the CCR4-NOT complex and promotes mRNA deadenylation activity of this complex. Interaction between BTG2 and CCR4-NOT is needed for the antiproliferative activity of BTG2, but the underlying mechanism has not been elucidated (Rouault et al. 1998, Mauxion et al. 2008, Horiuchi et al. 2009, Doidge et al. 2012, Ezzeddine et al. 2012). Two polo-like kinases, PLK2 and PLK3, are direct transcriptional targets of TP53. TP53-mediated induction of PLK2 may be important for prevention of mitotic catastrophe after spindle damage (Burns et al. 2003). PLK2 is involved in the regulation of centrosome duplication through phosphorylation of centrosome-related proteins CENPJ (Chang et al. 2010) and NPM1 (Krause and Hoffmann 2010). PLK2 is frequently transcriptionally silenced through promoter methylation in B-cell malignancies (Syed et al. 2006). Induction of PLK3 transcription by TP53 (Jen and Cheung 2005) may be important for coordination of M phase events through PLK3-mediated nuclear accumulation of CDC25C (Bahassi et al. 2004). RGCC is induced by TP53 and implicated in cell cycle regulation, possibly through its association with PLK1 (Saigusa et al. 2007). PLAGL1 (ZAC1) is a zinc finger protein directly transcriptionally induced by TP53 (Rozenfeld-Granot et al. 2002). PLAGL1 expression is frequently lost in cancer (Varrault et al. 1998) and PLAGL1 has been implicated in both cell cycle arrest and apoptosis (Spengler et al. 1997), but its mechanism of action remains unknown.

References

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Birot AM, Corbo L, Berthet C, Billaud M, Rouault JP, Magaud JP & Prévôt D (1998). Interaction of BTG1 and p53-regulated BTG2 gene products with mCaf1, the murine homolog of a component of the yeast CCR4 transcriptional regulatory complex. *J. Biol. Chem.*, 273, 22563-9. [🔗](#)

Hoffmann I & Krause A (2010). Polo-like kinase 2-dependent phosphorylation of NPM/B23 on serine 4 triggers centriole duplication. *PLoS ONE*, 5, e9849. [🔗](#)

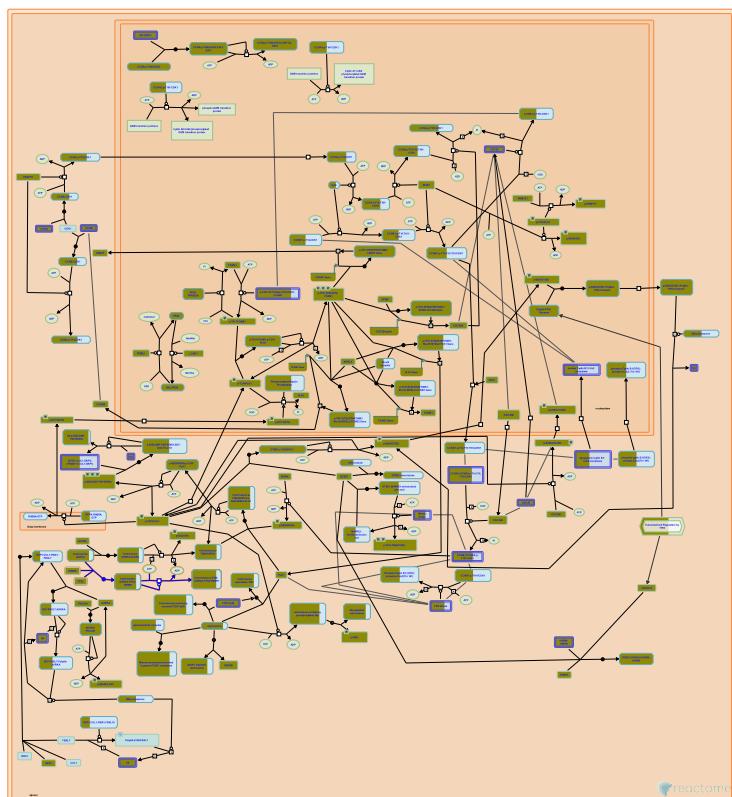
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2015-10-14	Authored	Orlic-Milacic M
2016-02-04	Reviewed	Zaccara S, Inga A

20 submitted entities found in this pathway, mapping to 25 Reactome entities

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ENSG00000125107	A5YKK6	ENSG00000138767	Q96LI5	ENSG00000141510	P04637
ENSG00000144580	Q92600	ENSG00000145632	Q9NYY3	ENSG00000149115	Q9C0C2
ENSG00000151849	Q9HC77	ENSG00000158402	P30307	ENSG00000158435	Q9UKZ1
ENSG00000159388	P78543	ENSG00000173846	Q9H4B4	ENSG00000182973	Q9H9A5
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ENSG00000159388	ENSG00000159388	ENSG00000173846	ENSG00000173846		

14. AURKA Activation by TPX2 ([R-HSA-8854518](#))



TPX2 binds to aurora kinase A (AURKA) at centrosomes and promotes its activation by facilitating AURKA active conformation and autophosphorylation of the AURKA threonine residue T288 (Bayliss et al. 2003, Xu et al. 2011, Giubettini et al. 2011, Dodson and Bayliss 2012).

References

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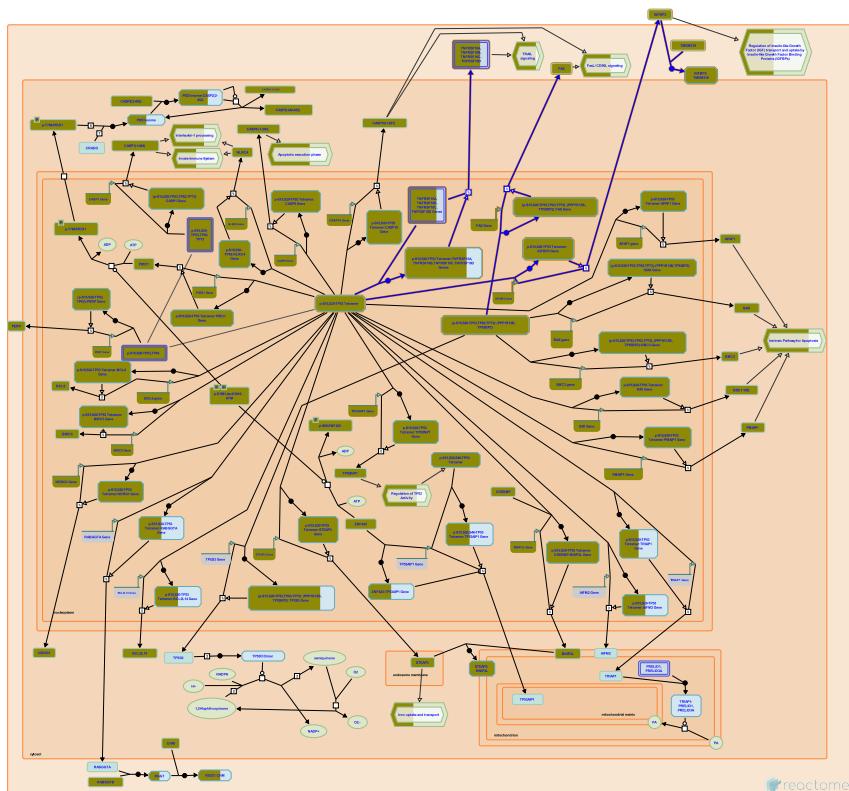
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2016-01-27	Authored	Orlic-Milacic M
2016-01-27	Created	Orlic-Milacic M
2016-02-16	Reviewed	Chen H, Maxwell CA
2024-05-25	Modified	Weiser JD

60 submitted entities found in this pathway, mapping to 60 Reactome entities

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ENSG00000077380	Q13409	ENSG00000078674	Q15154	ENSG00000080824	P07900
ENSG00000087586	O14965	ENSG00000088325	Q9ULW0	ENSG00000092036	Q9H6D7
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ENSG00000213066	O95684	ENSG00000213397	Q99871	ENSG00000213923	P49674
ENSG00000214367	Q68CZ6	ENSG00000227739	P07437	ENSG00000249115	O94927

15. TP53 Regulates Transcription of Death Receptors and Ligands (R-HSA-6803211)



Pro-apoptotic transcriptional targets of TP53 are TRAIL death receptors TNFRSF10A (DR4), TNFRSF10B (DR5), TNFRSF10C (DcR1) and TNFRSF10D (DcR2), as well as the FASL/CD95L death receptor FAS (CD95). TRAIL receptors and FAS induce pro-apoptotic signaling in response to external stimuli via extrinsic apoptosis pathway (Wu et al. 1997, Takimoto et al. 2000, Guan et al. 2001, Liu et al. 2004, Ruiz de Almodovar et al. 2004, Liu et al. 2005, Schilling et al. 2009, Wilson et al. 2013). IGF-BP3 is a transcriptional target of TP53 that may serve as a ligand for a novel death receptor TMEM219 (Buckbinder et al. 1995, Ingermann et al. 2010).

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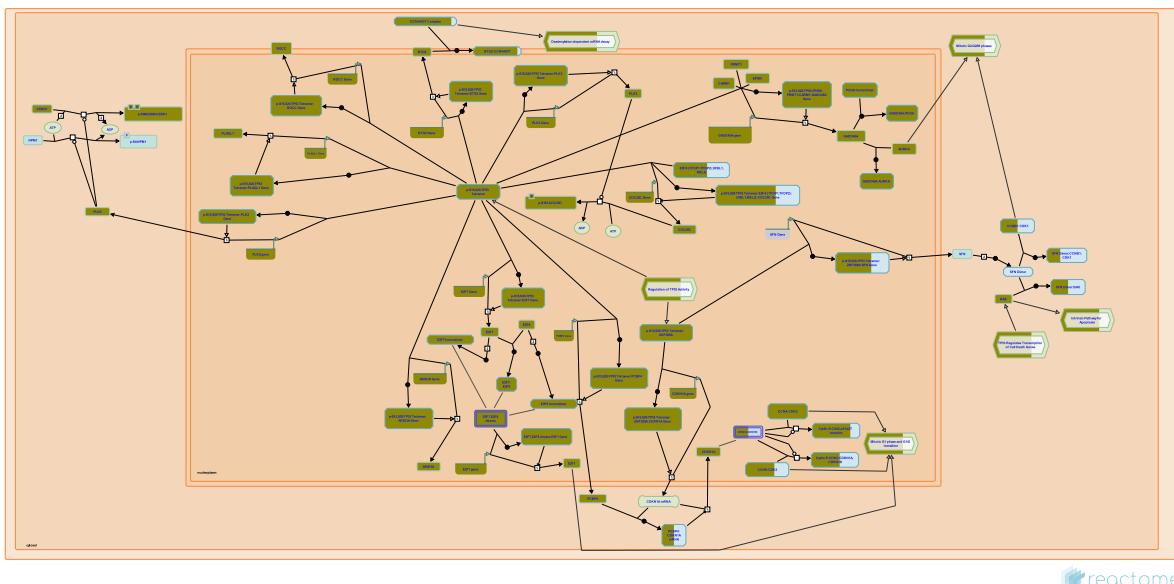
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2015-10-14	Authored	Orlic-Milacic M
2016-02-04	Reviewed	Zaccara S, Inga A
2024-05-25	Modified	Weiser JD

11 submitted entities found in this pathway, mapping to 16 Reactome entities

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ENSG0000149932	Q86XT9	ENSG0000173530	Q9UBN6		

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ENSG0000146674	ENSG0000146674	ENSG0000173530	ENSG0000173530		

16. TP53 Regulates Transcription of Cell Cycle Genes ([R-HSA-6791312](#))



Under a variety of stress conditions, TP53 (p53), stabilized by stress-induced phosphorylation at least on S15 and S20 serine residues, can induce the transcription of genes involved in cell cycle arrest. Cell cycle arrest provides cells an opportunity to repair the damage before division, thus preventing the transmission of genetic errors to daughter cells. In addition, it allows cells to attempt a recovery from the damage and survive, preventing premature cell death.

TP53 controls transcription of genes involved in both G1 and G2 cell cycle arrest. The most prominent TP53 target involved in G1 arrest is the inhibitor of cyclin-dependent kinases CDKN1A (p21). CDKN1A is one of the earliest genes induced by TP53 (El-Deiry et al. 1993). CDKN1A binds and inactivates CDK2 in complex with cyclin A (CCNA) or E (CCNE), thus preventing G1/S transition (Harper et al. 1993). Nevertheless, under prolonged stress, the cell destiny may be diverted towards an apoptotic outcome. For instance, in case of an irreversible damage, TP53 can induce transcription of an RNA binding protein PCBP4, which can bind and destabilize CDKN1A mRNA, thus alleviating G1 arrest and directing the affected cell towards G2 arrest and, possibly, apoptosis (Zhu and Chen 2000, Scoumanne et al. 2011). Expression of E2F7 is directly induced by TP53. E2F7 contributes to G1 cell cycle arrest by repressing transcription of E2F1, a transcription factor that promotes expression of many genes needed for G1/S transition (Aksoy et al. 2012, Carvajal et al. 2012). ARID3A is a direct transcriptional target of TP53 (Ma et al. 2003) that may promote G1 arrest by cooperating with TP53 in induction of CDKN1A transcription (Lestari et al. 2012). However, ARID3A may also promote G1/S transition by stimulating transcriptional activity of E2F1 (Suzuki et al. 1998, Peeper et al. 2002).

TP53 contributes to the establishment of G2 arrest by inducing transcription of GADD45A and SFN, and by inhibiting transcription of CDC25C. TP53 induces GADD45A transcription in cooperation with chromatin modifying enzymes EP300, PRMT1 and CARM1 (An et al. 2004). GADD45A binds Aurora kinase A (AURKA), inhibiting its catalytic activity and preventing AURKA-mediated G2/M transition (Shao et al. 2006, Sanchez et al. 2010). GADD45A also forms a complex with PCNA. PCNA is involved in both normal and repair DNA synthesis. The effect of GADD45 interaction with PCNA, if any, on S phase progression, G2 arrest and DNA repair is not known (Smith et al. 1994, Hall et al. 1995, Sanchez et al. 2010, Kim et al. 2013). SFN (14-3-3-sigma) is induced by TP53 (Hermeking et al. 1997) and contributes to G2 arrest by binding to the complex of CDK1 and CCNB1 (cyclin B1) and preventing its translocation to the nucleus. Phosphorylation of a number of nuclear proteins by the complex of CDK1 and CCNB1 is needed for G2/M transition (Chan et al. 1999). While promoting G2 arrest, SFN can simultaneously inhibit apoptosis by binding to BAX and preventing its translocation to mitochondria, a step involved in cytochrome C release (Samuel et al. 2001). TP53 binds the promoter of the CDC25C gene in cooperation with the transcriptional repressor E2F4 and represses CDC25C transcription, thus maintaining G2 arrest (St Clair et al. 2004, Benson et al. 2014).

Several direct transcriptional targets of TP53 are involved in cell cycle arrest but their mechanism of action is still unknown. BTG2 is induced by TP53, leading to cessation of cellular proliferation (Rouault et al. 1996, Duriez et al. 2002). BTG2 binds to the CCR4-NOT complex and promotes mRNA deadenylation activity of this complex. Interaction between BTG2 and CCR4-NOT is needed for the antiproliferative activity of BTG2, but the underlying mechanism has not been elucidated (Rouault et al. 1998, Mauxion et al. 2008, Horiuchi et al. 2009, Doidge et al. 2012, Ezzeddine et al. 2012). Two polo-like kinases, PLK2 and PLK3, are direct transcriptional targets of TP53. TP53-mediated induction of PLK2 may be important for prevention of mitotic catastrophe after spindle damage (Burns et al. 2003). PLK2 is involved in the regulation of centrosome duplication through phosphorylation of centrosome-related proteins CENPJ (Chang et al. 2010) and NPM1 (Krause and Hoffmann 2010). PLK2 is frequently transcriptionally silenced through promoter methylation in B-cell malignancies (Syed et al. 2006). Induction of PLK3 transcription by TP53 (Jen and Cheung 2005) may be important for coordination of M phase events through PLK3-mediated nuclear accumulation of CDC25C (Bahassi et al. 2004). RGCC is induced by TP53 and implicated in cell cycle regulation, possibly through its association with PLK1 (Saigusa et al. 2007). PLAGL1 (ZAC1) is a zinc finger protein directly transcriptionally induced by TP53 (Rozenfeld-Granot et al. 2002). PLAGL1 expression is frequently lost in cancer (Varrault et al. 1998) and PLAGL1 has been implicated in both cell cycle arrest and apoptosis (Spengler et al. 1997), but its mechanism of action remains unknown.

The zinc finger transcription factor ZNF385A (HZF) is a direct transcriptional target of TP53 that can form a complex with TP53 and facilitate TP53-mediated induction of CDKN1A and SFN (14-3-3 sigma) transcription (Das et al. 2007).

For a review of the role of TP53 in cell cycle arrest and cell cycle transcriptional targets of TP53, please refer to Riley et al. 2008, Murray-Zmijewski et al. 2008, Bieging et al. 2014, Kruiswijk et al. 2015.

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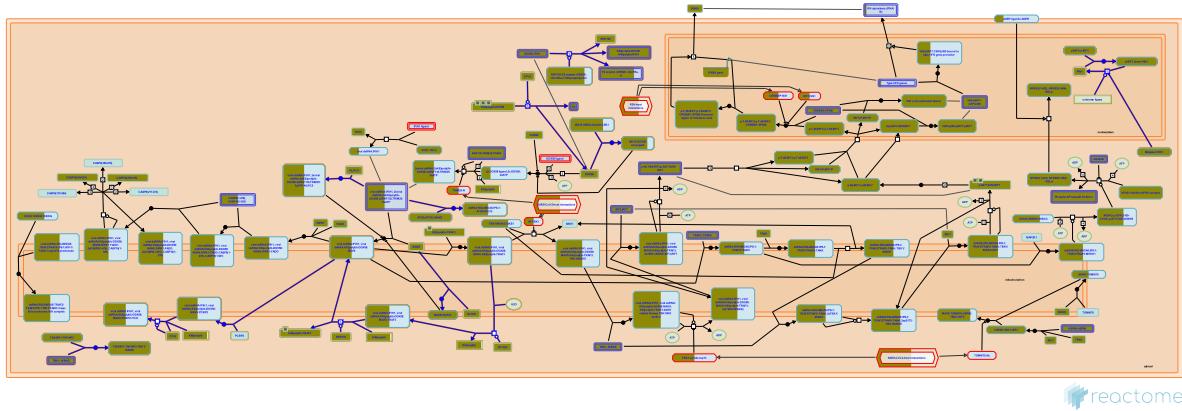
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2015-10-14	Authored	Orlic-Milacic M
2016-02-04	Reviewed	Zaccara S, Inga A
2024-05-25	Modified	Weiser JD

43 submitted entities found in this pathway, mapping to 55 Reactome entities

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ENSG00000111596	Q9NZN8	ENSG00000113300	Q9ULM6	ENSG00000116017	Q99856
ENSG00000116717	P24522	ENSG00000118495	Q9UM63	ENSG00000123374	P24941
ENSG00000124762	P38936	ENSG00000125107	A5YKK6	ENSG00000126457	Q99873
ENSG00000129173	A0AVK6	ENSG00000132646	P12004	ENSG00000133101	P78396
ENSG00000134057	P14635	ENSG00000138767	Q96LI5	ENSG00000141510	P04637
ENSG00000142453	Q86X55	ENSG00000144580	Q92600	ENSG00000145386	P20248
ENSG00000145632	Q9NYY3	ENSG00000149115	Q9C0C2	ENSG00000151849	Q9HC77
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ENSG00000161642	Q96PM9	ENSG00000165891	Q96AV8	ENSG00000173846	Q9H4B4
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ENSG00000124762	ENSG00000124762	ENSG00000145632	ENSG00000145632	ENSG00000158402	ENSG00000158402
ENSG00000159388	ENSG00000159388	ENSG00000165891	ENSG00000165891	ENSG00000173846	ENSG00000173846

17. Negative regulators of DDX58/IFIH1 signaling (R-HSA-936440)



reactome

As with other cytokine systems, production of type I IFN is a transient process, and can be hazardous to the host if unregulated, resulting in chronic cellular toxicity or inflammatory and autoimmune diseases. RIG-I-mediated production of IFN can, in turn, increase the transcription of RIG-I itself, thus setting into motion an IFN amplification loop, which if left unchecked, could become deleterious to the host. This module mainly focuses on the endogenous negative regulation of the RIG-I-like receptor (RLR) family proteins RIG-I and MDA5.

References

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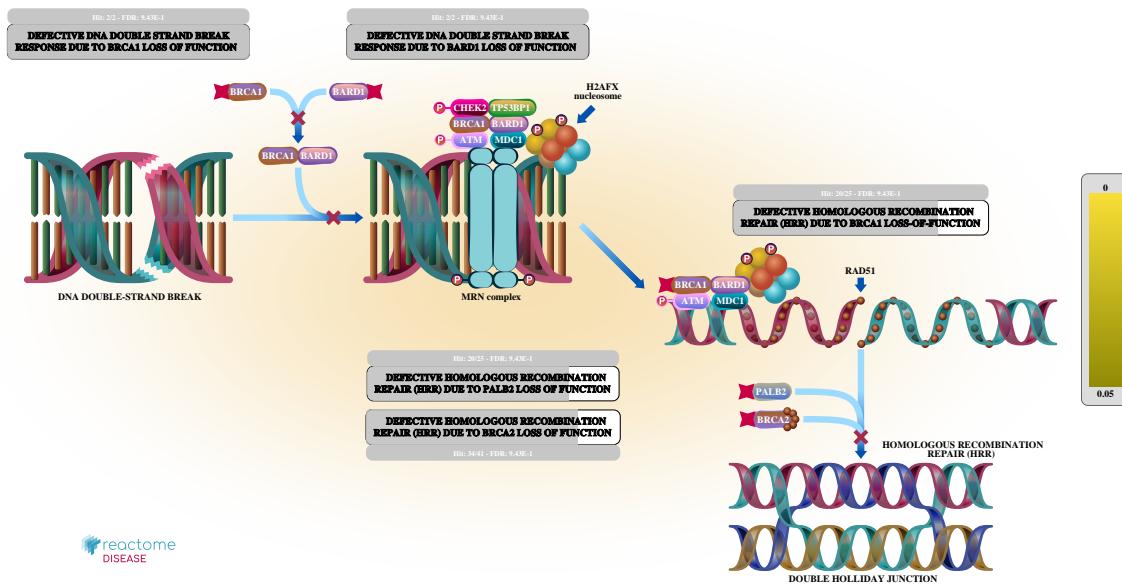
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2010-08-23	Created	Garapati P V
2010-10-30	Reviewed	Akira S, Kawai T
2024-05-25	Modified	Weiser JD

30 submitted entities found in this pathway, mapping to 31 Reactome entities

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ENSG00000083799	Q9NQC7	ENSG00000088888	Q7Z434	ENSG00000101695	Q96EQ8
ENSG00000106052	Q86VP1	ENSG00000107201	O95786	ENSG00000109332	P61077
ENSG00000115267	Q9BYX4	ENSG00000118503	P21580	ENSG00000121060	Q14258
ENSG00000126456	Q14653	ENSG00000127445	Q13526	ENSG00000131323	Q13114
ENSG00000140853	Q86WI3	ENSG00000145782	O94817	ENSG00000146833	Q9C037
ENSG00000150991	P0CG48	ENSG00000156587	O14933	ENSG00000160703	Q86UT6
ENSG00000170315	P0CG47, P62987	ENSG00000181481	Q8IUD6	ENSG00000182179	P41226
ENSG00000183735	Q9UHD2	ENSG00000187608	P05161	ENSG00000263528	Q14164

18. Diseases of DNA Double-Strand Break Repair (R-HSA-9675136)



Diseases: cancer.

Diseases of DNA double-strand break repair (DSBR) are caused by mutations in genes involved in repair of double strand breaks (DSBs), one of the most cytotoxic types of DNA damage. Unrepaired DSBs can lead to cell death, cellular senescence, or malignant transformation.

Germline mutations in DSBR genes are responsible for several developmental disorders associated with increased predisposition to cancer:

Ataxia telangiectasia, characterized by cerebellar neurodegeneration, hematologic malignancies and immunodeficiency, is usually caused by germline mutations in the ATM gene;

Nijmegen breakage syndrome 1, characterized by microcephaly, short stature and recurrent infections, is caused by germline mutations in the NBN (NBS1) gene;

Seckel syndrome, characterized by short stature, skeletal deformities and microcephaly, is caused by germline mutations in the ATR or RBBP8 (CtIP) genes.

Heterozygous germline mutations in BRCA1, BRCA2 or PALB2 cause the hereditary breast and ovarian cancer syndrome (HBOC), while homozygous germline mutations in BRCA2 and PALB2 cause Fanconi anemia, a developmental disorder characterized by short stature, microcephaly, skeletal defects, bone marrow failure, and predisposition to cancer.

Somatic mutations in DSBR genes are also frequently found in sporadic cancers.

The pathways "Defective DNA double strand break response due to BRCA1 loss of function" describes defects in DSB response caused by loss-of-function mutations in BRCA1 which prevent the formation of the BRCA1:BARD1 complex.

The pathway "Defective DNA double strand break response due to BARD1 loss of function" describes defects in DSB response caused by loss-of-function mutations in BARD1, the heterodimerization partner of BRCA1, which prevent the formation of the BRCA1:BARD1 complex.

The pathway "Defective homologous recombination repair (HRR) due to BRCA1 loss of function" describes defects in HRR caused by loss-of-function mutations in BRCA1 that impair its association with PALB2.

The pathway "Defective homologous recombination repair (HRR) due to BRCA2 loss of function" describes defects in HRR caused by loss-of-function mutations in BRCA2 that impair either its association with SEM1 (DSS1), its translocation to the nucleus, its binding to RAD51, or its binding to PALB2.

The pathway "Defective homologous recombination repair (HRR) due to PALB2 loss of function" describes defects in HRR caused by loss-of-function mutations in PALB2 that impair its association with BRCA2/RAD51/RAD51C.

For review, please refer to McKinnon and Caldecott 2007, Keijzers et al. 2017, and Jachimowicz et al. 2019.

References

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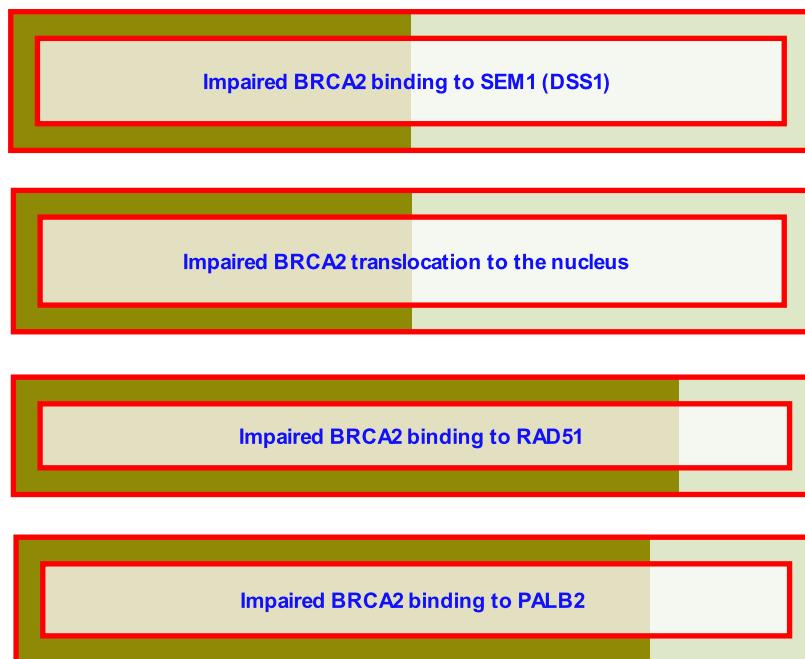
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2020-11-11	Authored	Orlic-Milacic M
2020-11-12	Edited	Orlic-Milacic M
2023-10-12	Modified	Weiser JD

35 submitted entities found in this pathway, mapping to 36 Reactome entities

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ENSG0000197299	P54132	ENSG0000276618	O75943		

19. Defective homologous recombination repair (HRR) due to BRCA2 loss of function ([R-HSA-9701190](#))



 reactome

Cellular compartments: nucleoplasm.

Diseases: cancer.

BRCA2 (FANCD1) is a tumor suppressor gene located on chromosomal arm 13q. BRCA2 protein is a mediator of the core mechanism of homologous recombination repair (HRR), essential for the recruitment of RAD51 recombinase to resected DNA double-strand breaks (DSBs). Monoallelic pathogenic germline mutations in BRCA2 are one of the underlying causes of the hereditary breast and ovarian cancer (HBOC) syndrome, with carriers having close to 50% lifetime risk for development of breast cancer and about 15% lifetime risk for development of ovarian cancer. In addition, BRCA2 germline mutation carriers are predisposed to cancers of the fallopian tube, pancreas, stomach, larynx and prostate. Biallelic germline mutations in BRCA2 cause Fanconi anemia subtype characterized by brain and soft tissue tumors, including medulloblastoma and Wilms tumor. BRCA2-deficient cells are defective in the formation of RAD51 foci upon treatment with DSB-inducing DNA damaging agents and accumulate chromatid breaks and radial chromosomes.

Besides its crucial role in HRR, BRCA2 is also implicated in protection of replication forks, centrosome duplication, spindle assembly checkpoint and cytokinesis. Recently published studies show the involvement of BRCA2 in the turnover of R-loops (hybrids between RNA and single strand DNA that are generated as intermediates of gene transcription). Unscheduled accumulated R-loops may be processed into DSBs, leading to genomic instability. Finally, BRCA2 is involved in pathway choice of DSB repair by inhibiting DNA polymerase theta-mediated end-joining (TMEJ) until M-phase (reviewed in Petropoulos and Halazonetis 2021, and Llorens-Agost et al. 2021). TMEJ is the predominant pathway for microhomology-mediated end joining MMEJ/alternative-nonhomologous end joining (alt-NHEJ, a-EJ) in mammals (reviewed in Ramsden et al. 2022).

BRCA2 haploinsufficiency is frequently observed in cancers, with close to 50% of BRCA2-mutant breast cancers retaining one wild type allele, suggesting that in some tissues at least heterozygous loss of BRCA2 function is sufficient for carcinogenesis. Promoter hypermethylation is not an obvious contributor to BRCA2 gene inactivation and no pathogenic mutations in the promoter region have been identified so far.

For review, please refer to Roy et al. 2011, Nalepa and Clapp 2018, Santana dos Santos et al. 2018, Venkitaraman 2019, Le et al. 2021, and Llorens-Agost et al. 2021.

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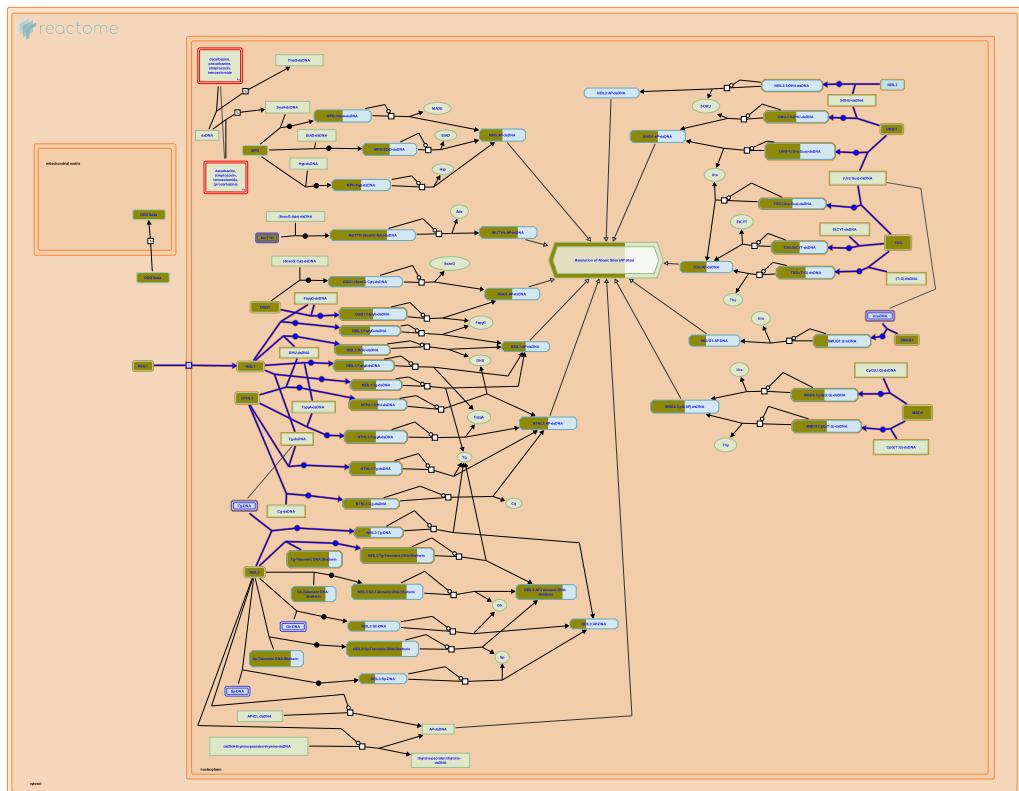
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2022-01-26	Reviewed	Le HP, Liu J, Heyer WD
2022-02-04	Edited	Orlic-Milacic M
2023-03-08	Modified	Matthews L

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ENSG0000152942	O60671, O75943	ENSG0000163781	Q92547	ENSG0000163918	P35249
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ENSG0000178966	Q9H9A7	ENSG0000185379	O75771	ENSG0000196584	O43543
ENSG0000197299	P54132	ENSG0000276618	O75943		

20. Recognition and association of DNA glycosylase with site containing an affected pyrimidine (R-HSA-110328)



Cellular compartments: nucleoplasm.

Base excision repair is initiated by a DNA glycosylase which first recognizes and removes a damaged or incorrect (e.g. mismatched) base (Sokhansanj et al. 2002).

References

Fitch JP, Sokhansanj BA, Rodrigue GR & Wilson DM 3rd (2002). A quantitative model of human DNA base excision repair. I. Mechanistic insights. Nucleic Acids Res, 30, 1817-25. [🔗](#)

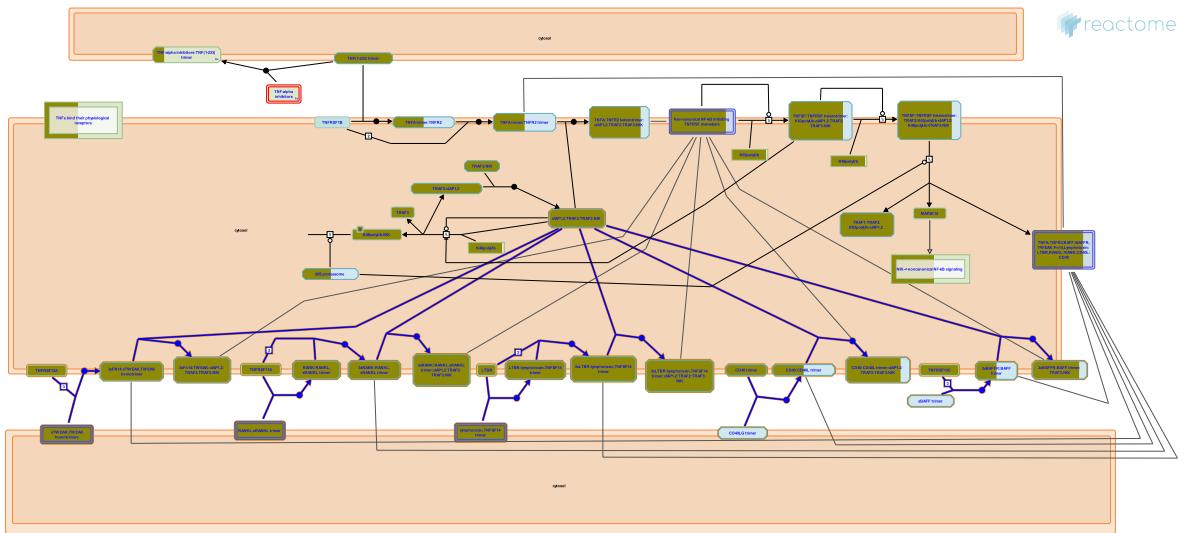
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2004-02-03	Authored	Matthews L
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2014-12-04	Edited	Orlic-Milacic M
2014-12-22	Reviewed	Borowiec JA
2024-05-25	Modified	Weiser JD

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ENSG00000233822	Q99877, Q99879	ENSG00000234289	P57053	ENSG00000270276	P62805
ENSG00000270882	P62805	ENSG00000273802	P62807	ENSG00000274183	P0C5Y9
ENSG00000274290	P62807	ENSG00000277075	P04908		

21. TNF receptor superfamily (TNFSF) members mediating non-canonical NF- κ B pathway (R-HSA-5676594)



Cellular compartments: plasma membrane, extracellular region, cytosol.

Activation of NF- κ B is fundamental to signal transduction by members of the TNFRSF. Expression of NF- κ B target genes is essential for mounting innate immune responses to infectious microorganisms but is also important for the proper development and cellular compartmentalization of secondary lymphoid organs necessary to orchestrate an adaptive immune response.

NF- κ B transcription factor family is activated by two distinct pathways: the canonical pathway involving NF- κ B1 and the non-canonical pathway involving NF- κ B2. Unlike NF- κ B1 signalling, which can be activated by a wide variety of receptors, the NF- κ B2 pathway is typically activated by a subset of receptor and ligand pairs belonging to the tumor necrosis factor receptor (TNF) super family (TNFRSF) members. These members include TNFR2 (Rauert et al. 2010), B cell activating factor of the TNF family receptor (BAFFR also known as TNFRSF13C) (Kayagaki et al. 2002, CD40 (also known as TNFRSF5) (Cooke et al. 2002), lymphotoxin beta-receptor (LTBR also known as TNFRSF3) (Dejardin et al. 2002), receptor activator for nuclear factor κ B (RANK also known as TNFRSF11A) (Novack et al. 2003), CD27 and Fibroblast growth factor-inducible immediate-early response protein 14 (FN14 also known as TNFRSF12A) etc. These receptors each mediate specific biological roles of the non-canonical NF- κ B. These non-canonical NF- κ B-stimulating receptors have one thing in common and is the presence of a TRAF-binding motif, which recruits different TNF receptor-associated factor (TRAF) members, particularly TRAF2 and TRAF3, to the receptor complex during ligand ligation (Grech et al. 2004, Bishop & Xie 2007). Receptor recruitment of these TRAF members leads to their degradation which is a critical step leading to the activation of NIK and induction of p100 processing (Sun 2011, 2012).

References

- Razani B, Reichardt AD & Cheng G (2011). Non-canonical NF- κ B signaling activation and regulation: principles and perspectives. *Immunol. Rev.*, 244, 44-54. [🔗](#)
- Sun SC (2011). Non-canonical NF- κ B signaling pathway. *Cell Res.*, 21, 71-85. [🔗](#)

Mahoney DJ, Wang Y, Shiba T, Mak TW, Yeh WC, Cheng G, ... Zarnegar BJ (2008). Noncanonical NF- κ B activation requires coordinated assembly of a regulatory complex of the adaptors cIAP1, cIAP2, TRAF2 and TRAF3 and the kinase NIK. *Nat. Immunol.*, 9, 1371-8. [🔗](#)

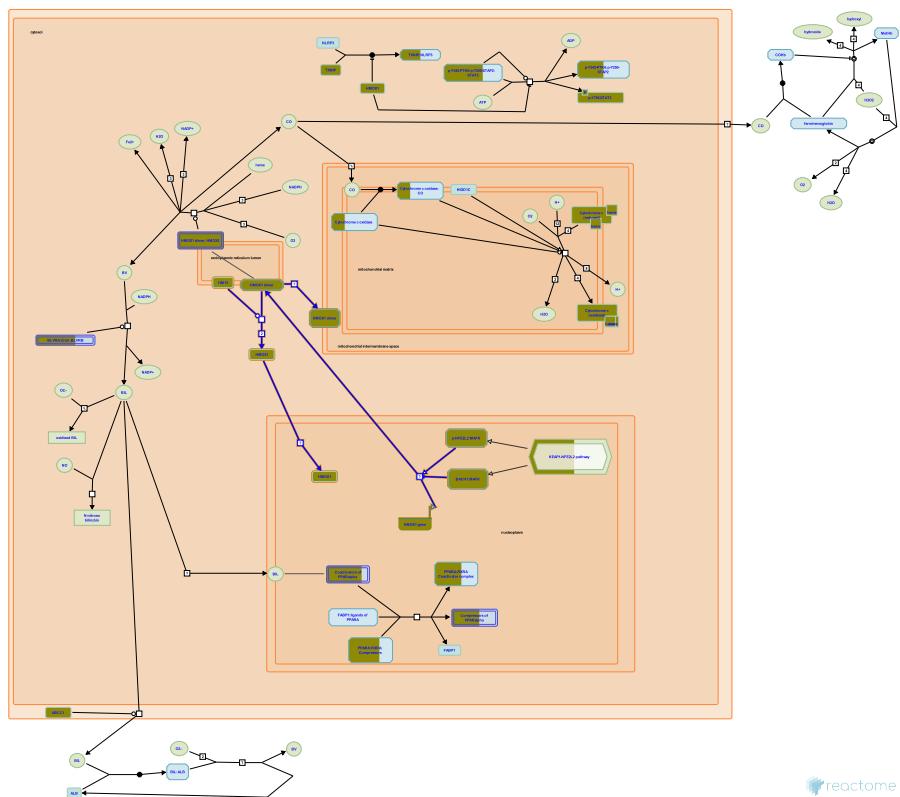
Edit history

Date	Action	Author
2015-01-26	Edited	Garapati P V
2015-01-26	Authored	Garapati P V
2015-02-20	Created	Garapati P V
2015-05-12	Reviewed	Virgen-Slane R, Ware CF, Rajput A
2024-05-25	Modified	Weiser JD

15 submitted entities found in this pathway, mapping to 15 Reactome entities

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ENSG00000131323	Q13114	ENSG00000141655	Q9Y6Q6	ENSG00000159958	Q96RJ3
ENSG00000223448	Q06643	ENSG00000231408	P01374	ENSG00000239697	O43508

22. Regulation of HMOX1 expression and activity (R-HSA-9707587)



Heme oxygenase 1 (HMOX1) is regulated at the level of gene transcription, mRNA translation, localization and degradation. Its gene is often activated under a wide range of stressful conditions. The transcriptional control of HMOX1 is determined by inducible regulatory elements localized in the 5' region of the promoter, so called antioxidant response elements (ARE)(Raghunath et al, 2018).

AREs on the HMOX1 gene are ultimately controlled by the enhancing NFE2L2:MAFK dimer and the repressing BACH1:MAFK dimer, both of which are influenced by a multitude of processes. Less specific enhancement occurs via AP-1 (FOS:JUN) dimers (Funes et al, 2020).

HMOX1 activity depends on dimerization in the ER membrane. Its membrane localization is abandoned by cleavage of the membrane domain by HM13. The resulting soluble enzyme is found in the cytosol, mitochondria, and the nucleus (Schaefer et al, 2017).

References

- Sethi G, Kumar AP, Sundarraj K, Perumal E, Arfuso F, Raghunath A, ... Nagarajan R (2018). Antioxidant response elements: Discovery, classes, regulation and potential applications. *Redox Biol*, 17, 297-314. [🔗](#)
- Behrends S, Schaefer B & Moriishi K (2017). Insights into the mechanism of isoenzyme-specific signal peptide peptidase-mediated translocation of heme oxygenase. *PLoS One*, 12, e0188344. [🔗](#)
- Kalergis AM, Fernández-Fierro A, Funes SC, Mackern-Oberti JP, Bueno SM, Covián C, ... Riedel CA (2020). Naturally Derived Heme-Oxygenase 1 Inducers and Their Therapeutic Application to Immune-Mediated Diseases. *Front Immunol*, 11, 1467. [🔗](#)
- Alam J, Choi AM & Ryter SW (2006). Heme oxygenase-1/carbon monoxide: from basic science to therapeutic applications. *Physiol Rev*, 86, 583-650. [🔗](#)

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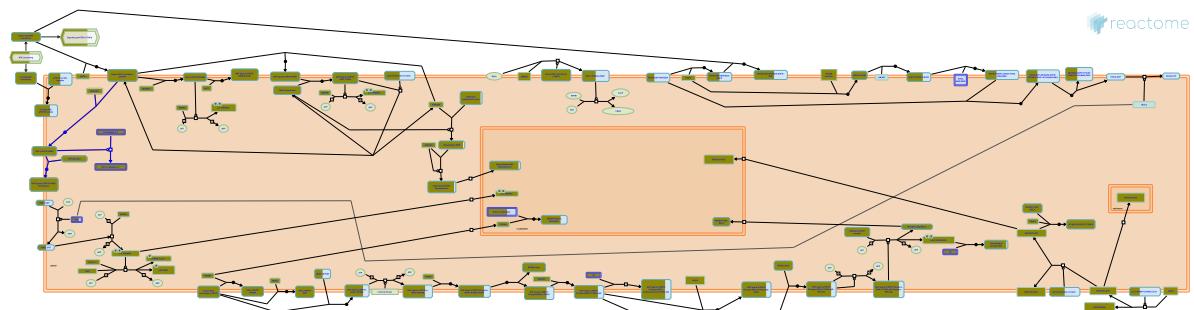
Date	Action	Author
2020-11-12	Edited	Stephan R
2020-11-12	Authored	Stephan R
2020-11-19	Created	Stephan R
2021-01-23	Reviewed	Somers J
2022-02-24	Revised	Rothfels K
2024-05-25	Modified	Weiser JD

5 submitted entities found in this pathway, mapping to 6 Reactome entities

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ENSG00000156273	O14867	ENSG00000198517	O60675		

Input	Ensembl Id
ENSG00000100292	ENSG00000100292

23. NADE modulates death signalling (R-HSA-205025)



NADE protein (p75NTR-associated cell death executor) may induce cell death upon NGF binding, but not BDNF, NT3, or NT4/5 binding, to p75NTR. The NADE-dependent apoptosis is modulated by the 14-3-3-epsilon protein (Kimura MT et al, 2001).

References

Irie S, Sato TA, Mukai J, Shoji-Hoshino S, Oshimura M, Nadano D & Kimura MT (2001). 14-3-3 is involved in p75 neurotrophin receptor-mediated signal transduction. *J Biol Chem*, 276, 17291-300.



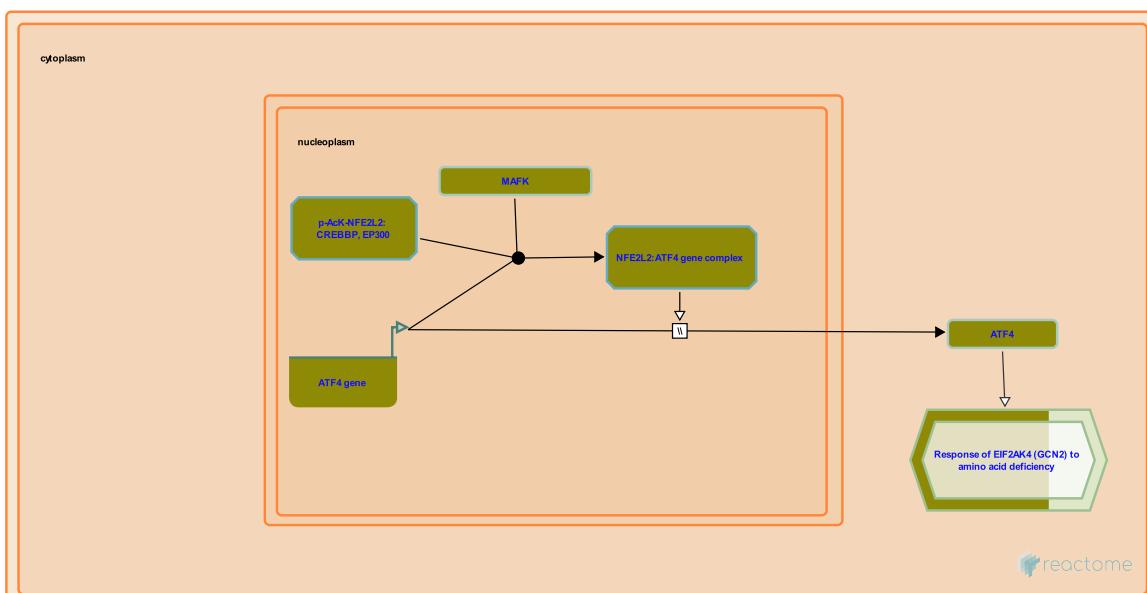
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Date	Action	Author
2006-10-10	Authored	Annibali D, Nasi S
2007-12-06	Created	Jassal B
2008-05-20	Edited	Jassal B
2008-05-20	Reviewed	Friedman WJ
2008-05-28	Reviewed	Chao MV
2024-05-25	Modified	Weiser JD

6 submitted entities found in this pathway, mapping to 6 Reactome entities

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ENSG00000064300	P08138	ENSG00000106144	P42575	ENSG00000108953	P62258
ENSG00000134259	P01138	ENSG00000164305	P42574	ENSG00000166681	Q00994

24. NFE2L2 regulating ER-stress associated genes (R-HSA-9818035)



Cellular compartments: nucleoplasm.

Subpathway representing ER-stress-associated genes regulated by NFE2L2 (NRF2). Activating transcription factor 4 (ATF4) is a stress-induced transcription factor that is frequently upregulated in cancer cells. ATF4 controls the expression of a wide range of adaptive genes that allow cells to endure periods of stress, such as hypoxia or amino acid limitation. However, under persistent stress conditions, ATF4 promotes the induction of apoptosis (Wortel et al, 2017). ATF4 is also known to regulate serine and glycine biosynthesis in NSCLC (Denicola et al, 2016)

References

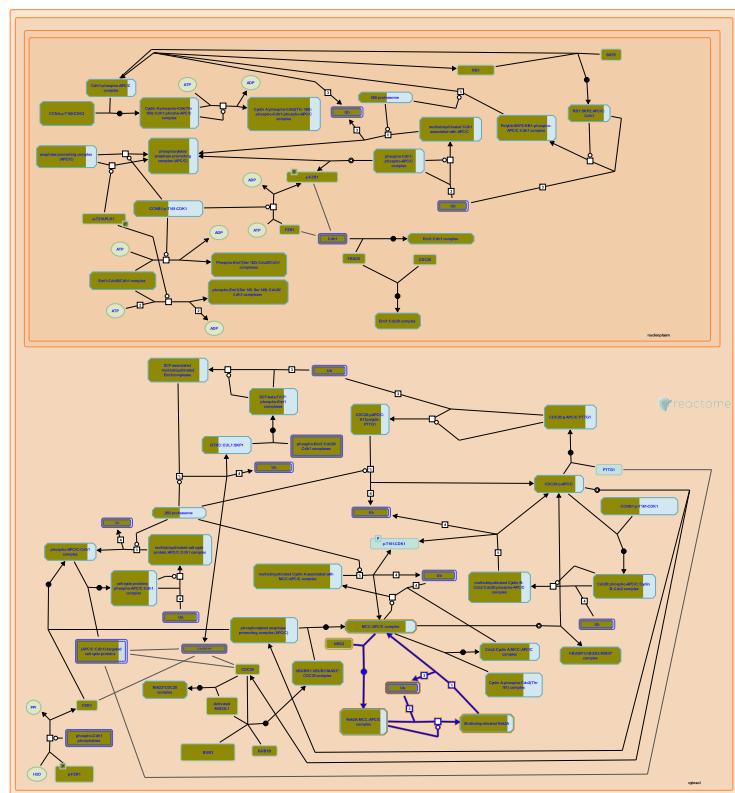
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2022-10-10	Created	Tiwari K
2023-08-08	Edited	Tiwari K
2023-08-08	Authored	Tiwari K
2023-08-21	Modified	Matthews L

5 submitted entities found in this pathway, mapping to 6 Reactome entities

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ENSG00000128272	P18848	ENSG00000198517	O60675		
Input		Ensembl Id			
ENSG00000128272		ENSG00000128272			

25. APC-Cdc20 mediated degradation of Nek2A (R-HSA-179409)



Cellular compartments: cytosol.

Like Cyclin A, NIMA-related kinase 2A (Nek2A) is degraded during pro-metaphase in a checkpoint-independent manner.

References

Fry AM, Bacchieri R, Yamano H, Wattam SL & Hames RS (2001). APC/C-mediated destruction of the centrosomal kinase Nek2A occurs in early mitosis and depends upon a cyclin A-type D-box. EMBO J, 20, 7117-27. [\[PubMed\]](#)

Fry AM, Mao G, Kimata Y, Hayes MJ, Lindon C, Yamano H & Wattam SL (2006). Early mitotic degradation of Nek2A depends on Cdc20-independent interaction with the APC/C. Nat Cell Biol, 8, 607-14. [\[PubMed\]](#)

Edit history

Date	Action	Author
2006-01-26	Authored	Castro A, Lorca T
2006-03-28	Reviewed	Peters JM
2006-04-28	Created	Matthews L
2006-07-11	Edited	Matthews L

21 submitted entities found in this pathway, mapping to 22 Reactome entities

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ENSG00000154473	O43684	ENSG00000156970	O60566	ENSG00000164109	Q13257
ENSG00000164162	Q9UM13	ENSG00000170142	P51965	ENSG00000170315	P0CG47, P62987
ENSG00000175063	O00762	ENSG00000176248	Q9UJX6	ENSG00000176386	Q8NHZ8

6. Identifiers found

Below is a list of the input identifiers that have been found or mapped to an equivalent element in Reactome, classified by resource.

6189 of the submitted entities were found, mapping to 6842 Reactome entities

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7. Identifiers not found

These 4810 identifiers were not found neither mapped to any entity in Reactome.

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