ウイルス感染現象における
宿主細胞コンピテンシーの分子基盤

領域番号：3405

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研究成果報告書

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はしがき

ウイルス感染における宿主特異的な子孫ウイルス複製と病原性発現は、ウイルスの増殖能とこれを抑制する宿主細胞機能との攻防の結果である。本領域の研究目的は、最終的には病原性発現に帰結する宿主特異的なウイルス複製と細胞内防御メカニズムとの拮抗の分子基盤を理解することである。ウイルスの複製にはウイルス側の因子に加えて、宿主（の因子）が必須である。細胞の機能／因子群を自身の感染および複製過程に動員・奪取することで増殖する。一方、宿主は個体レベルのみならず、細胞レベルでも防御系を発動する。すなわち、ウイルスは、自身にとってポジティブおよびネガティブな効果を持つ宿主環境の中で、感染サイクルを動かしていることになる。宿主は感染状況の中では、多くの生命プロセスを正常状態とは異なる均衡の中で維持するか、細胞内防御系を含む緊急応答を発動しなければならない。つまり、ウイルスは自然宿主の中では高い病原性は示さず、感染現象と細胞内防御系を含む生命プロセスが折り合った状態で感染サイクルを繰り返しながら存続するか、もしくは、この均衡がウイルス側に偏ることで高い病原性が発現する。本研究領域では、このような結果に繋がる細胞の特性を『宿主細胞コンピテンシー』と捉え、この均衡の中で、ウイルスが宿主を選択し、また宿主に適合した戦略的なメカニズム（感染の細胞・組織特異性、あるいは種特異性）を明らかにする。研究手法としては、ウイルス感染現象を対象とする学問・研究領域で遅れている構造生物学的解析、数理モデル解析、およびポストゲノム時代の考え方と方法を取り入れ、これらの領域の専門家とウイルス研究者が協業する体制を構築し、これまでもオリジナリティーある研究成果をあげてきた我が国のウイルス関連研究をさらに推進する。

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交付決定額（配分額）

	合計	直接経費	間接経費
平成 24 年度	144,950,000 円	111,500,000 円	33,450,000 円
平成 25 年度	298,350,000 円	229,500,000 円	68,850,000 円
平成 26 年度	299,650,000 円	230,500,000 円	69,150,000 円
平成 27 年度	298,350,000 円	229,500,000 円	68,850,000 円
平成 28 年度	289,510,000 円	222,700,000 円	66,810,000 円
総計	1,330,810,000 円	1,023,700,000 円	307,110,000 円

研究発表

雑誌論文（全点査読有）

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研究成果

研究計画① マイナス鎖RNA ウイルスの複製におけるウイルスと宿主の攻防

研究代表者：永田恭介（筑波大学）

研究分担者：朴三用（横浜市立大学）

ウイルスゲノムの転写・複製には、多様な宿主因子が関与しており、宿主因子をウイルス複製系と細胞生理系の間で奪い合う分子レベルでの競合（攻防）が起こっている。本計画班では、インフルエンザウイルスを対象として、その攻防の構図を明らかにする。これまでの成果より、スプライシング因子であるUAP56は分子シャペロンとしてNPを新規複製鎖にリクルートし、RNP複合体形成と協調して伸長反応を促進することを見出した。UAP56との結合に必須なNPのN末端20アミノ酸は、誘導適合により機能的な構造を形成すると予測され、NP－UAP56 複合体の立体構造を解析中である。酵母内ウイルスRNA合成系を用いた遺伝学的解析により、NPの分子シャペロンとして、スプライシング因子であるPrp18を新たに同定した。また、子孫ウイルスゲノムの細胞内動態を決定する宿主因子としてYB-1を同定した。YB-1は、ウイルスゲノムと共に中心体に集積し、中心体の成熟化を促進する。それによって、小胞輸送を介したウイルスゲノムの輸送を活性化することを明らかにした。完全長RdR Pol複合体の精製にも成功し、公募班 岩崎との協業により、クライオ電顕観察による構造解析も開始しており、原子構造の決定まであと少しである。

研究計画② プラス鎖RNA ウイルスの複製におけるウイルスと宿主の攻防

研究代表者：脇田隆字（国立感染症研究所）

研究分担者：竹安邦夫（京都大学）

本計画では、C 型肝炎ウイルス（HCV）の複製場である細胞内膜系、脂質膜ラフト、脂肪滴等でゲノム複製と粒子形成に関わる宿主因子を同定してその機能を明らかにし、ウイルスと宿主の間で起こる分子レベルでの競合（攻防）を解明する。HCV 複製に必須な膜小胞の形成に関与するNS4B と結合する宿主タンパク質のプロテオミクス解析と siRNA を用いたスクリーニングより、

prolactin regulatory element binding protein （PREB）および Surfeit 4（SURF4）を同定した。PREB および SURF4 はそれぞれ Sec12、ERV29 とも呼ばれ、COPII、COPI を介した小胞輸送に関与するタンパク質として知られており、小胞輸送が HCV 複製複合体を含む膜小胞の形成に関与する可能性が考えられた。そこで、COPII および COPI 関連タンパク質 Sec23、Sec24、Sec13、Sec31、SAR1、Sec16、RAB1、CSNK1 の HCV 複製における機能についても解析した。さらに“RNA を見る”ための技術開発を行った。原子間力顕微鏡（AFM）を用いた一本鎖 RNA の可視化方法を、①cRNA（2 kb）、②Poly(A) tail の cRNA、③18S/28S rRNA で確立し、④ HCV（9 kb）でも可視化できることを示した。ついで、画像解析の自動化プログラムを開発し、28S rRNA 全長の構造をモデリングすることも可能になった。

研究計画③ 細胞内ウイルス防御系とウイルスの攻防
研究代表者：藤田尚志（京都大学・ウイルス再生医学研究所）
研究分担者：高折晃史（京都大学）

RIG-I 様受容体（RLR）はウイルス由来の RNA を感知して「自然免疫」を誘導する受容体である。また、APOBEC3、TRIM5 など、HIV-1 感染を制御する宿主因子は「内因性免疫」として理解されている。本研究では自然免疫および内因性免疫の制御機構を解明し、様々なウイルスがどのような戦略でそれらを阻害しているかを明らかにする事で感染の細胞・組織特異性（感染コンピテンシー）の理解を深める事を目的とする。これまでの成果より、ウイルスの増殖は細胞内の特定の場で行なわれるが、それとは別に抗ウイルスストレス顆粒（avSG）が誘導されることを明らかにした。特に、RIG-I 様受容体は avSG に局在しており、シグナル伝達のプラットフォームであることが示唆された。DExDH-box 型の RNA ヘリカーゼである DHX36 が RIG-I と PKR と複合体を形成し、ウイルス由来の二本鎖 RNA を認識して PKR を活性化することを見出した。ニューキャッスル病ウイルス由来のキャップ構造を持たないリードスルー転写産物を RIG-I がストレス顆粒内で認識してインターフェロン応答を活性化することも明らかにした。また、RNA 結合タンパク質である Pumilio が RLR の一つである LGP2 によるウイルス RNA 認識を増強することを明らかにした。高折は、Vif の補助因子として CBFβを同定し、Vif 変異体の作製により、E88、W89 が CBFβとの相互作用に重要であることを明らかにした。Vif の誘導する細胞周期停止には、Vif による脱リン酸化酵素 PP2A のユビキチン化を介したプロテアソーム分解が必須であることを明らかにした。また、CBFβは MDM2 による Vif のプロテアソーム分解を抑制することで、Vif の発現維持に関与する。

研究計画④ ウイルスの宿主細胞選択における攻防
研究代表者：柳雄介（九州大学）
研究分担者：荒瀬尚（大阪大学・微生物病研究所）

柳は主に麻疹ウイルスを取り上げ、ウイルスの宿主細胞選択における攻防について研究を進める。膜融合と細胞侵入機構、自然免疫との攻防、宿主因子との相互作用を明らかにすることにより、ウイルスの感染成立機構を明らかにする。麻疹ウイルスの細胞侵入には、ウイルスエンベロープ上

の H タンパク質、F タンパク質と宿主細胞上のレセプターの相互作用が関わっている。H タンパク質の変異体の構造と機能を解析することにより、H タンパク質四量体（dimer of dimers）の構造変化が F タンパク質を活性化して膜融合を誘導するのに重要であることを明らかにした。また、神経細胞への麻疹ウイルス感染には、細胞外領域の変異による F タンパク質の膜融合能亢進が重要であることを明らかにした。麻疹ウイルスは、ウイルス粒子中に複数のゲノムをもつことがあり（polyploidy）、それぞれのウイルスゲノムから発現した F タンパク質が三量体を形成することにより、個々のウイルスゲノムでコードされた F タンパク質にはない、新たな性質を獲得しうることを明らかにし、ウイルスの新しい進化メカニズムとして提唱した。さらに、ウイルス RNA 合成に重要な宿主タンパク質 SHCBP1 を同定した。荒瀬は、単純ヘルペスウイルスレセプターの PILRαの認識機構と構造を解析することにより、糖鎖構造、タンパク質構造の双方を認識するユニークなレセプターであることを見出した。ウイルスが産生される際の糖鎖構造がウイルスのトロピズムを規定している可能性が示唆されている。また、ウイルス感染等で引き起こされる炎症の制御に PILRαが関与していることも明らかにした。

研究計画⑤ ウイルスの標的組織決定における攻防
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ポリオウイルス（PV）やエンテロウイルス 71 （EV71）は、ヒトに経口的に感染し、中枢神経系に達すると運動神経細胞などの神経細胞を標的として爆発的に増殖し、脊髄炎や脳炎を引き起こす。マウスはこれらのウイルスに非感受性であるが、ヒトの受容体を発現させたトランスジェニックマウスはウイルス感受性を獲得し、ヒトと類似の病態を再現することが可能である。本研究では、受容体の発現分布を人為的に改変した Tg マウスモデルや、自然免疫系を破壊したマウスなどを用いて、特定の組織によるウイルスー宿主の攻防がウイルス側に傾いて標的組織となるのか、宿主側に傾いて非標的となるのか、その決定メカニズムを明らかにすることを目標とする。現在までに、我々は EV71 受容体としてウイルスの細胞への結合、侵入、脱殻を行う Scavenger receptor B2（SCARB2）を同定し、これを発現するトランスジェニックマウスはウイルス感受性を獲得することを明らかにした。これから SCARB2 は EV71 の種特異性を決定している分子であることが判明した。SCARB2 以外にウイルスと結合はするが脱殻を起こさない attachment receptor として機能するとされるヘパラン硫酸の役割を調べた。ヘパラン硫酸は培養細胞では感染に有利に働くが、個体内では不利に働くことが判明した。また、PVR-Tg マウスモデルを用いて、ポリオウイルス経口感染時における IFN-α/β ならびに IFN-λの役割を調べた。腸管における攻防においては両方の IFN 受容体をノックアウトした場合に感染効率は上昇したことから、腸管でのウイルス増殖は両方の IFN システムによって防御されていることが分った。

研究計画⑥ ポストゲノム解析による感染体−宿主ネットワーク
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ウイルスの感染・侵入から、感染性ゲノムの複製・遺伝子発現と、ウイルス粒子へのパッケージング・放出に至るまでには、多くの宿主因子とウイルス因子との相互作用が存在し、大きな感染体－宿主ネットワークを形成していると考えられる。本計画では、超高感度・ハイスループット質量分析システムを活用した感染側因子と宿主因子の網羅的な相互作用解析と、ウイルス感染による宿主細胞のタンパク質発現変動を解析する。これまでに、インフルエンザ NS1 タンパク質、インフルエンザ RNP の輸送に関わる YB−1、ウイルス受容体タンパク質 RIG-I と相互作用する因子の網羅的解析を行った。また、HSV-1 感染細胞での新生タンパク質のプロテオミクス解析も進めている。伊庭は、細胞レベルでのウイルスと宿主の攻防に関わる宿主 miRNA について miR-199a-5p/3p および miR-214 に注目して、これらの miRNA が宿主細胞のコンピテンシーにどのように関与し、細胞の抗ウイルス活性を規定する分子スイッチとして機能するのかを解析した。*miR199* 遺伝子クラスター、*Egr1*、*Brm* の間に double-negative feedback loop が形成されていて、Brm を発現に必要とし、かつ miR-199a の標的となっている *CD44*、*Met*、*Caveolin 1* の発現がヒト上皮細胞においてall-or-non に発現を制御されていることを明らかにした。また、miR-199a の強制発現により、*trans*-ゴルジネットワークでの HSV-1 の Secondary envelopment が抑制されることを見出し、これは、miR-199a が *ARHGAP21* 遺伝子を抑制するためであると示唆された。

研究計画⑦ ウイルスー宿主攻防の数理科学解析
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宿主内でのウイルスと宿主の攻防の結果、ウイルスはダイナミックな遺伝的変化をとげる。本研究計画では、数理解析と実証実験の真の融合を目指す。これまでに、EV71 感染の数理モデル解析を行い、ウイルス株間でのそのバーストサイズおよび基本再生産数が、感染細胞の半減期に比べて顕著に異なることを見出した。また、宿主内の複数の組織で増殖する能力をもつウイルスの動態を、それぞれの組織での増殖と、ウイルス粒子の組織間移動を取り入れたモデルとして解析した。R0 中心性の概念と摂動展開を用いることにより、病原体が最も高い増殖率をもつ部位だけに集中的に介入する戦略が極めて有効であることを示した。ヒトの対レトロウイルス防御タンパク質であるAPOBEC3G と、それを阻害する HIV のタンパク質 Vif の共進化の数理モデル化を行い、ウイルス突然変異率を巡る宿主とウイルスの攻防の進化動態モデルを構築した。HIV-1 の抑制因子であるAPOBEC3H（A3H）は 7 つの遺伝子多型をもつ。A3H を拮抗阻害できないウイルス型の Vif は、2ヶ所のアミノ酸変異により、A3H に対する拮抗阻害活性を獲得することを明らかにした。数理モデル解析と HIV ゲノム配列ならびにヒトゲノムのデータベース解析により、同定した変異部位の多型とヒト集団内での A3H の遺伝子多型に相関性を見出し、ヒト集団の中で HIV が流行拡大する過程において、ウイルスが A3H をどのように回避・克服してきたのかを明らかにした。