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Localization of the Human Gene Allowing Infection by Gibbon Ape Leukemia Virus to Human Chromosome Region 2q11-q14 and to the Homologous Region on Mouse Chromosome 2

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Retrovirus receptors remain a largely unexplored group of proteins. Of the receptors which allow infection of human and murine cells by various retroviruses, only three have been identified at the molecular level. These receptors include CD4 for human immunodeficiency virus, *Rec-1* for murine ecotropic virus, and GLVR1 for gibbon ape leukemia virus. These three proteins show no homology to one another at the DNA or protein level. Therefore, work to date has not shown any general relationship or structural theme shared by retroviral receptors. Genes for two of these receptors (CD4 and *Rec-1*) and several others which have not yet been cloned have been localized to specific chromosomes. In order to assess the relationship between GLVR1 and other retroviral receptors, we mapped the chromosome location of GLVR1 in human and mouse. GLVR1 was found to map to human chromosome 2q11-q14 by in situ hybridization and somatic-cell hybrid analysis. This location is distinct from those known for receptors for retroviruses infecting human cells. *Glvr-1* was then mapped in the mouse by interspecies backcrosses and found to map to chromosome 2 in a region of linkage conservation with human chromosome 2. This mouse chromosome carries *Rec-2*, the likely receptor for M813, a retrovirus derived from a feral Asian mouse. These data raise the interesting possibility that *Rec-2* and *Glvr-1* are structurally related.

The first stage in infection of a cell by a retrovirus involves specific interaction between a retroviral envelope glycoprotein and a cell surface receptor. For retroviruses that infect human cells, eight interference groups have been identified, implying the existence of eight receptors (25, 27). For retroviruses that infect mouse cells, at least five receptors are known to exist (11). Three receptor genes have been cloned, these being CD4 for human immunodeficiency virus (14, 15), *Rec-1* for murine ecotropic virus (1), and GLVR1 for gibbon ape leukemia virus (GALV) (18). Expression of the human homolog of GLVR1 permits infection of mouse cells by GALV, but the protein has not yet been demonstrated to bind virus directly.

The proteins encoded by these three genes display no homology to one another. This diversity suggests the possibility that receptors defining different interference groups may be generally unrelated. Nonetheless, because so few receptors have been cloned and sequenced, the possibility still exists that some receptors might be related. We therefore compared the location of GLVR1 with the locations of other receptor genes in the hope that this might reveal a similarity between some of these receptors. The receptor genes which have been mapped include CD4 and *Rec-1*, which map to human chromosome 12 and mouse chromosome 5, respectively (6, 11, 12, 19), the RD114 receptor on human chromosome 19 (27), the human T-cell leukemia virus types I and II (HTLV-I and HTLV-II) receptor on human chromosome 17 (26, 27), the murine amphotropic receptor on mouse chromosome 8 (4), the mink cell focus-forming and wild mouse xenotropic virus receptors on mouse chromosome 1 (9, 10), and the M813 virus (a murine ecotropic virus from a feral Asian mouse) receptor (*Rec-2*) on mouse chromosome 2 (19).

By in situ hybridization and somatic-cell hybrid analysis, GLVR1 was mapped to human chromosome 2, in the region 2q11-q14. This location is distinct from other known receptor locations in human cells. In the mouse, *Glvr-1* was found to map to chromosome 2, in a region of linkage conservation with human chromosome 2. Since *Rec-2*, the receptor for M813 virus, has also been mapped to mouse chromosome 2, this raises the possibility that *Glvr-1* may be related to *Rec-2*.

MATERIALS AND METHODS

In situ hybridization. The probe consisted of a 2,129-bp *Nde*I-*Bgl*II fragment of pOJ4, a derivative of the GLVR1 cDNA-containing plasmid pHGR6-1. pOJ4 was constructed by introducing an *Nde*I site (by in vitro mutagenesis) at the ATG codon initiating the long open reading frame of pHGR6-1 and a *Bgl*II site (by linker insertion) at the *Hpa*I site in the 3′ untranslated region of the cDNA (18). The probe was labeled with [^{3}H]TTP by nick translation and hybridized to bromodeoxyuridine-containing lymphocyte preparations (28) by the method of Harper and Saunders (5). Grain counting and statistical analysis were done as described before (8).

Somatic-cell hybrid analysis. The hybrids in the somatic-

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TABLE 1. Segregation of GLVR1 with human chromosomes in *Eco*RI-digested human-mouse cell hybrid DNA[a]

Hybrid	DNA no.	GLVR1 present	Human chromosome																							Translocation(s)
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	X	
ATR-13	660	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	+	+	−	−	+	t	5/X
DUA-3BSAGA	233	+	−	+	−	−	−	−	+	+	−	−	−	−	+	+	−	−	+	−	−	−	−	−	−	
DUA-5BSAGA	197	−	−	−	+	−	+	−	−	−	−	−	−	+	−	−	+	−	−	+	+	−	−	+	−	−	
DUA-6	859	+	−	+	−	+	+	−	−	−	−	−	−	−	−	−	−	+	−	−	+	+	−	−	−	+	
DUM-13	186	+	+	+	+	−	+	+	+	−	−	+	+	+	−	+	t	+	+	+	+	+	+	+	t	X/15, 15/X
GAR-1	1185	−	−	−	+	−	+	−	−	+	−	+	−	+	+	−	+	+	−	−	−	+	−	−	+	
ICL-15	18	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	−	−	+	−	−	+	+	−	−	
JSR-2	389	−	−	−	+	+	−	−	+	−	−	−	−	−	+	+	−	−	−	−	−	−	−	−	+	
JSR-14	795	+	−	+	+	+	+	−	−	−	−	−	−	+	−	+	−	−	+	−	−	+	+	−	−	
JSR-17S	44	+	+	+	+	−	+	−	t	+	+	+	+	+	+	+	+	+	+	+	−	+	+	+	−	7/9
JWR-22H	653	+	t	t	+	+	−	+	−	+	−	+	+	+	+	+	+	−	+	+	−	+	+	−	−	2/1
JWR-26C	187	+	t	+	+	+	+	+	+	−	+	+	+	+	−	+	+	+	+	+	−	+	+	−	+	1/2
NSL-16	192	−	−	−	+	+	+	−	+	+	t	+	−	+	−	+	+	+	+	+	−	+	+	−	−	17/9
REW-11	42	−	−	−	−	+	−	−	+	−	−	−	+	+	+	−	−	+	−	−	−	+	+	+	+	
REW-15	17	+	+	+	+	+	+	+	+	+	−	+	+	+	+	+	+	−	+	+	+	+	+	+	+	
REX-11BSAgB	184	−	−	−	+	−	−	−	−	−	−	+	−	−	−	+	+	−	−	+	−	−	−	−	−	
REX-11BSHF	254	−	−	−	+	−	−	−	−	−	−	+	−	−	−	+	−	−	−	+	−	−	−	t	t	22/X
REX-26	394	+	+	+	+	+	−	−	+	+	+	+	+	+	−	+	+	+	+	+	+	−	+	t	t	22/X
RSR-3	1162	−	−	−	−	+	−	−	+	−	−	+	+	−	−	+	−	+	+	−	−	−	+	−	+	
SIR-11	390	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	−	−	+	+	+	
TSL-2	644	+	−	+	t	−	+	+	−	+	−	+	−	+	−	+	+	−	t	+	−	+	+	−	+	17/3
VTL-6	395	+	−	+	−	−	−	+	+	+	−	+	+	−	−	−	+	−	+	−	+	+	+	+	−	
VTL-14	1095	−	−	−	−	−	−	−	−	−	−	−	+	−	−	−	−	−	+	−	−	−	−	−	−	
VTL-17	407	−	−	−	−	−	+	−	−	+	−	−	+	+	−	+	+	−	−	+	−	−	+	+	−	
W12	559	+	−	+	−	−	+	−	−	−	−	−	−	+	−	−	+	−	−	+	−	+	+	+	+	−	11p-
WIL-1	20	−	−	−	−	−	−	−	−	+	−	−	−	+	−	+	−	−	+	+	−	−	+	−	+	
WIL-2	12	−	−	−	−	−	−	−	−	+	−	−	−	+	−	−	+	−	+	−	−	−	+	−	+	
WIL-2CSAZ	403	−	−	−	−	−	−	−	−	+	−	+	−	+	−	−	−	−	+	−	−	−	+	−	−	
WIL-6	425	+	−	+	−	+	+	+	+	+	−	+	+	−	−	+	−	−	+	−	+	+	+	−	+	
WIL-8X	772	−	−	−	+	+	+	−	+	+	−	+	+	+	−	+	−	−	+	+	+	+	+	−	+	
WIL-8Y	423	−	−	−	+	−	−	+	+	+	−	+	+	−	−	+	+	+	+	+	+	+	+	+	+	
WIL-14	347	−	+	−	+	−	+	−	+	+	−	+	−	+	−	+	+	−	+	−	−	−	−	−	+	
WIL-15	25	+	−	+	+	+	−	+	+	−	−	+	+	+	+	+	+	−	+	+	−	+	+	−	+	
XER-11	33	−	+	−	+	+	−	+	+	+	−	+	t	+	+	−	+	+	+	+	+	+	+	+	t	11/X, X/11
XOL-6	534	−	t	−	−	−	+	+	+	−	−	+	+	+	−	+	−	−	+	−	+	+	−	+	t	1/X
XOL-21	1107	−	−	−	+	−	−	−	t	+	+	+	+	+	−	+	−	+	+	−	+	−	−	+	+	ISO7p
XTR-2	332	−	−	−	t	−	+	−	−	+	−	+	−	+	+	+	−	−	−	+	−	+	+	−	t	3/X
XTR-3BSAgB	57	−	−	−	t	−	−	−	−	−	+	t	−	+	−	−	−	−	−	−	−	+	+	−	t	3/X, 10q−
No. of concordant hybrids			25	37	19	26	25	29	20	20	24	19	23	19	22	22	26	22	21	23	27	22	20	23	13	
No. of discordant hybrids			10	0	16	12	13	9	16	18	13	18	14	19	16	16	11	16	16	15	11	16	18	13	17	
% Discordancy			29	0	46	32	34	24	44	47	35	49	38	50	42	42	30	42	43	39	29	42	47	36	57	

[a] Data were compiled for 38 cell hybrids involving 17 unrelated human cell lines and four mouse cell lines (21–23). The hybrids were characterized by karyotypic analysis and by mapped enzyme markers (20–22). A t indicates a chromosome translocation with no intact chromosome present. The probe was hybridized to Southern blots containing *Eco*RI-digested DNA from the human × mouse cell hybrids. Scoring was determined by the presence (+) or absence (−) of the 4-kb human band and the presence or absence of human chromosomes in the hybrids. The hybrid JWR-22H with the 2/1 translocation (2pter→2q37::1p11→1pter) excludes only the tip of 2q.

cell hybrid panel and the methods used in their characterization are shown in Table 1. Southern analysis was performed as described before (18); hybridization was done at 30°C in 50% formamide–5× Denhardt's solution–5× SSC–0.1% sodium dodecyl sulfate (SDS)–200 μg of sonicated denatured salmon sperm DNA per ml (1× Denhardt's solution is 0.02% each bovine serum albumin, Ficoll, and polyvinylpyrrolidone; 1× SSC is 0.15 M NaCl plus 0.015 M sodium citrate). The probe used consisted of a 916-bp *Eco*RI fragment of pHGR6-1, corresponding to bases 1744 to 2659 of the cDNA for GLVR1 (18), labeled by nick translation.

Interspecies backcross analysis. Interspecific backcross progeny were generated by mating (C57BL/6J × *Mus spretus*)F_1 females and C57BL/6J males as described previously (2). A total of 204 N_2 progeny were obtained; a random subset of these N_2 mice was used to map the *Glvr-1* locus. DNA isolation, restriction enzyme digestion, agarose gel electrophoresis, Southern blot transfer, and hybridization were performed essentially as described before (7). All blots were prepared with Zetabind nylon membrane (AMF-Cuno). The *Glvr-1* probe (a 3′ *Pst*I fragment of mouse *Glvr-1* cDNA; unpublished data) was labeled with [α-^{32}P]dCTP by using a multiprime DNA labeling kit (Amersham) for gel-purified fragments. Washing was done to a final stringency of 0.4× SSC–0.1% SDS, 65°C. Fragments of 6.0 and 1.2 kb were detected in *Eco*RI-digested C57BL/6J DNA; fragments of 6.0 and 2.1 kb were detected in *M. spretus* DNA. A description of the probes and restriction fragment length polymorphisms (RFLPs) for the loci linked to the *Glvr-1* locus has been given previously (24).

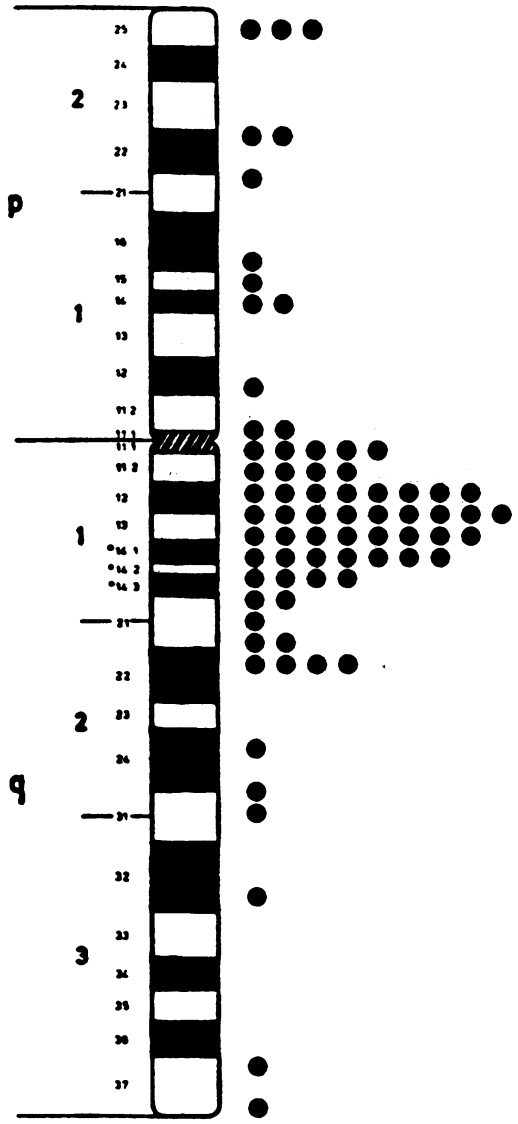

FIG. 1. Idiogram of human chromosome 2, showing the distribution of silver grains obtained after in situ hybridization of metaphase chromosomes with a GLVR1-specific probe.

RESULTS

In situ hybridization with human metaphase chromosomes. To localize GLVR1, in situ hybridization with a GLVR1 cDNA probe on human metaphase chromosomes was used. Of 201 silver grains on or touching these chromosomes in 130 metaphase spreads, 73 (36.3%) were found on chromosome 2. No other notable concentration of grains was observed. Of the 73 grains associated with chromosome 2, 47 (64.4%) were found in the region 2q11-q14, with a peak over 2q12 (Fig. 1).

Analysis of human × mouse somatic-cell hybrids. Southern analysis of *Eco*RI-digested mouse DNA with a GLVR1-specific probe showed the presence of two bands of 6.6 and 1.2 kb which were invariant among the hybrids. Human DNA showed a main band of 4 kb (Fig. 2). Table 1 summarizes the results obtained with the hybrids and shows that GLVR1 can be unambiguously assigned to human chromosome 2. This result is in agreement with that found in the in situ hybridization experiments.

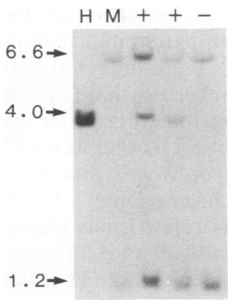

FIG. 2. Southern analysis of *Eco*RI-digested human (H), mouse (M), and somatic-cell hybrid DNAs with a GLVR1-specific probe. The first two hybrids (W12 and JSR-14, lanes +) contain the human-specific 4-kb fragment; the last (WIL-8Y, lane —) does not.

Interspecies backcross analysis. The chromosome location of the *Glvr-1* locus in the mouse was determined by interspecific backcross analysis with progeny derived from matings of [(C57BL/6J × *M. spretus*)F_1 × C57BL/6J] mice. This interspecific backcross mapping panel has been typed for over 500 loci distributed among all the mouse autosomes as well as on the X chromosome. C57BL/6J and *M. spretus* DNAs were digested with several restriction enzymes and analyzed by Southern blot hybridization for informative RFLPs with a *Glvr-1*-specific probe. A 2.1-kb *M. spretus*-specific *Eco*RI RFLP was used to follow the segregation of *Glvr-1* in backcross mice. The mapping results indicated that

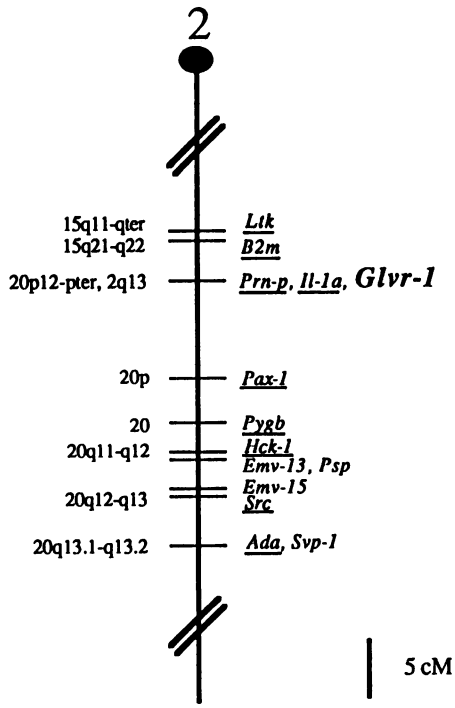

FIG. 3. Position of the *Glvr-1* locus on mouse chromosome 2. For a description of other distal chromosome 2 loci previously typed in the interspecific backcross panel, see Siracusa et al. (24). Loci which have also been mapped in humans are underlined, and their chromosome location in humans is listed on the left.

Glvr-1 is located on mouse chromosome 2, tightly linked to the prion protein (*Prn-p*) and interleukin-1-α (*Il-1α*) loci (Fig. 3). No recombinants were detected between *Glvr-1*, *Prn-p*, and *Il-1α* in 130 backcross mice typed in common for all three loci, indicating that these loci are located within 2.3 centimorgans (cM) of each other at the 95% confidence level.

The tight linkage of *Glvr-1* and *Il-1α*, which have been assigned to human chromosome 2, bands q11.2-q14 and q13, respectively (13; this report), has identified a new region of synteny between mouse and human (Fig. 3). While no recombinants have been detected between *Prn-p* and *Il-1α* in our interspecific mapping panel, the previous studies of Carlson et al. (3) have shown that *Prn-p* maps distal to *Il-1α*, consistent with its human chromosome 20 location (Fig. 3). The human chromosome 2 localization of GLVR1 strongly predicts that *Glvr-1* will map proximal to *Prn-p* as did *Il-1α*.

DISCUSSION

Expression of GLVR1 in mouse cells renders them susceptible to infection by GALV (18). It therefore seems likely that the protein derived from this gene acts as a receptor for the virus, although direct binding of GALV envelope glycoprotein to GLVR1 has not yet been demonstrated. In this study, GLVR1 was mapped in human and mouse DNA to determine whether a relationship between receptors could be deduced from similarities in their locations. At least two situations can be envisaged in which a relationship would become evident from a study of chromosome location. First, if receptors for retroviruses from separate interference groups were derived from a family of genes restricted to a specific location, then a relationship would be immediately evident. Second, homologs of a receptor in different species might act as receptors for different, species-specific viruses. Such a situation would be reflected in chromosomal locations if the homologs belonged to a conserved linkage group.

The results of the mapping study for human GLVR1 allow us to assign the gene to chromosome 2, in the region 2q11-q14 and most likely within 2q12. Of the mapped receptors for retroviruses which infect human cells, none is located at the same position or on the same chromosome as GLVR1. These include the receptors for human immunodeficiency virus, RD114, and HTLV. This result therefore indicates that no two of these four receptors are derived from a family of genes restricted to a specific location. The analysis of interspecies backcross mice allows assignment of murine *Glvr-1* to mouse chromosome 2 within 2.3 cM of *Il-1α*, which has been mapped previously to chromosome 2 (24). Of the receptors mapped in the mouse, most are asyntenic with *Glvr-1*. However, *Rec-2*, a gene (most likely encoding a receptor) required for replication of M813 virus and mink cell focus-forming viruses from C3H mice, has been mapped to mouse chromosome 2 (19), though the subchromosomal localization of the gene is not known. It is thus possible that *Glvr-1* and *Rec-2* may be related or identical genes. If they are identical, this would be the first example of homologous genes being used as retroviral receptors in distantly related species. If such is the case, then GALV and M813 virus envelope glycoproteins may have a similar origin and may have coevolved with GLVR1/*Rec-2* as the receptor. This could have involved separate maintenance of the viruses in their respective hosts from before the point of divergence of the species or the transfer of a progenitor virus between species. Alternatively, the viral envelope glycoprotein genes may have developed by convergent evolution to the use of GLVR1/*Rec-2* as the receptor. Any relationship between these loci will be become fully evident only when *Rec-2* is cloned or if *Glvr-1* can be shown to allow infection by M813 virus. If these genes are related, it will be important to determine the sequences of viruses using *Rec-2* as a receptor and to compare these with that of GALV.

Another example of a possible relationship between different retroviral receptors involves the *Tea* gene (which is closely related to *Rec-1*, a murine ecotropic virus receptor [16]) and *Ram-1*, the receptor for murine amphotropic virus. Because of the homology between *Tea* and *Rec-1* and the fact that both *Tea* and *Ram-1* are on mouse chromosome 8, it is possible that *Tea* and *Ram-1* are related or identical genes.

Despite the tentative suggestion that GLVR1 is related to *Rec-2*, the available data suggest that receptors defining different interference groups are generally unrelated. These data include the distinct locations (with the possible exceptions discussed) of those receptors which have been mapped and the lack of homology between the three receptors cloned to date, CD4, *Rec-1*, and GLVR1. Because it is difficult to envisage a common function being carried out by such a heterogeneous group, it may be that receptors act merely as attachment points for envelope glycoproteins and that the envelope glycoproteins are primarily responsible for effecting virus entry.

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