## Interstellar Molecular Clouds

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The interstellar medium in our galaxy contains matter in a variety of states ranging from hot plasma to cold and dusty molecular gas. The molecular phase consists of giant clouds, which are the largest gravitationally bound objects in the galaxy, the primary reservoir of material for the ongoing birth of new stars, and the medium regulating the evolution of galactic disks.

The DISCOVERY OF LINES IN THE OPTICAL SPECTRA OF emission nebulae, such as the Great Nebula in Orion, by Sir William Huggins more than a century ago provided the first direct evidence for the existence of a gaseous interstellar medium (I). We now know that luminous, hot, young stars, which emit ionizing ultraviolet radiation, are often surrounded by clouds of ionized atomic hydrogen, the so-called HII regions. With the discovery of interstellar molecules, it has become generally recognized that the HII regions are relatively small, hot blisters formed at the edges or inside much more massive molecular clouds from which the hot stars were born. Even though it is now believed that molecular clouds contain most of the mass in the interstellar medium, they remained undiscovered until recently.

The interstellar medium contains a variety of phases with greatly varying temperatures, densities, and physical conditions. Because of their bright optical emission, the ionized nebulae such as the Orion Nebula represented the first phase of the interstellar medium to be discovered. A colder, neutral atomic phase was discovered in the early part of this century from the absorption lines of sodium and calcium seen toward bright, distant stars. The detection of neutral atomic hydrogen (HI) in 1951 (2) by means of its 1.4-GHz (21-cm wavelength) spectral line led to the recognition that the warm atomic phase of the interstellar medium, which has temperatures ranging from a few tens to thousands of Kelvins and densities between 0.1 to about 100 atoms cm<sup>-3</sup>, is widespread. Our galaxy was found to have about  $3 \times 10^9$  solar masses (1 solar mass =  $2 \times 10^{33}$  grams, the mass of the sun) of HI (3), which represents several percent of the total mass of all observed matter, mostly in the form of stars in the galaxy. In the 1960's, observations at ultraviolet wavelengths made from satellites and rockets revealed that between 10 to 50 percent of the volume of the interstellar medium is filled with hot  $(10^5 \text{ to } 10^6 \text{ K})$  bubbles of low-density plasma formed by supernova explosions and the winds from hot stars (4). As a result of the low density (<0.1 particle cm<sup>-3</sup>) of this "coronal" phase (so named because the temperature is similar to that in the solar corona), the total mass of hot plasma in the galaxy is negligible compared with the mass of the atomic phase.

Since the 1930's, the widespread existence of dust in interstellar space has become accepted. In some directions, clouds of dust were seen to obscure completely the stars lying behind them. Little was known about the composition and physical conditions of these opaque objects until the late 1960's, when the development of sensitive radio receivers and the application of new technology to radio astronomy led to the accidental discovery of radio frequency spectral emission lines of several molecules, such as OH, H<sub>2</sub>O, NH<sub>3</sub>, and  $H_2CO$ , in interstellar space. Although these species were at first seen only in a few distinct directions, the discovery of CO (5) led to the recognition that cold molecular gas represents a major, previously unrecognized phase of the interstellar medium, having a total mass comparable to that of the HI phase but occupying only about 1 percent of the volume of the galactic disk. Early surveys (6) of the 115 GHz (wavelength, 2.6 mm) ground-state rotational transition of CO revealed that it is an excellent tracer of the distribution of molecular hydrogen. Molecular clouds were found to be widespread and closely associated with the dark clouds of dust responsible for obscuration at optical wavelengths. These clouds contain sites of active star formation. In this article, I will review the physical properties of the molecular phase of the interstellar medium and how it has contributed to our understanding of star formation and the structure of our galaxy.

### Tools Used to Study Molecular Clouds

Molecular clouds are the coldest form of matter in the universe, with temperatures ranging from a few Kelvins to more than 100 K in regions of active star formation. Most of the detectable radiation from these clouds is emitted by dust in the far infrared portion of the electromagnetic spectrum and by rotational transitions of molecules in the far infrared and millimeter-wavelength spectral region. Spectral lines provide information about the temperature, density, mass, and size of the clouds, and, by virtue of the Doppler effect, we can probe the radial component of the gas velocity.

The most abundant species in these clouds is the H2 molecule, but because of its symmetric structure it does not radiate unless the gas temperature exceeds 500 K. Helium occurs in high abundance but has no detectable transitions in the cold environment of molecular clouds. Although large quantities of atomic hydrogen may be present in molecular clouds, its emission can not be distinguished from that of the HI clouds. Carbon monoxide, the most abundant molecule after hydrogen, has its lowest lying J = 1-0 rotational transition at 115 GHz (2.6 mm), a region of the spectrum where Earth's atmosphere is relatively transparent to radiation. The CO molecule is therefore used as a tracer of the distribution of molecular hydrogen in space. The abundance of CO in clouds near the sun has been measured to be approximately  $10^{-4}$  of the molecular hydrogen abundance (7). However, the conversion of observed CO intensity to H<sub>2</sub> column density or mass depends on the constancy of the H<sub>2</sub>:CO ratio. Variations in the temperature of the gas, the properties of the ambient radiation field, the relative abundance of the

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elements, and the properties of the dust grains embedded in the clouds may cause the CO abundance to vary. At the edges of molecular clouds and in very low density clouds, the fractional abundance of CO can be as small as  $10^{-6}$ . As a consequence of these variations, estimates of the total mass and density of molecular clouds are uncertain by at least a factor of 2 in the solar neighborhood and by even larger factors in distant regions of our galaxy and in other galaxies.

The brightness of a spectral line is determined by the number of molecules in the quantum state from which the line originates. The states are populated through collisions, mostly with hydrogen (8). Significant excitation of a level (thermalization) occurs only if the collision rate exceeds the rate of radiative decay of the state. Emission from CO is detectable for total particle densities greater than 200 particle cm<sup>-3</sup>. Most other molecules have faster radiative decay rates than CO in their ground state rotational transitions and require higher gas density for excitation of their emission lines. Such molecules are useful as tracers of higher density gas. The CS molecule requires a density of a  $4 \times 10^4$  molecule cm<sup>-3</sup> for significant excitation of its 49-GHz J = 1-0 transition. The radiative decay rates increase with increasing rotational quantum number, so that excitation of populations at detectable levels in high-lying states requires greater density than the excitation of low-lying states. Density structure in the range  $10^2$  to  $10^6$  particle cm<sup>-3</sup> can be probed by observations of several low-lying transitions of CO and CS.

In addition to sufficient excitation of the radiating level, it is necessary that the total column density of molecules in the state be large enough to produce a detectable flux of photons. As the total amount of a particular species along the line of sight (column



Fig. 1. A <sup>12</sup>CO integrated intensity map showing a small molecular cloud near the Pleiades star cluster, located at a distance of 125 pc from the sun. This cloud has a mass of about 10 solar masses, a density of  $10^3$  cm<sup>-3</sup>, and a gas temperature of 26 K. The Pleiades and the cloud are colliding with a relative velocity of about 10 km sec<sup>-1</sup>. The cluster mass is exerting a tidal force on the cloud that has caused an east-to-west velocity gradient to be set up; this may also be responsible for the cloud elongation seen in this direction. Contours are at intervals of 2.0 K km sec<sup>-1</sup>. This map was made with the Crawford Hill 7-m millimeter-wavelength telescope.

density) is increased, the optical depth in the line grows and the peak brightness approaches the flux density that would be produced by a blackbody radiator at the excitation temperature. The excitation temperature equals the gas temperature for densities larger than those required to thermalize the line; for much lower densities, the excitation temperature becomes 3 K, which is the temperature of the cosmic microwave background. The CO 1–0 line saturates when the total number of CO molecules in the line of sight (the column density) is roughly  $4 \times 10^{15}$  molecules, which corresponds to a hydrogen column density of about  $10^{20}$  H<sub>2</sub> molecules. An optically thick and thermalized transition (such as the 115 GHz line of CO) provides a measurement of the gas temperature near the cloud surface where the opacity is near unity.

Molecules containing rare isotopic species of one or more atoms occur with a relative abundance in approximate proportion to the isotopic abundance ratio. The opacity of molecules in which isotopic substitution has occurred is correspondingly less. Thus <sup>13</sup>CO has an opacity approximately 40 to 90 times smaller than the common <sup>12</sup>CO species and can be used to probe deeper into the interior of clouds. Although  $^{12}\mathrm{CO}$  is totally opaque in most clouds (in the 1–0 transition), the less abundant <sup>13</sup>CO species is usually optically thin. Where <sup>13</sup>CO saturates, C<sup>18</sup>O can be used as an optically thin probe. Not only are the isotopic species useful in providing a variety of optically thin tracers, they can be used to study the actual isotopic abundances at various places in the galaxy (9). Such studies suggest that the central regions of the galaxy contain a larger abundance of elements relative to hydrogen than does the solar neighborhood. It has also been shown that in cold regions chemical fractionation may enhance the relative abundance of the more massive isotopic species (such as  $^{13}CO$ ) relative to the less massive species (such as  $^{12}CO$ ) by factors of 2. The abundance of deuterated versions of molecules, such as the DCO<sup>+</sup> isotopic variant of HCO<sup>+</sup>, can be enhanced by factors of several hundred by chemical fractionation.

In addition to direct detection of molecular emission lines, the gas can be studied by observing molecular absorption in the ultraviolet, optical, and near infrared spectra of stars located either behind or inside a molecular cloud. This method provides information about the properties of the gas on very narrow lines of sight in the direction of bright background stars (10).

Mixed with the molecular gas is a large amount of interstellar dust (roughly 1 percent of the cloud mass is in solid material) whose presence can be inferred from its wavelength-dependent extinction and far infrared emission. The far infrared emission (20- $\mu$ m to 1mm wavelength) from the grains provides a measure of the dust temperature and column density. The IRAS satellite has recently surveyed 98 percent of the sky in four infrared bands (centered at 12, 25, 60, and 100  $\mu$ m), yielding maps of the distribution of dust at temperatures of 20 K or more with a resolution of a few arc minutes (11).

Most observations of molecular clouds are made with single-dish, high-surface precision radio telescopes, such as the 45-m-diameter dish in Nobeyama, Japan, the 14-m dish at the University of Massachusetts in Amherst, the 12-m dish operated by the National Radio Astronomy Observatory on top of Kitt Peak, Arizona, or the 7-m telescope at AT&T Bell Laboratories in Holmdel, New Jersey. A 1-m-diameter dish at Columbia University in the middle of Manhattan in New York and a sister dish located at the Cerro Tololo Inter-American Observatory in Chile have produced the first complete maps of the molecular cloud distribution in the galaxy (12). The best angular resolution attainable is about 0.2 to 1 arc minute, about 10 to 50 times worse than that available at optical wavelengths. Even in the nearest molecular clouds, this implies that the smallest structures that we can resolve are of order  $10^{17}$  cm in diameter [about 0.1 light year or 0.03 parsec (pc)]. Thus our understanding of the structure of molecular clouds is restricted to large-scale phenomena; only in a few cases where absorption line techniques or radio interferometric methods have been used, or shorter wavelength observations have been obtained, do we have information on small-scale behavior. The next generation of infrared and millimeter-wavelength telescopes should enable us to probe small-scale structure comparable in dimensions to the solar system.

#### Molecular Clouds

Although the early studies of molecular emission lines concentrated on the vicinity of nearby compact HII regions, it is now clear that CO-emitting molecular gas is wide spread. The emission comes mostly from clouds confined to a thin layer lying near the plane of the galaxy that is about 150 pc thick near the sun and a little thinner in the inner parts of the galaxy. From our vantage point inside the galaxy, the galactic plane appears as a narrow band of emission, the Milky Way. Since the molecular gas layer is very thin (200 times thinner than the diameter of the galaxy), most of the emission is seen confined to a 2°-wide band circling the sky. Only the nearest clouds are seen in directions far off the plane of the Milky Way.

Molecular clouds exist in a large variety of sizes, masses, and morphologies. The smallest clouds, the so-called Bok globules (13), were first recognized by Barnard around the turn of the century as nearby regions of high obscuration on photographs. Studies of CO emission show that Bok globules have masses ranging from only a few solar masses to hundreds of solar masses, are often round, and appear to be in nearly hydrostatic equilibrium (the sum of the internal thermal pressure of the gas and subsonic turbulence supports the cloud against gravitational collapse). Some of these objects have formed low-mass stars that are visible at infrared wavelengths (14).

Recently, a population of low-mass, low-density ( $<10^3$  molecule cm<sup>-3</sup>) molecular clouds has been discovered at large angles from the plane of the Milky Way (15). These so-called high-latitude clouds do not appear to be forming stars and may be the nearest examples of interstellar molecular gas. An example of a small, high-latitude molecular cloud having a mass of about 10 solar masses is shown in Fig. 1. This cloud is now undergoing a nearly head-on collision with the Pleiades star cluster, toward which it is moving at a relative velocity of about 10 km sec<sup>-1</sup>. The gravitational field of the cluster is tidally distorting the cloud, and starlight is heating and accelerating the gas and photodissociating the molecules on its surface.

Denser small clouds in the mass range 10 to 1000 solar masses are observed in isolation or in groups, often exhibiting complicated internal structure consisting of filaments and condensations of highdensity gas in which low- and intermediate-mass stars are forming. Small clouds often cluster into cloud complexes such as the Taurus molecular clouds (16), the nearest grouping of clouds in the sky (at a distance of about 150 pc). Here a total of about  $5 \times 10^4$  solar masses of gas is observed in filaments consisting of numerous small molecular clouds. The filamentary morphology of these clouds may be related to the interstellar magnetic field (17), whose anisotropic pressure allows gas flow and condensation to take place only along the field lines, resulting in the formation of flattened structures. The Taurus clouds have given birth to a gravitationally unbound association of low- to intermediate-mass stars that is observed as a concentration of pre-main sequence T-Tauri type variable stars (18). A complex of clouds associated with the star-forming region ON-1, at a distance of 1000 pc from the sun and similar to the Taurus molecular clouds, is shown in Fig. 2.

Most of the molecular gas in our galaxy is in immense clouds containing between  $5 \times 10^4$  and  $10^6$  solar masses of gas and with

diameters on the order of 40 pc. These clouds, which have come to be known as giant molecular clouds (GMC's), are the largest selfgravitating bodies in the disk of our galaxy. They constitute a reservoir from which most stars in our galaxy are presently created. The GMC's are gravitationally bound structures with much internal substructure. High-resolution observations show extensive fragmentation into small condensations (19). In some clouds, such as the Orion GMC, the individual lumps are so numerous that they give rise to a relatively smooth CO surface brightness over the face of the cloud with several individual lumps visible along each line of sight. When observed in optically thin species, such as C<sup>18</sup>O, each lump has a slightly different radial velocity, so that the substructure is revealed by multiple emission line components. Massive stars formed from the GMC generate bubbles of ionized gas (HII regions) and can disrupt large parts of the cloud by the combined action of ionization, powerful stellar winds, and supernova explosions (20). In some spiral arm locations, the GMC's cluster to form GMC complexes, which contain nearly  $10^7$  solar masses of gas (21).

Molecular gas is also seen to enshroud mass-losing red giants, which are stars in the last phases of evolution (22). These stars shed their outer layers back into the interstellar medium at rates ranging from  $10^{-5}$  to  $10^{-3}$  solar masses per year at velocities of a few tens of kilometers per second. Some of the material in the stellar envelopes condenses into grains as the outflowing gas cools. The grains can completely obscure the star at optical wavelengths and radiate the stellar energy in the middle infrared portion of the spectrum, making these stars the brightest infrared sources in the sky (23). As the remaining gas is rapidly condensed into molecules, an expanding, spherically symmetric molecular cloud forms around the star. Not until the density in the expanding cloud drops to a value sufficiently low that the general interstellar ultraviolet radiation field photodissociates the molecules is the envelope destroyed, often at a radius of  $10^{18}$  cm or more from the stellar surface.

The total amount of molecular gas in the galaxy, mostly in the form of molecular hydrogen, is in the range  $2 \times 10^9$  to  $4 \times 10^9$ 



Fig. 2. The filamentary molecular complex containing the star-forming region ON1 in Cygnus. ON1, the only B-type star forming in this complex, is contained by the dense knot in the right middle of the figure. This <sup>13</sup>CO map was made from 7000 spectra obtained with the Crawford Hill 7-m telescope. Contours show the integrated line intensity in steps of 2.0 K km  $sec^{-1}$ .

solar masses, comparable to or perhaps slightly greater than the amount in atomic form (24). Most of the gas is contained in about 6000 GMC's and is primarily confined to the spiral arms of our galaxy (25); the rest is in tens of thousands of smaller clouds distributed throughout the disk. Although there are probably tens of thousands of mass-losing giant stars blowing shells back into the interstellar medium, the total mass of molecular gas in stellar envelopes is of order  $10^4$  solar masses, which is negligible in comparison with other clouds (22).

The properties of the various kinds of molecular clouds are summarized in Table 1. Most clouds have mean gas number densities in the range 2  $\times$  10  $^2$  to 2  $\times$  10  $^3$  particle cm  $^{-3}$  and kinetic temperatures around 10 K. Roughly 10 percent of the mass of gas is in dense cores having densities 10 to 100 times greater than the cloud surface and containing recently formed stars that may heat the gas to temperatures up to several hundred Kelvins. In low-density interior regions far from buried stars, the gas is heated directly by collisions with cosmic rays (mostly 100-MeV protons) that penetrate the cloud. The balance between heating and the cooling provided by molecular line radiation determines the observed cloud temperature (26), usually close to 10 K. Near the outer edges of clouds, interstellar ultraviolet radiation indirectly heats the gas by photoemission of electrons from dust grains, making cloud surfaces hotter (40 to 60 K) than cloud interiors (27). In dense cloud cores, where particle number densities are greater than 10<sup>5</sup> particle cm<sup>-2</sup> collisions between molecules and dust grains couple the gas and dust temperatures. Since dust absorbs stellar radiation, raising the temperature to the value determined by radiative equilibrium (the power absorbed equals the power radiated by the grains), the temperature in such regions is closely coupled to the radiation environment. One of the nearest dense cloud cores is behind the Orion Nebula (Fig. 3). Several recently formed stars radiate about  $10^5$  solar luminosities of energy (1 solar luminosity =  $4 \times 10^{33}$  erg  $sec^{-1}$ , which is the total power radiated by the sun) into the dense  $(>10^{6} \text{ cm}^{-3})$  cloud core, raising its gas temperature to greater than 100 K.

Most molecular clouds exhibit highly supersonic emission line widths. Hydrodynamic considerations suggest that supersonic motions should be damped by shock waves in roughly one cloud

crossing time (the cloud size divided by the internal velocity dispersion of the gas), resulting in gravitational collapse and star formation, which would occur in roughly a free-fall time scale  $(\tau_{\rm ff} = 1/\sqrt{G\rho} \approx 10^6$  years, where G is the gravitational constant and  $\rho$  is the cloud density). The resulting galaxy-wide star formation rate would be in excess of 1000 solar masses per year, which is about 300 times greater than the deduced rate of 3 solar masses per year (28). Either the turbulence is rapidly regenerated by an agent such as stellar winds, or the motion above the sound speed is not as dissipative as pure hydrodynamic considerations suggest. The presence of a 0.05- to 1-mG magnetic field in the clouds can make the gas less dissipative for relative velocities under the Alfven velocity, which is about 2 to 5 km sec<sup>-1</sup>. Some evidence for magnetic fields of this magnitude exists in the form of measurements of Zeeman splitting in the 18 cm transition of the OH molecule, the 21-cm atomic hydrogen line, and polarization of far infrared radiation (29).

The thermal gas pressure inside molecular clouds  $(5 \times 10^{-12} \text{ dyne cm}^{-2})$  exceeds the pressure in the interstellar medium  $(1 \times 10^{-12} \text{ dyne cm}^{-2})$ . Since the clouds are not observed to be expanding, they must be bound by their own self-gravitation. In addition to being gravitationally bound by their own mass, the molecular clouds seem to be in virial equilibrium. That is, the typical turbulent velocity of the gas inside the cloud has a magnitude roughly one-half as large as the velocity required for a mass to escape from the gravitational field of the cloud.

The differential rotation of our galaxy imposes a tidal stress that tends to disrupt the clouds (30). For a cloud to remain bound, it must have a mean density in excess of a critical density, which increases with decreasing distance from the galactic center. Near the position of the sun, this critical density is only about 10 particle cm<sup>-3</sup>, which is less than the density of the observed molecular clouds. On the other hand, near the galactic center a mean density greater than  $10^4$  particle cm<sup>-3</sup> is required for a cloud to remain gravitationally bound against the galactic shear. Molecular clouds near the galactic center are observed to have much higher densities than those near the sun.

Giant molecular clouds may form primarily by mutual inelastic collisions between smaller clouds (31). Modeling of this process shows that in equilibrium most of the mass is tied up in the largest

Type of cloud	Mass (solar masses)	Mean particle number density (cm <sup>-3</sup> )	Typical size (pc)	Internal velocity dispersion (km sec <sup>-1</sup> )	Temp- erature (Kelvins)	Example	Comments
Giant star	0.1 to 5	$10^2$ to $10^5$	0.1 to 3	10 to 30	10 to 100	IRC + 10216	Expanding, spherically symmetric envelope*
Globules	1 to 500	$10^3$ to $10^4$	0.1 to 10	0.2 to 2	5 to 15	B335	Round, isolated, small clouds, little star formation
Small molecular clouds	1 to 10 <sup>3</sup>	200 to 10 <sup>4</sup>	1.0 to 10	0.5 to 5	5 to 25	Pleiades cloud	Complex or filamentary structure. Mostly low- mass star formation
Small cloud complex	$\frac{10^2 \text{ to}}{5 \times 10^4}$	$200 \text{ to } 10^4$	10 to 50	2 to 10	5 to 30	ON1 clouds	Complex structure, low- to intermediate-mass star formation
GMC	$5 imes10^4$ to $10^6$	$200 \text{ to } 10^4$	20 to 150	5 to 15	5 to 100	Orion clouds	Complex structure; all stellar masses form
GMC complex	$10^6$ to $10^7$	$200 \text{ to } 10^4$	100 to 300	10 to 20	5 to 100	l = 110 complex	Ensemble of GMC's in spiral arms
Galactic center cloud	10 <sup>4</sup> to 10 <sup>7</sup>	$10^{4}$ to $10^{6}$	10 to 50	20 to 50	20 to 200	Sgr BŹ	Located in inner 1 kpc of galaxy only; star formation poorly understood

Table 1. Properties of interstellar molecular clouds.

\*Envelopes expand with a constant radial velocity of 10 to 30 km sec<sup>-1</sup>; density, n, decreases with distance from the star, r, as n proportional to  $r^{-2}$ .

stable structures (32). The process of cloud buildup is terminated by the destructive effects of massive star formation, which through the action of ionizing radiation, winds, and supernovae can shatter a GMC. The cloud is partially dissociated into atomic hydrogen and ionized to form an HII region, whose high pressure accelerates and disperses the remaining molecular cloud. The cloud fragments start the cycle anew; they can accrete gas from the atomic phase of the interstellar medium and accumulate into a GMC by collisions with other molecular clouds. Observational evidence indicates that cloud destruction occurs at masses slightly above  $10^6$  solar masses. Near this mass, cloud equilibrium may be disrupted by the passage of the cloud through a spiral arm of the galaxy, which may induce gravitational collapse and produce a burst of massive star formation.

Estimates for the lifetimes of molecular clouds range from  $10^7$  years (from the ages of stars believed to be born from a given cloud) to  $10^9$  years (from arguments that molecular clouds may survive several passages through spiral arms) (33). From our vantage point



in the galaxy, it is difficult to tell how well clouds are confined to the galactic spiral arms lying inside the solar circle (the roughly circular orbit of the solar system about the center of our galaxy) and much controversy has erupted over this issue. Observers agree that the regions of the most active star formation do delineate spiral arms and that the associated CO-emitting clouds reflect this activity by their high temperature. Although molecular clouds are observed in abundance in the interarm regions, they appear to be smaller and, on the average, colder than the clouds lying near galactic spiral arms. The apparent confinement of GMC's to the spiral arms of our galaxy suggests that a GMC can maintain its identity for a time of order 2  $\times$  $10^7$  to 5  $\times$  10<sup>7</sup> years. Since smaller clouds are observed in the interarm regions, there is little information to constrain their lifetimes. In discussing cloud lifetimes, it is important to remember that the time for which a given parcel of gas survives in the molecular state may differ from the time for which a particular cloud retains its identity.

It is generally believed that molecular hydrogen is formed on grain surfaces, thus making interstellar dust vital to the existence of molecular clouds. Once molecular hydrogen exists in the cloud, cosmic ray ionization and photoionization at the cloud surfaces produce the radical  $H_3^+$ , which is the cornerstone of the gas-phase ion-molecule chemistry thought to be responsible for most of the observed species in molecular clouds (34). Observations indicate that there are well over 100 different chemical species (including



Fig. 3. (Left) The central portion of the Orion molecular cloud, the nearest giant molecular cloud, showing the total integrated intensity of <sup>12</sup>CO in false color. Data were taken at the Five College Radio Astronomy Observatory 14-m telescope. [Photograph by P. Shcloerb, R. Snell, P. Goldsmith] (Right) An optical photograph showing the Orion Nebula with the HII region lying in front of the molecular cloud core.

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isotopic substitutions) in molecular clouds. The ion-molecule chemistry explains the abundance of the most common observed species, such as CO and CS. Excellent reviews of this subject are available (34).

#### **Star Formation**

The observed proximity of molecular clouds to HII regions, O and B type stars, and low-mass pre-main sequence objects such as T-Tauri stars and the presence of large populations of buried infrared sources leaves little doubt that star formation in our galaxy occurs in molecular clouds. Within the past few years, it has become generally recognized that most stars undergo an episode of energetic mass loss while still buried in their parent molecular clouds (35). Luminous stars drive outflows that may accelerate up to 100 solar masses of ambient gas to velocities of tens of kilometers per second. In many sources, the accelerated gas shows a pronounced bipolar morphology, indicating collimation of the outflow into two oppositely directed streams. In the case of low-mass stars, the outflows are often highly collimated into spectacular jets of gas that are visible even at optical wavelengths (36). The end points of these jets often contain shock-excited nebulae (the so-called Herbig-Haro objects), which have velocities up to 500 km sec $^{-1}$ . The outflows associated



with more luminous sources often exhibit powerful maser emission in certain transitions of  $H_2O$  and OH and weak masers in other molecules (37). Outflows from recently formed stars may generate supersonic cloud turbulence and thereby control the rate of cloud collapse and the rate of star formation (38). Massive outflows may be the first visible sign of the birth of new stars in a cloud.

Most luminous stars of spectral type O and B are concentrated in gravitationally unbound groups (OB associations) that disperse in about 10<sup>7</sup> to 10<sup>8</sup> years. Such groupings may form by a process of self-induced star formation toward the end of the lifetime of a GMC. Soon after their birth, OB stars ionize their surroundings, creating HII regions and raising the local temperature from that of the molecular cloud from which they were born to about 10<sup>4</sup> K. The rapidly expanding ionized cavities drive shock waves into the remaining molecular cloud at velocities around 5 km sec<sup>-1</sup> (39). Gas compressed by the passing shock wave may undergo further gravitational collapse, resulting in more star formation. If O and B stars are the result, the process may continue as a wave of massive star formation propagating into the GMC at a velocity of 2 to 5 km  $sec^{-1}$ , converting the remaining gas into stars or dispersing it. This scenario of propagating OB star formation may explain the observed sequential nature of the OB subgroups (40) and provide a mechanism for the destruction of GMC's.

Although low-mass stars can form throughout the star-forming life of a cloud, the formation of O and B stars and the onset of ionization marks the termination of star formation. As the hot, ionized gas expands, it disperses the remaining gas near the ionizing stars (39). If only a small fraction of the molecular gas has been converted into stars by the time O and B stars disperse the remaining gas, thereby removing most of the gravitating mass, an expanding, gravitationally unbound association results. On the other hand, if more than 50 percent of the mass of the preexisting cloud has been converted into stars, then the resulting star cluster contains sufficient mass to remain bound even after gas dispersal (41); a self-gravitating star cluster is the result. Many bound clusters (open star clusters such as the Pleiades) are seen in the plane of the Milky Way with ages, in some cases, greater than 10<sup>9</sup> years. Whereas the GMC's in Orion are believed to be forming an unbound OB association, the cloud associated with the star p-Ophiuchi is believed to be giving birth to a bound star cluster (42). At the present time, no sufficiently luminous stars have yet formed to initiate the process of cloud dispersal, and the nascent cluster is only visible at infrared wavelengths.

#### Molecular Clouds and the Structure of Our Galaxy

A number of <sup>12</sup>CO surveys conducted along the galactic plane have shown that, to first order, the GMC population of the galaxy forms a ring with an inner radius at 3 kpc from the galactic center and an outer radius somewhere outside the solar circle beyond 13 kpc (24, 25). The greatest concentration of molecular clouds occurs around 5 kpc and drops in a roughly exponential fashion with radius (Fig. 4). Superimposed on this radial distribution is a spiral pattern that can be most clearly seen outside the solar circle (radius, 10 kpc). Here, the Perseus arm of our galaxy can be traced for more than 6 kpc in the CO data (43). Inside the solar circle at least two spiral arm segments, those associated with the Sagittarius arm and the Scutum arm, can be traced for at least several kiloparsecs around the galaxy (24). Contrast between the CO luminosity in the spiral arms and between the spiral arms is at least 10 to 1 outside the solar circle but only 3 to 1 near the peak of the molecular ring. There is controversy over whether GMC's in the molecular ring are strictly confined to spiral arms or whether they are simply hotter and therefore more visible in the arms.

There is evidence for at least one well-defined, large-scale spiral arm feature inside the molecular ring between 3 to 4 kpc; this has been labeled the "3-kpc arm." This feature has a distinct -50 km sec<sup>-1</sup> radial velocity component toward the direction of the galactic center, allowing it to be clearly distinguished from the rest of the galactic disk (which has, on the average, no radial velocity in this direction). This feature can be traced over nearly 30° in the plane of the galaxy, so that it is at least 5 or 6 kpc in extent.

The region between galactocentric radius of 0.5 kpc and 3 kpc contains relatively little gas. One suggestion for the origin of this hole is that mass loss from giant stars in the galactic bulge, which has much less angular momentum than the disk of the galaxy, has in interacting with the interstellar medium removed its orbital angular momentum. This would cause it to fall close to the galactic center (44).

Within 0.5 kpc of the galactic center, the abundance of molecular gas increases dramatically (Fig. 5). The CO and <sup>13</sup>CO surface brightness (averaged over all velocities) of the galactic center region exceeds that seen in any other part of the sky by one or two orders of magnitude. Recent surveys of molecular clouds in the galactic center indicate that their properties are different from the clouds in the disk (45). The mean gas density in these clouds is on the average about  $10^4$  particle cm<sup>-3</sup> or higher, which is sufficient to excite the 98-GHz CS J = 2-1 line. The tidal stress generated by the gravitational field of the galaxy requires any clouds that are self-gravitating to have a mean density higher than this value. In the disk of the galaxy, only the dense star-forming cores exhibit such high densities. Within a few parsecs of the compact radio source believed to mark the position of the galactic center, molecular gas forms a complete ring of emission that can be seen in CO and in near infrared emission lines of shocked molecular hydrogen (46). This gas is probably being sheared by the tidal force and is not bound by its own gravity. The widths of the emission lines produced in the galactic center clouds have values around 20 to 50 km sec<sup>-1</sup>, which is an order of magnitude larger than values found in disk GMC's. The temperature of the gas is also higher (>30 K and possibly as)high as 200 K in some places).

Some clouds near the galactic center have velocities strictly forbidden by models postulating uniform circular motion about the center. Violations of 150 km sec<sup>-1</sup> occur. Furthermore, some molecular gas is located many scale heights above or below the mean galactic plane (47). These kinematic oddities have been interpreted in terms of powerful quasar-like explosions that produce large radial velocities in the gas near the galactic center (48). An alternative interpretation of the kinematics is that the gas is moving in highly elongated and inclined orbits about the galactic center. Such motion may be stable if stars responsible for the gravitational potential of the galaxy form a bar-of-soap-shaped configuration (a triaxial ellipsoid). Many external galaxies are observed to have barlike distributions in their centers and highly elongated dust lanes. The observed motions near our nucleus may indicate the presence of a kiloparsec-sized stellar bar.

If the H<sub>2</sub>:CO conversion ratio found in the solar neighborhood is applied to the gas lying within 500 pc of the galactic center, the total amount of matter in this relatively small region is estimated to be about  $2 \times 10^8$  solar masses, which is about 10 percent of the molecular mass of the entire galaxy. Surprisingly little star formation occurs in this region for this much mass. Although there are some spectacular HI regions, their number is much less than would be expected given the density and mass of gas present. One possible explanation is that the large internal turbulence exhibited by these clouds prevents gravitational collapse. Long-range gravitational interactions between the clouds and stars in the disk of the galaxy result in the exchange of momentum and energy between the two populations. Stars born out of the molecular gas initially have galactic kinematics and distributions similar to those of the gas. The motions of recently formed stars reflect the motions of the parent clouds. Over time, gravitational interactions in the form of encounters between clouds and individual stars transfer kinetic energy from the massive GMC's to the much lower mass stars (49). This process increases the star-to-star velocity dispersion, and the stars enter orbits that take them a greater distance from the galactic plane. Older stellar populations have undergone this interaction for a long time, and they are now observed to have a larger scale height in the galaxy than stars formed recently. Thus the molecular clouds play a crucial role in the evolution of the kinematic properties of stars in our galaxy.

Star formation produces more low-mass, long-lived stars than high-mass, short-lived stars. While the high-mass stars eventually return most of their mass, after nuclear processing, to the interstellar medium via mass loss in the form of winds and supernova explosions, gas used to produce low-mass stars is effectively removed from the interstellar medium. Thus star formation is depleting the interstellar medium, converting more gas into stars than stars return to the interstellar medium. The amount of gas accreted by the galaxy is probably less than the amount converted into low-mass stars (50). From the total observed amount of molecular gas in the galaxy and the deduced galaxy-wide rate of formation of low-mass stars, the half-life of the interstellar medium can be estimated to be only about  $5 \times 10^9$  years, which is only one-third the age of the galaxy. These arguments suggest that the total amount of gas in the interstellar medium may be shrinking. However, what gas remains is continuously enriched in its heavy element content by thermonuclear processing in the deep interiors of massive stars.

Studies of the morphology and amount of molecular gas in other galaxies are being vigorously pursued. Carbon monoxide has been detected in well over 200 galaxies and mapped in several dozen (51).



Fig. 5. (A) A comparison of the emission line profile seen in <sup>13</sup>CO at 110 GHz between a nearby molecular cloud core (NGC 2024) and a molecular cloud near the galactic center (Sgr B2). (B and C) Maps showing the integrated <sup>13</sup>CO emission at blue-shifted velocities ( $V_{\rm LSR}$ ) from -200 to -20 km sec<sup>-1</sup> (indicating approaching gas) (B) and red-shifted velocities from 20 to 200 km sec<sup>-1</sup> (indicating receding gas) (C). To first order, this velocity pattern describes rotation of the interstellar medium in the inner regions of our galaxy about the center. Strong deviations from simple circular motion are indicated. Contour intervals are set at 10 K km sec<sup>-1</sup>. The velocity range surrounding  $V_{\rm LSR} = 0$  has been eliminated from the galactic center.  $T_{\rm A}^*$  is the antenna temperature corrected for atmospheric attenuation;  $\ell$  and b are galactic longitude and latitude in degrees. The galactic center lies very close to  $\ell = 0$ , b = 0.

A portion of our closest spiral neighbor, the Andromeda galaxy, has been mapped in this molecule and found to exhibit high-contrast (25 to 1) spiral structure in molecular clouds. The total molecular gas content of the Andromeda galaxy is only about 10 percent of our galaxy, indicating that the molecular gas content of otherwise similar galaxies can be very different. In more distant systems, current telescopes do not clearly resolve the spiral pattern because of the large beam size of the present single-dish telescopes and the small angular diameter of the galaxies. We can only determine the global molecular cloud content and possibly the nature of the radial distribution of the molecular gas in most external galaxies.

It is evident that the most luminous galaxies in CO are those peculiar systems that are very bright at far infrared wavelengths (52). Most of these systems are undergoing a violent burst of star formation in which gas is being converted into stars at a rate one or two orders of magnitude higher than that in our galaxy. Such star bursts are seen primarily in systems showing evidence of recent tidal interactions with other galaxies. In such encounters, gravitational forces greatly disturb the interstellar medium of the galaxies involved. Some or all of the gas of one galaxy may be transferred to the other system, and the compression by large-scale shock waves may produce the increase in the star formation rate. In some nearby galaxies, such as M82, the star burst is confined to the nuclear regions of the galaxy. The large molecular luminosity of star-burst galaxies may be a direct consequence of star formation. The ionization, winds, and explosions of massive stars that are formed may heat and fragment the optically thick GMC's. Cloud fragmentation lowers the mean opacity of optically thick molecules and increases the radiating surface area of the gas. More radiation capable of reaching a distant observer is produced, increasing the luminosity of the gas in the star-burst galaxy.

The nuclear activity associated with the quasar phenomenon and their weaker counterparts, the so-called Seyfert galaxies, does not appear to be related to the molecular content of these systems. The CO luminosity and inferred molecular gas content of nearby Seyfert galaxies is the same as those of normal galaxies of the same morphological type (53).

The relation between CO emission, molecular gas content, and other properties of normal galaxies is slowly being clarified. Very massive galaxies containing much dust and well-developed spiral structure exhibit, on the average, the largest CO luminosities. Spiral galaxies having only little dust, such as the Andromeda galaxy, show weak CO emission. No CO emission has ever been detected from an elliptical galaxy. Although some low-mass galaxies (dwarf galaxies such as the Magellenic Clouds in the southern sky, our nearest extragalactic neighbor) exhibit spectacular star-forming regions, they tend to have very few molecular clouds and exhibit weak CO emission. There is speculation that some dwarf galaxies may have very low heavy-element abundances and very little dust. Molecular clouds do not form easily, and stars may form directly from the gravitational collapse of the atomic phase of their interstellar medium.

The best information about the relation of CO emission to other galaxian characteristics will probably come from extensive surveys of the CO emission of nearby objects such as the Virgo cluster, the nearest concentration of galaxies in the sky. Initial results of the first efforts to study the CO properties of Virgo spirals suggest correlations among total CO content, disk radio continuum luminosity (a measure of the number of HII regions and supernova remnants), and far infrared luminosity (a measure of total dust content) (54). Although the total CO content may correlate with total galaxian mass, there is little evidence for correlations with the amount of blue light emitted (a measure of the abundance of hot, young stars modified by dust extinction) or morphological type. The apparent

correlation between CO emission from the inner regions of these galaxies and morphological type may be explained by the removal of gas from the bulge-dominated inner parts of the early type (Sa and early Sb) galaxies.

#### Conclusions

Studies of molecular clouds within our galaxy and in other galaxies has revolutionized our understanding of the interstellar medium, star formation, and the manner in which galaxies evolve. We now believe (i) that most of the mass of the interstellar medium of our galaxy is in the form of giant molecular clouds; (ii) that the largest clouds and those responsible for most massive star formation, are concentrated in spiral arms; (iii) that molecular clouds are the sites of ongoing star formation and play a key role in the chemical evolution of the galaxy; (iv) that giant molecular clouds determine the evolution of the kinematic properties of galactic disk stars; (v) that the total gas content of the galaxy is diminishing with time; and (vi) that most clouds have supersonic internal motions and do not form stars on a free-fall time scale.

Although we have learned much, we still have a long way to go before we can claim an understanding of the basic process of star and planet formation that almost certainly must accompany it. The organization and evolution of the interstellar media of the galaxies as well as the factors determining their global structure remain poorly understood. Most of the data discussed in this article were collected with instruments having a resolution not much better than that of the human eye. We do not yet have the power to inspect the processes operating within stellar nurseries or even to study the distribution of the molecular clouds in all but the nearest galaxies. A number of very powerful instruments are now being contemplated by the astronomical community; these may enable us to make measurements with orders of magnitude better sensitivity and resolution. Currently on the drawing board are the Very Long Baseline Array (already under construction), which will be used for milliarc-second imaging of masers in star-forming regions; the space infrared telescope facility, which will be used to study infrared radiation from celestial sources with several orders of magnitude improvement in sensitivity; the large deployable reflector, a spacebased 25-m telescope designed to work from infrared to submillimeter wavelengths; the submillimeter array, an interferometric instrument consisting of six dishes proposed by the Smithsonian Astrophysical Observatory; the new technology telescope, a 15-m optical to near infrared telescope; and the millimeter-wave array, an aperture-synthesis instrument designed to make maps of the molecular line and continuum radiation with a resolution of 0.1 arc second. This latter instrument is perhaps the least expensive of the lot and the one that would most revolutionize our understanding of star formation, molecular clouds, and the behavior of the cold component of the interstellar medium.

#### REFERENCES AND NOTES

- W. Huggins, Proc. R. Soc. London Ser. A 13, 492 (1864). For a historical review, see H. M. Johnson, in Nebulae and Interstellar Matter, B. M. Middlehurst and L. H. Aller, Eds. (Univ. of Chicago Press, Chicago, 1968), pp. 65-118.
   H. I. Ewen and E. M. Purcell, Nature (London) 168, 356 (1951). For review, see W. T. Sullivan III, Ed., The Early Years of Radio Astronomy (Cambridge Univ. Press, Cambridge, 1984).
   W. B. Burton A univ Peri Astron. Astrophys. 14, 275 (1976); P. L. Baker and W. B.
- Press, Cambridge, 1984).
  W. B. Burton, Annu. Rev. Astron. Astrophys. 14, 275 (1976); P. L. Baker and W. B. Burton, Astrophys. J. 198, 281 (1975).
  J. Castor, R. McCray, R. Weaver, Astrophys. J. Lett. 200, 107 (1975); C. F. McKee and J. P. Ostriker, Astrophys. J. 218, 148 (1977).
  A. A. Penzias, K. B. Jefferts, R. W. Wilson, Astrophys. J. 165, 229 (1971).
  N. Z. Scoville and P. M. Solomon, Astrophys. J. Lett. 199, 105 (1975); M. A. Gordon and W. B. Burton, Astrophys. J. 208, 346 (1976).
  R. L. Dickman, Astrophys. J. 202, 50 (1975); M. A. Frerking, W. D. Langer, R. W. Wilson, ibid. 262, 590 (1982).

- P. Goldreich and J. Kwan, *ibid.* 189, 441 (1974); N. Z. Scoville and P. M. Solomon, Astrophys. J. Lett. 187, 67 (1975).
   A. A. Penzias, Science 208, 663 (1980).
   J. H. Black and S. P. Willner, Astrophys. J. 279, 673 (1984).
   G. Neugebauer et al., Astrophys. J. Lett. 278, 1 (1984).
   T. M. Dame and P. Thaddeus, Astrophys. J. 297, 751 (1985).
   E. E. Barnard, in Photographic Atlas of Science Regions of the Milky Way, E. B. Frost and M. R. Calverd, Eds. (Carnegie Institution of Washington, Washington, DC, 1927); B. Bok and E. Reilly, Astrophys. J. 21, 143 (1983); P. C. Meyers and P. J. Benson, *ibid.* 266, 309 (1983); P. C. Meyers, *ibid.* 270, 105 (1983); P. J. Benson, P. C. Meyers, E. L. Wright, Astrophys. J. Lett. 279, 27 (1984).
   L. Blitz, L. Magnani, L. Mundy, Astrophys. J. Lett. 282, L9 (1984).
   G. Baran, thesis, Columbia University (1981).
   A. Monet et al., Astrophys. J. 282, 508 (1984); F. J. Vrba, S. E. Strom, K. M. Strom, Astron. J. 81, 958 (1976).
   M. Cohen and L. Kuhi, Astrophys. J. Suppl. 41, 743 (1979).

- M. Cohen and L. Kuhi, Astrophys. J. Suppl. 41, 743 (1979).
   L. Blitz and A. A. Stark, Astrophys. J., in press.
   J. Bally and N. Z. Scoville, *ibid.* 239, 121 (1980); C. J. Lada, B. G. Elmegreen, L. Blitz, in Prototars and Planets, T. Gehrels, Ed. (Univ. of Arizona Press, Tucson, 1967).
- Blitz, in Protostars and Planets, I. Gehrels, Ed. (Univ. of Arizona Press, Tucson, 1984), pp. 341-367.
  21. R. S. Cohen et al., Astrophys. J. Lett. 290, 15 (1985).
  22. B. Zuckerman, Annu. Rev. Astron. Astrophys. 18, 263 (1980); G. R. Knapp and M. Morris, Astrophys. J. 292, 640 (1985).
  23. R. D. Gehrz and N. J. Woolf, Astrophys. J. 165, 285 (1971).
  24. D. B. Sanders, P. M. Solomon, N. Z. Scoville, ibid. 276, 182 (1985); T. M. Dame, thesis, Columbia University (1983).
  25. D. B. Sanders, N. Z. Scoville, P. M. Solomon, Astrophys. J. 289, 373 (1985); A. A. Strat, thesis, Princeton University (1979).

- Stark, thesis, Princeton University (1979).
  26. P. G. Goldsmith and W. D. Langer, Astrophys. J. 222, 881 (1978).
  27. G. M. Tielens and D. Hollenbach, *ibid.* 291, 722 (1985).
- L. F. Smith, P. Biermann, P. G. Mezger, Astron. Astrophys. 66, 65 (1978); B. M. Tinsley, Astrophys. J. 208, 797 (1976).
   T. H. Troland and C. Heiles, Astrophys. J. Lett. 260, 23 (1982); S. S. Hansen,

- Astrophys. J. 260, 104 (1982); M. Dragovan, thesis, University of Chicago (1985).
  30. A. A. Stark and L. Blitz, Astrophys. J. Lett. 225, 15 (1978).
  31. G. B. Field and W. C. Saslaw, Astrophys. J. 142, 568 (1965).
  32. J. Kwan, *ibid.* 229, 567 (1979); N. Z. Scoville and K. Hersch, *ibid.*, p. 578.
  33. L. Blitz and F. Shu, *ibid.* 238, 148 (1980).
  34. W. D. Langer, *ibid.* 225, 860 (1978); in Birth and Infancy of Stars, R. Lucas, A. Omont, R. Stora, Eds. (North-Holland, Amsterdam, 1985), pp. 279-348.
  35. J. Bally and C. J. Lada, Astrophys. J. 265, 154 (1983); J. Welch et al., Science 228, 1389 (1985).
- 1389 (1985)
  - R. Mundt and J. W. Fried, Astrophys. J. Lett. 274, 83 (1983).
     M. J. Reid and J. M. Moran, Annu. Rev. Astron. Astrophys. 19, 231 (1981). 36. 37.
  - M. J. Reid and J. M. Moran, Annu. Rev. Astron. Astrophys. 19, 231 (1981).
     C. Norman and J. Silk, Astrophys. J. 238, 158 (1980).
     L. Spitzer, Physical Processes in the Interstellar Medium (Wiley, New York, 1978).
     B. G. Elmegreen and C. J. Lada, Astrophys. J. 214, 725 (1977).
     C. J. Lada, M. Margulis, D. Dearborn, *ibid.* 285, 141 (1984).
     R. S. Cohen et al., Astrophys. J. Lett. 239, 53 (1980).
     I. E. Gunn, in Active Galactic Nuclei, C. Hazard and S. Mitton, Eds. (Cambridge Univ. Press, Cambridge, 1979), p. 213; E. Bajaja et al., Astrophys. 141, 309 (1984). (1984)
  - J. Bally et al., in preparation; G. Heiligman, thesis, Princeton University (1982); J. T. Armstrong and A. H. Barrett, Astrophys. J. Suppl. 57, 535 (1984).
     I. Gatley et al., Mon. Not. R. Astron. Soc. 210, 565 (1985); H. S. Liszt, W. B.
  - Burton, J. M. van der Hulst, Astron. Astrophys. 142, 237 (1985).
  - 47. T. M. Bania, Astrophys. J. 216, 381 (1977
  - 48. J. Oort, Annu. Rev. Astron. Astrophys. 15, 295 (1977)
  - 49. L. Spitzer and M. Schwarzschild, Astrophys. J. 114, 385 (1951).
  - 50. I. F. Mirabel and R. Morras, ibid. 279, 86 (1984).
  - 51. F. Verter, thesis, Princeton University (1983)
  - 52. J. Young et al., Astrophys. J. Lett. 287, 65 (1984).

  - J. H. Bieging et al., Astrophys. J. 247, 443 (1981).
     J. Young, N. Z. Scoville, E. Brady, *ibid.* 288, 487 (1985); A. A. Stark et al., in preparation.

**Research Articles** 

# Molecular Genetics of Human Color Vision: The Genes Encoding Blue, Green, and **Red Pigments**

JEREMY NATHANS, DARCY THOMAS, DAVID S. HOGNESS

Human color vision is based on three light-sensitive pigments. The isolation and sequencing of genomic and complementary DNA clones that encode the apoproteins of these three pigments are described. The deduced amino acid sequences show  $41 \pm 1$  percent identity with rhodopsin. The red and green pigments show 96 percent mutual identity but only 43 percent identity with the blue pigment. Green pigment genes vary in number among color-normal individuals and, together with a single red pigment gene, are proposed to reside in a head-to-tail tandem array within the X chromosome.

ISUAL PIGMENTS ARE THE LIGHT-ABSORBING MOLECULES that mediate vision. They consist of an apoprotein, opsin, that is covalently linked to 11-cis-retinal or, in rare instances, 11-cis-dehydroretinal. Visual pigments are integral mem-

brane proteins: in vertebrates they reside in the plasma and disk membranes of the photoreceptor outer segment. Vision begins when a photon is absorbed by a visual pigment, isomerizing retinal from the 11-cis to the all-trans configuration. Photoisomerized retinal triggers a series of conformational changes in the attached apoprotein which creates or unveils an enzymatic site on its cytosolic face. During its brief lifetime one enzymatically active visual pigment catalyzes the conversion of several hundred second messengers from an inert to an active state. This conversion is the first step in a cascade of enzymatic reactions that ultimately produces a neural signal (1).

All visual pigment absorption spectra have nearly the same characteristic bell shape (2). Each pigment is therefore specified by its wavelength of maximal absorption. The three pigments that mediate human color vision have absorption maxima at approxi-

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