

Cryptochrome

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Cryptochromes (from the Greek κρυπτός χρώμα, "hidden colour") are a class of flavoproteins that are sensitive to blue light. They are found in plants and animals. Cryptochromes are involved in the circadian rhythms of plants and animals, and in the sensing of magnetic fields in a number of species. The name *cryptochrome* was proposed as a *portmanteau* combining the cryptic nature of the photoreceptor, and the cryptogamic organisms on which many blue-light studies were carried out.^[5]

The two genes *Cry1* and *Cry2* code for the two cryptochrome proteins CRY1 and CRY2.^[6] In insects and plants, CRY1 regulates the circadian clock in a light-dependent fashion, whereas, in mammals, CRY1 and CRY2 act as light-independent inhibitors of CLOCK-BMAL1 components of the circadian clock.^[7] In plants, blue-light photoreception can be used to cue developmental signals.^[8] Besides chlorophylls, cryptochromes are the only proteins known to form photoinduced radical-pairs in vivo.^[9]

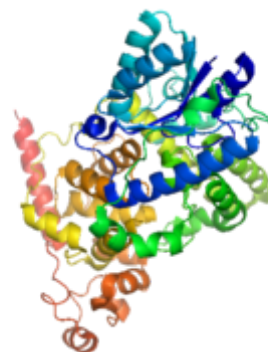
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Discovery

Although Charles Darwin first documented plant responses to blue light in the 1800s, it was not until the 1980s that research began to identify the pigment responsible.^[10] In 1980, researchers discovered that

CRY1



Available structures

PDB Ortholog search: PDBe (<https://www.ebi.ac.uk/pdbe/searchResults.html?display=both&term=P97784%20or%20Q16526%20or%20A2I2P0>) RCSB (<http://www.rcsb.org/pdb/search/smartSubquery.do?smartSearchSubtype=UpAccessionIdQuery&accessionIdList=P97784,Q16526,A2I2P0>)

List of PDB id codes

4CT0 (<http://www.rcsb.org/pdb/explore/explore.do?pdbId=4CT0>), 4K0R (<http://www.rcsb.org/pdb/explore/explore.do?pdbId=4K0R>)

Identifiers

Aliases (**h** CRY1 (http://www.genenames.org/cgi-bin/gene_symbol_report?hgnc_id=2384), cryptochrome
wikipedi circadian clock 1, PHL1
a.org/wik
i/Human
_Genome
_Organis
ation)

External OMIM: 601933 (<https://omim.org/entry/601933>)
IDs MGI: 1270841 (<http://www.informatics.jax.org/marker/MGI:1270841>) HomoloGene: 7042 (https://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=homologene&dopt=HomoloGene&list_uids=7042) GeneCards: CRY1 (<https://www.genecards.org/cgi-bin/carddisp.pl?gene=CRY1>)

Gene ontology

the HY4 gene of the plant *Arabidopsis thaliana* was necessary for the plant's blue light sensitivity, and, when the gene was sequenced in 1993, it showed high sequence homology with photolyase, a DNA repair protein activated by blue light.^[11] By 1995, it became clear that the products of the HY4 gene and its two human homologs did not exhibit photolyase activity and were instead a new class of blue light photoreceptor hypothesized to be circadian photopigments.^[12] In 1996 and 1998, *Cry* homologs were identified in *Drosophila* and mice, respectively.^{[13][14]}

Evolutionary history and structure

Cryptochromes (CRY1, CRY2) are evolutionarily old and highly conserved proteins that belong to the flavoproteins superfamily that exists in all kingdoms of life.^[8] All members of this superfamily have the characteristics of an N-terminal photolyase homology (PHR) domain. The PHR domain can bind to the flavin adenine dinucleotide (FAD) cofactor and a light-harvesting chromophore.^[8] Cryptochromes are derived from and closely related to photolyases, which are bacterial enzymes that are activated by light and involved in the repair of UV-induced DNA damage. In eukaryotes, cryptochromes no longer retain this original enzymatic activity.^[15] The structure of cryptochrome involves a fold very similar to that of photolyase, with a single molecule of FAD noncovalently bound to the protein.^[8] These proteins have variable lengths and surfaces on the C-terminal end, due to the changes in genome and appearance that result from the lack of DNA repair enzymes. The Ramachandran plot^[16] shows that the secondary structure of the CRY1 protein is primarily a right-handed alpha helix with little to no steric overlap.^[17] The structure of CRY1 is almost entirely made up of alpha helices, with several loops and few beta sheets. The molecule is arranged as an orthogonal bundle.^[8]

Function

Phototropism

Molecular function	• deoxyribodipyrimidine photo-lyase activity (http://amigo.geneontology.org/amigo/term/GO:0003904) • DNA binding (http://amigo.geneontology.org/amigo/term/GO:0003677) • nucleotide binding (http://amigo.geneontology.org/amigo/term/GO:0000166) • phosphatase binding (http://amigo.geneontology.org/amigo/term/GO:0019902) • transcription factor activity, transcription factor binding (http://amigo.geneontology.org/amigo/term/GO:0000989) • core promoter binding (http://amigo.geneontology.org/amigo/term/GO:0001047) • blue light photoreceptor activity (http://amigo.geneontology.org/amigo/term/GO:0009882) • transcription factor binding (http://amigo.geneontology.org/amigo/term/GO:0008134) • histone deacetylase binding (http://amigo.geneontology.org/amigo/term/GO:0042826) • nuclear hormone receptor binding (http://amigo.geneontology.org/amigo/term/GO:0035257) • DNA (6-4) photolyase activity (http://amigo.geneontology.org/amigo/term/GO:0003914) • core promoter sequence-specific DNA binding (http://amigo.geneontology.org/amigo/term/GO:0001046) • kinase binding (http://amigo.geneontology.org/amigo/term/GO:0019900) • ubiquitin binding (http://amigo.geneontology.org/amigo/term/GO:0043130) • protein binding (http://amigo.geneontology.org/amigo/term/GO:0005515) • photoreceptor activity (http://amigo.geneontology.org/amigo/term/GO:0009881) • double-stranded DNA binding (http://amigo.geneontology.org/amigo/term/GO:0003690) • protein kinase binding (http://amigo.geneontology.org/amigo/term/GO:0019901) • lyase activity (http://amigo.geneontology.org/amigo/term/GO:0016829)
Cellular component	• cytoplasm (http://amigo.geneontology.org/amigo/term/GO:0005737) • mitochondrion (http://amigo.geneontology.org/amigo/term/GO:0005739)

In plants, cryptochromes mediate phototropism, or directional growth toward a light source, in response to blue light. This response is now known to have its own set of photoreceptors, the phototropins.

Unlike phytochromes and phototropins, cryptochromes are not kinases. Their flavin chromophore is reduced by light and transported into the cell nucleus, where it affects the turgor pressure and causes subsequent stem elongation. To be specific, *Cry2* is responsible for blue-light-mediated cotyledon and leaf expansion. *Cry2* overexpression in transgenic plants increases blue-light-stimulated cotyledon expansion, which results in many broad leaves and no flowers rather than a few primary leaves with a flower.^[18] A double loss-of-function mutation in *Arabidopsis thaliana* Early Flowering 3 (*elf3*) and *Cry2* genes delays flowering under continuous light and was shown to accelerate it during long and short days, which suggests that *Arabidopsis* CRY2 may play a role in accelerating flowering time during continuous light.^[19]

In the sponge eyes, blue-light-receptive cryptochrome is also expressed. Most animals have some form of visual structure that allowed them to navigate the world, from simple eyespots up to complex refractive and compound eyes. The eyes utilize photo-sensitive opsin proteins expressed in neurons to communicate information of the light environment to the nervous system, whereas sponge larvae use pigment ring eyes to mediate phototactic swimming. However, despite possessing many other G-protein-coupled receptors (GPCRs), the fully sequenced genome of *Amphimedon queenslandica*, a demosponge larvae, lacks one vital visual component: a gene for a light-sensitive opsin pigment – which is essential for vision in other animals – suggesting that the sponge's unique eyes might have evolved a completely novel light-detection mechanism. By using RNA probes, Todd Oakley research group determined that one of the two cryptochromes, Aq-Cry2, was produced near the sponge's simple eye cells. Aq-Cry2 lacks photolyase activity and contains a flavin-based co-factor that is responsive to wavelengths of light that also mediate larval photic behavior. Defined as opsin-clade GPCRs, it possess a conserved Schiff base lysine that is central to opsin function. Like other sponges, *A. queenslandica* lacks a nervous system. This indicates that opsin-less sponge eyes utilize cryptochrome, along with other proteins, to direct or act in eye-mediated phototactic behavior. Therefore, *A.*

Biological process

- nucleus (<http://amigo.geneontology.org/amigo/term/GO:0005634>)
- gluconeogenesis (<http://amigo.geneontology.org/amigo/term/GO:0006094>)
- negative regulation of glucocorticoid receptor signaling pathway (<http://amigo.geneontology.org/amigo/term/GO:2000323>)
- response to glucagon (<http://amigo.geneontology.org/amigo/term/GO:0033762>)
- regulation of transcription, DNA-templated (<http://amigo.geneontology.org/amigo/term/GO:0006355>)
- glucose homeostasis (<http://amigo.geneontology.org/amigo/term/GO:0042593>)
- response to stimulus (<http://amigo.geneontology.org/amigo/term/GO:0050896>)
- rhythmic process (<http://amigo.geneontology.org/amigo/term/GO:0048511>)
- negative regulation of circadian rhythm (<http://amigo.geneontology.org/amigo/term/GO:0042754>)
- lipid storage (<http://amigo.geneontology.org/amigo/term/GO:0019915>)
- negative regulation of transcription from RNA polymerase II promoter (<http://amigo.geneontology.org/amigo/term/GO:0000122>)
- circadian regulation of gene expression (<http://amigo.geneontology.org/amigo/term/GO:0032922>)
- transcription, DNA-templated (<http://amigo.geneontology.org/amigo/term/GO:0006351>)
- response to insulin (<http://amigo.geneontology.org/amigo/term/GO:0032868>)
- negative regulation of protein ubiquitination (<http://amigo.geneontology.org/amigo/term/GO:0031397>)
- regulation of circadian rhythm (<http://amigo.geneontology.org/amigo/term/GO:0042752>)
- regulation of DNA damage checkpoint (<http://amigo.geneontology.org/amigo/term/GO:2000001>)
- DNA damage induced protein phosphorylation (<http://amigo.geneontology.org/amigo/term/GO:0006975>)
- protein-chromophore linkage (<http://amigo.geneontology.org/amigo/term/GO:0006975>)

queenslandica pigment ring eyes likely evolved convergently in the absence of opsins and nervous systems, and probably use as-yet-unknown molecular mechanisms that are fundamentally different from those employed by other animal eyes.^[20]

Photomorphogenesis

Cryptochromes receptors cause plants to respond to blue light via photomorphogenesis. Cryptochromes help control seed and seedling development, as well as the switch from the vegetative to the flowering stage of development. In *Arabidopsis*, it is shown that cryptochromes controls plant growth during sub-optimal blue-light conditions.^[21]

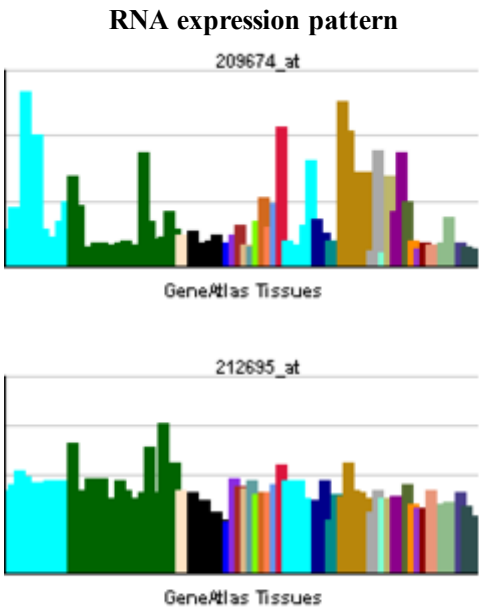
Light capture

Despite much research on the topic, cryptochrome photoreception and phototransduction in *Drosophila* and *Arabidopsis thaliana* is still poorly understood. Cryptochromes are known to possess two chromophores: pterin (in the form of 5,10-methenyltetrahydrofolic acid (MTHF)) and flavin (in the form of FAD).^[22] Both may absorb a photon, and in *Arabidopsis*, pterin appears to absorb at a wavelength of 380 nm and flavin at 450 nm. Past studies have supported a model by which energy captured by pterin is transferred to flavin.^[23] Under this model of phototransduction, FAD would then be reduced to FADH, which probably mediates the phosphorylation of a certain domain in cryptochrome. This could then trigger a signal transduction chain, possibly affecting gene regulation in the cell nucleus.

A new hypothesis^[24] proposes that in plant cryptochromes, the transduction of the light signal into a chemical signal that might be sensed by partner molecules could be triggered by a photo-induced negative charge within the protein - on the FAD cofactor or on the neighbouring aspartic acid.^{[25][26]} This negative charge would electrostatically repel the protein-bound ATP molecule and thereby also the protein C-terminal domain, which covers the ATP binding pocket prior to photon absorption. The resulting change in protein conformation could lead to phosphorylation of previously inaccessible phosphorylation sites on the C-terminus and the given phosphorylated segment could then liberate the

- ontology.org/amigo/term/GO:0018298)
- negative regulation of G-protein coupled receptor protein signaling pathway (<http://amigo.geneontology.org/amigo/term/GO:0045744>)
 - negative regulation of transcription, DNA-templated (<http://amigo.geneontology.org/amigo/term/GO:0045892>)
 - negative regulation of glucocorticoid secretion (<http://amigo.geneontology.org/amigo/term/GO:2000850>)
 - entrainment of circadian clock by photoperiod (<http://amigo.geneontology.org/amigo/term/GO:0043153>)
 - blue light signaling pathway (<http://amigo.geneontology.org/amigo/term/GO:0009785>)
 - circadian rhythm (<http://amigo.geneontology.org/amigo/term/GO:0007623>)

Sources:Amigo (<http://amigo.geneontology.org/>) / QuickGO (<https://www.ebi.ac.uk/QuickGO/>)



More reference expression data (<http://biogps.org/gene/1407/>)

Orthologs		
Species	Human	Mouse
Entrez	1407 (https://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene&cmd=retrieve&dopt=default&list_uids=1407&rn=1)	12952 (https://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene&cmd=retrieve&dopt=default&list_uids=12952&rn=1)
Ensembl		

transcription factor HY5 by competing for the same binding site at the negative regulator of photomorphogenesis COP1.

A different mechanism may function in *Drosophila*. The true ground state of the flavin cofactor in *Drosophila* CRY is still debated, with some models indicating that the FAD is in an oxidized form,^[27] while others support a model in which the flavin cofactor exists in anion radical form, FAD^{•−}. Recently, researchers have observed that oxidized FAD is readily reduced to FAD^{•−} by light. Furthermore, mutations that blocked photoreduction had no effect on light-induced degradation of CRY, while mutations that altered the stability of FAD^{•−} destroyed CRY photoreceptor function.^{[28][29]} These observations provide support for a ground state of FAD^{•−}. Researchers have also recently proposed a model in which FAD^{•−} is excited to its doublet or quartet state by absorption of a photon, which then leads to a conformational change in the CRY protein.^[30]

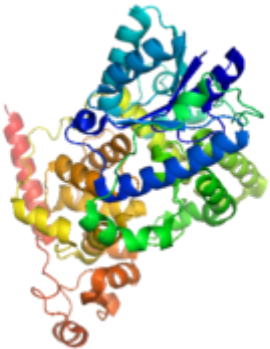
Circadian rhythm

Studies in animals and plants suggest that cryptochromes play a pivotal role in the generation and maintenance of circadian rhythms.^[31] Similarly, cryptochromes play an important role in the entrainment of circadian rhythms in plants.^[32] In *Drosophila*, cryptochrome (dCRY) acts as a blue-light photoreceptor that directly modulates light input into the circadian clock,^[33] while in mammals, cryptochromes (CRY1 and CRY2) act as transcription repressors within the circadian clockwork.^[34] Some insects, including the monarch butterfly, have both a mammal-like and a *Drosophila*-like version of cryptochrome, providing evidence for an ancestral clock mechanism involving both light-sensing and transcriptional-repression roles for cryptochrome.^{[35][36]}

Cry mutants have altered circadian rhythms, showing that *Cry* affects the circadian pacemaker. *Drosophila* with mutated *Cry* exhibit little to no mRNA cycling.^[37] A point mutation in *cry^b*, which is required for flavin association in CRY protein, results in no PER or TIM protein cycling in either DD or LD.^[38] In addition, mice lacking *Cry1* or *Cry2* genes exhibit

	ENSG00000008405 (http://www.ensembl.org/Homo_sapiens/geneview?gene=ENSG00000008405;db=core)	ENSMUSG00000020038 (http://www.ensembl.org/Mus_musculus/geneview?gene=ENSMUSG00000020038;db=core)
UniProt	Q16526 (http://www.uniprot.org/uniprot/Q16526)	P97784 (http://www.uniprot.org/uniprot/P97784)
RefSeq (mRNA)	NM_004075 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=N	NM_007771 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=N
RefSeq (protein)	NP_004066 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_004066) NP_004066.1 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_004066.1)	NP_031797.1 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_031797.1) NP_031797 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_031797)
Location (UCSC)	Chr 12: 106.99 – 107.09 Mb (https://genome.ucsc.edu/cgi-bin/hgTracks?org=Human&db=hg38&position=chr12:106991364-107093829)	Chr 10: 85.13 – 85.19 Mb (https://genome.ucsc.edu/cgi-bin/hgTracks?org=Human&db=mm0&position=chr10:85131700-85185064)
PubMed search	[1]	[2]
	Wikidata	
	View/Edit Human	View/Edit Mouse

CRY1



differentially altered free running periods, but are still capable of photoentrainment. However, mice that lack both *Cry1* and *Cry2* are arrhythmic in both LD and DD and always have high *Per1* mRNA levels. These results suggest that cryptochromes play a photoreceptive role, as well as acting as negative regulators of *Per* gene expression in mice.^[39]

In *Drosophila*

In *Drosophila*, cryptochrome functions as a blue light photoreceptor. Exposure to blue light induces a conformation similar to that of the always-active CRY mutant with a C-terminal deletion (CRYΔ).^[30] The half-life of this conformation is 15 minutes in the dark and facilitates the binding of CRY to other clock gene products, PER and TIM, in a light-dependent manner.^{[7][30][33][40]} Once bound by dCRY, dTIM is committed to degradation by the ubiquitin-proteasome system.^{[30][40]}

Although light pulses do not entrain, full photoperiod LD cycles can still drive cycling in the ventral-lateral neurons in the *Drosophila* brain. These data along with other results suggest that CRY is the cell-autonomous photoreceptor for body clocks in *Drosophila* and may play a role in nonparametric entrainment (entrainment by short discrete light pulses). However, the lateral neurons receive light information through both the blue light CRY pathway and the rhodopsin pathway. Therefore, CRY is involved in light perception and is an input to the circadian clock, however it is not the only input for light information, as a sustained rhythm has been shown in the absence of the CRY pathway, in which it is believed that the rhodopsin pathway is providing some light input.^[41] Recently, it has also been shown that there is a CRY-mediated light response that is independent of the classical circadian CRY-TIM interaction. This mechanism is believed to require a flavin redox-based mechanism that is dependent on potassium channel conductance. This CRY-mediated light response has been shown to increase action potential firing within seconds of a light response in opsin-knockout *Drosophila*.^[42]

Cryptochrome, like many genes involved in circadian rhythm, shows circadian cycling in mRNA and protein levels. In *Drosophila*, *Cry* mRNA concentrations cycle under a light-dark cycle (LD), with high levels in light and low levels in the dark.^[37] This cycling persists in

Available structures

PDB Ortholog search: PDBe (<https://www.ebi.ac.uk/pdbe/searchResults.html?display=both&term=P97784%20or%20Q16526%20or%20A2I2P0>) RCSB (<http://www.rcsb.org/pdb/search/smartSubquery.do?smartSearchSubtype=UpAccessionIdQuery&accessionIdList=P97784,Q16526,A2I2P0>)

List of PDB id codes

4CT0 (<http://www.rcsb.org/pdb/explore/explore.do?pdbId=4CT0>), 4K0R (<http://www.rcsb.org/pdb/explore/explore.do?pdbId=4K0R>)

Identifiers

Aliases (human) CRY1 (http://www.genenames.org/cgi-bin/gene_symbol_report?hgnc_id=2384), cryptochrome
wikipedia circadian clock 1, PHLL1

a.org/wiki/
i/Human
_Genome
_Organisation)

External IDs OMIM: 601933 (<https://omim.org/entry/601933>)
MGI: 1270841 (<http://www.informatics.jax.org/marker/MGI:1270841>) HomoloGene: 7042 (http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?cmd=Retrieve&db=homologene&dopt=HomoloGene&list_uids=7042) GeneCards: CRY1 (<https://www.genecards.org/cgi-bin/carddisp.pl?gene=CRY1>)

Gene ontology

Molecular function

- deoxyribodipyrimidine photo-lyase activity (<http://amigo.geneontology.org/amigo/term/GO:0003904>)
- DNA binding (<http://amigo.geneontology.org/amigo/term/GO:0003677>)
- nucleotide binding (<http://amigo.geneontology.org/amigo/term/GO:0000166>)
- phosphatase binding (<http://amigo.geneontology.org/amigo/term/GO:0019902>)
- transcription factor activity, transcription factor binding (<http://amigo.geneontology.org/amigo/term/GO:0000989>)
- core promoter binding (<http://amigo.geneontology.org/amigo/term/GO:0001047>)
- blue light photoreceptor activity (<http://amigo.geneontology.org/amigo/term/GO:0001047>)

constant darkness (DD), but with decreased amplitude.^[37] The transcription of the *Cry* gene also cycles with a similar trend.^[37] CRY protein levels, however, cycle in a different manner than *Cry* transcription and mRNA levels. In LD, CRY protein has low levels in light and high levels in dark, and, in DD, CRY levels increase continuously throughout the subjective day and night.^[37] Thus, CRY expression is regulated by the clock at the transcriptional level and by light at the translational and posttranslational level.^[37]

Overexpression of *Cry* also affects circadian light responses. In *Drosophila*, *Cry* overexpression increases flies' sensitivity to low-intensity light.^[37] This light regulation of CRY protein levels suggests that CRY has a circadian role upstream of other clock genes and components.^[37]

In mammals

Cryptochrome is one of the four groups of mammalian clock genes/proteins that generate a transcription-translation negative-feedback loop (TTFL), along with Period (PER), CLOCK, and BMAL1.^[43] In this loop, CLOCK and BMAL1 proteins are transcriptional activators, which together bind to the promoters of the *Cry* and *Per* genes and activate their transcription.^[43] The CRY and PER proteins then bind to each other, enter the nucleus, and inhibit CLOCK-BMAL1-activated transcription.^[43]

In mice, *Cry1* expression displays circadian rhythms in the suprachiasmatic nucleus, a brain region involved in the generation of circadian rhythms, with mRNA levels peaking during the light phase and reaching a minimum in the dark.^[44] These daily oscillations in expression are maintained in constant darkness.^[44]

While CRY has been well established as a TIM homolog in mammals, the role of CRY as a photoreceptor in mammals has been controversial. Early papers indicated that CRY has both light-independent and -dependent functions. A study in 2000 indicated that mice without rhodopsin but with cryptochrome still respond to light; however, in mice without either rhodopsin or cryptochrome, *c-Fos* transcription, a mediator of light sensitivity, significantly drops.^[45] In recent years, data have

geneontology.org/amigo/term/GO:0009882)

- transcription factor binding (<http://amigo.geneontology.org/amigo/term/GO:0008134>)
- histone deacetylase binding (<http://amigo.geneontology.org/amigo/term/GO:0042826>)
- nuclear hormone receptor binding (<http://amigo.geneontology.org/amigo/term/GO:0035257>)
- DNA (6-4) photolyase activity (<http://amigo.geneontology.org/amigo/term/GO:0003914>)
- core promoter sequence-specific DNA binding (<http://amigo.geneontology.org/amigo/term/GO:0001046>)
- kinase binding (<http://amigo.geneontology.org/amigo/term/GO:0019900>)
- ubiquitin binding (<http://amigo.geneontology.org/amigo/term/GO:0043130>)
- protein binding (<http://amigo.geneontology.org/amigo/term/GO:0005515>)
- photoreceptor activity (<http://amigo.geneontology.org/amigo/term/GO:0009881>)
- double-stranded DNA binding (<http://amigo.geneontology.org/amigo/term/GO:0003690>)
- protein kinase binding (<http://amigo.geneontology.org/amigo/term/GO:0019901>)
- lyase activity (<http://amigo.geneontology.org/amigo/term/GO:0016829>)

Cellular component

- cytoplasm (<http://amigo.geneontology.org/amigo/term/GO:0005737>)
- mitochondrion (<http://amigo.geneontology.org/amigo/term/GO:0005739>)
- nucleus (<http://amigo.geneontology.org/amigo/term/GO:0005634>)

Biological process

- gluconeogenesis (<http://amigo.geneontology.org/amigo/term/GO:0006094>)
- negative regulation of glucocorticoid receptor signaling pathway (<http://amigo.geneontology.org/amigo/term/GO:2000323>)
- response to glucagon (<http://amigo.geneontology.org/amigo/term/GO:0033762>)
- regulation of transcription, DNA-templated (<http://amigo.geneontology.org/amigo/term/GO:0006355>)
- glucose homeostasis (<http://amigo.geneontology.org/amigo/term/GO:0042593>)
- response to stimulus (<http://amigo.geneontology.org/amigo/term/GO:0009882>)

supported melanopsin as the main circadian photoreceptor, in particular melanopsin cells that mediate entrainment and communication between the eye and the suprachiasmatic nucleus (SCN).^[46] One of the main difficulties in confirming or denying CRY as a mammalian photoreceptor is that when the gene is knocked out the animal goes arrhythmic, so it is hard to measure its capacity as purely a photoreceptor. However, some recent studies indicate that human CRY may mediate light response in peripheral tissues.^[47]

Normal mammalian circadian rhythm relies critically on delayed expression of *Cry1* following activation of the *Cry1* promoter. Whereas rhythms in *Per2* promoter activation and *Per2* mRNA levels have almost the same phase, *Cry1* mRNA production is delayed by approximately four hours relative to *Cry1* promoter activation.^[48] This delay is independent of CRY1 or CRY2 levels and is mediated by a combination of E/E'-box and D-box elements in the promoter and RevErbA/ROR binding elements (RREs) in the gene's first intron.^[49] Transfection of arrhythmic *Cry1*^{-/-} *Cry2*^{-/-} double-knockout cells with only the *Cry1* promoter (causing constitutive *Cry1* expression) is not sufficient to rescue rhythmicity. Transfection of these cells with both the promoter and the first intron is required for restoration of circadian rhythms in these cells.^[49]

Magnetoception

Cryptochromes in the photoreceptor neurons of birds' eyes are involved in magnetic orientation during migration.^[50] Cryptochromes are also essential for the light-dependent ability of *Drosophila* to sense magnetic fields.^[51] Magnetic fields were once reported to affect cryptochromes also in *Arabidopsis thaliana* plants: growth behavior seemed to be affected by magnetic fields in the presence of blue (but not red) light.^[52] Nevertheless, these results have later turned out to be irreproducible under strictly controlled conditions in another laboratory,^[53] suggesting that plant cryptochromes do not respond to magnetic fields.

Cryptochrome forms a pair of radicals with correlated spins when exposed to blue light.^{[54][55]} Radical pairs can also be generated by the light-independent dark reoxidation of the flavin cofactor by molecular oxygen

y.org/amigo/term/GO:0050896)

- rhythmic process (<http://amigo.geneontology.org/amigo/term/GO:0048511>)
- negative regulation of circadian rhythm (<http://amigo.geneontology.org/amigo/term/GO:0042754>)
- lipid storage (<http://amigo.geneontology.org/amigo/term/GO:0019915>)
- negative regulation of transcription from RNA polymerase II promoter (<http://amigo.geneontology.org/amigo/term/GO:0000122>)
- circadian regulation of gene expression (<http://amigo.geneontology.org/amigo/term/GO:0032922>)
- transcription, DNA-templated (<http://amigo.geneontology.org/amigo/term/GO:0006351>)
- response to insulin (<http://amigo.geneontology.org/amigo/term/GO:0032868>)
- negative regulation of protein ubiquitination (<http://amigo.geneontology.org/amigo/term/GO:0031397>)
- regulation of circadian rhythm (<http://amigo.geneontology.org/amigo/term/GO:0042752>)
- regulation of DNA damage checkpoint (<http://amigo.geneontology.org/amigo/term/GO:2000001>)
- DNA damage induced protein phosphorylation (<http://amigo.geneontology.org/amigo/term/GO:0006975>)
- protein-chromophore linkage (<http://amigo.geneontology.org/amigo/term/GO:0018298>)
- negative regulation of G-protein coupled receptor protein signaling pathway (<http://amigo.geneontology.org/amigo/term/GO:0045744>)
- negative regulation of transcription, DNA-templated (<http://amigo.geneontology.org/amigo/term/GO:0045892>)
- negative regulation of glucocorticoid secretion (<http://amigo.geneontology.org/amigo/term/GO:2000850>)
- entrainment of circadian clock by photoperiod (<http://amigo.geneontology.org/amigo/term/GO:0043153>)
- blue light signaling pathway (<http://amigo.geneontology.org/amigo/term/GO:0009785>)

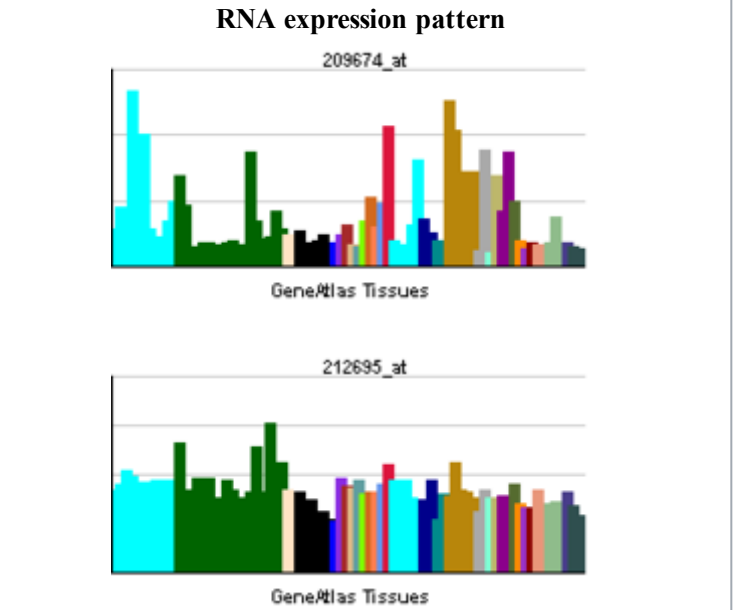
through the formation of a spin-correlated FADH-superoxide radical pairs.^[56] Magnetoception is hypothesized to function through the surrounding magnetic field's effect on the correlation (parallel or anti-parallel) of these radicals, which affects the lifetime of the activated form of cryptochrome. Activation of cryptochrome may affect the light-sensitivity of retinal neurons, with the overall result that the animal can "see" the magnetic field.^[57] Animal cryptochromes and closely related animal (6-4) photolyases contain a longer chain of electron-transferring tryptophans than other proteins of the cryptochrome-photolyase superfamily (a tryptophan tetrad instead of a triad).^{[58][59]} The longer chain leads to a better separation and over 1000× longer lifetimes of the photoinduced flavin-tryptophan radical pairs than in proteins with a mere triad of tryptophans.^{[58][59]} The absence of spin-selective recombination of these radical pairs on the nanosecond to microsecond timescales seems to be incompatible with the suggestion that magnetoreception by cryptochromes is based on the forward light reaction.

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• circadian rhythm (<http://amigo.geneontology.org/amigo/term/GO:0007623>)

Sources:Amigo (<http://amigo.geneontology.org/>) / QuickGO (<https://www.ebi.ac.uk/QuickGO/>)



More reference expression data (<http://biogps.org/gene/1407/>)

Orthologs		
Species	Human	Mouse
Entrez	1407 (https://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene&cmd=retrieve&dopt=default&list_uids=1407&rn=1)	12952 (https://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene&cmd=retrieve&dopt=default&list_uids=12952&rn=1)
Ensembl	ENSG00000008405 (http://www.ensembl.org/Homo_sapiens/geneview?gene=ENSG00000008405;db=core)	ENSMUSG00000020038 (http://www.ensembl.org/Mus_musculus/geneview?gene=ENSMUSG00000020038;db=core)
UniProt	Q16526 (http://www.uniprot.org/uniprot/Q16526)	P97784 (http://www.uniprot.org/uniprot/P97784)
RefSeq (mRNA)	NM_004075 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=Nm_004075)	NM_007771 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=Nm_007771)
RefSeq		

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(protein)	NP_004066 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_004066)	NP_031797.1 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_031797.1)
	NP_004066.1 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_004066.1)	NP_031797 (https://www.ncbi.nlm.nih.gov/entrez/viewer.fcgi?val=NP_031797)
Location (UCSC)	Chr 12: 106.99 – 107.09 Mb (https://genome.ucsc.edu/cgi-bin/hgTracks?org=Human&db=hg38&position=chr12:106991364-107093829)	Chr 10: 85.13 – 85.19 Mb (https://genome.ucsc.edu/cgi-bin/hgTracks?org=Human&db=mm0&position=chr10:85131700-85185064)
PubMed search	[3]	[4]
	Wikidata	
	View/Edit Human	View/Edit Mouse

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External links

- cryptochrome (https://www.nlm.nih.gov/cgi/mesh/2011/MB_cgi?mode=&term=cryptochrome) at the US National Library of Medicine Medical Subject Headings (MeSH)
- Cryptochrome circadian clock in Monarch Butterflies (<http://www.umassmed.edu/neuroscience/faculty/reppert.cfm?start=0>), by Steven M. Reppert, Department of Neurobiology, University of Massachusetts
- Cryptochrome and Magnetic Sensing (<http://www.ks.uiuc.edu/Research/cryptochrome/>), *Theoretical and Computational Biophysics Group* at the University of Illinois at Urbana-Champaign
- 2IJG (<http://www.rcsb.org/pdb/explore.do?structureId=2IJG>) at the Protein Data Bank; 3-D structure of *Arabidopsis* cryptochrome 3, obtained by X-ray crystallography.
- Animated model of Murine circadian pathway, including role of Cry (http://stke.sciencemag.org/cgi/content/full/sigtrans;CMP_13010/DC1)

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