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# Antigenic relationships between type A influenzaviruses of human, porcine, equine, and avian origin

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*This paper summarizes the available information on the relationship of two envelope antigens (haemagglutinin and neuraminidase) of influenzaviruses isolated from different hosts. The relationship of the haemagglutinin antigens was based on the results of haemagglutination inhibition tests with postinfection sera and that of the neuraminidase antigens on the results of neuraminidase inhibition and gel precipitation tests with hyperimmune and monospecific sera. On the basis of the antigenic specificity of the haemagglutinin, the influenzaviruses of human origin are divided into several subtypes (H0, H1, H2); viruses of equine origin could be divided into two subtypes (Heq1, Heq2). Porcine influenza strains are regarded as belonging to a single subtype, all of them being related to the prototype swine influenzavirus A (swine/Iowa/15/30). Within the avian influenzaviruses, 6 antigenic subtypes were described in earlier studies. Antigenic relationships between the haemagglutinin of strains from different hosts were infrequent but were demonstrated and confirmed between human A/Hong Kong/68 and equine viruses and between A/Hong Kong/68 and swine/Taiwan/69. The swine/Taiwan/69 virus also shared the related neuraminidase with A/Hong Kong/68 virus, and represents the only isolation from nonhuman sources of an influenzavirus identical with a human pandemic strain. The studies on the antigenic specificity of the neuraminidases demonstrated 8 antigenic varieties of neuraminidase among avian influenzaviruses and also that the neuraminidase grouping did not correspond with the antigenic grouping with regard to haemagglutinin. The relationships between human and nonhuman influenzaviruses are emphasized because of their significance to studies on the origin of influenza pandemics in man.*

The influenzaviruses form a morphologically homogeneous group of agents containing four major antigenic components. The type-specific ribonucleoprotein antigen is located internally in the virus particle and is antigenically stable, forming the basis for the division of influenza isolates into types A, B, and C. A further internal protein of the virus, antigenically distinct from ribonucleoprotein, is associated with a low molecular weight polypeptide component (Skehel & Schild, 1971; Schild, 1972) and also appears to be typespecific for influenza viruses type A and type B. The virus envelope contains two virus-coded antigenic components, the haemagglutinin and the neuraminidase, which are antigenically distinct and subtype-specific, and which undergo considerable antigenic variation.

The isolation of human influenzavirus A was first achieved in 1933 (Smith et al., 1933). However, even before this, virus isolations from nonhuman sources were reported that were only subsequently identified as type A influenzaviruses. Fowl plague viruses were isolated from domestic birds as early as 1902 and were recognized as a significant cause of avian disease (reviewed by Easterday & Tumová, 1971) and the virus of swine influenza was isolated in 1930 (Shope, 1931). On the basis of its morphology and the demonstration of antigenic relationships between its ribonucleoprotein antigen and that of human type A influenzaviruses, Schafer (1955) suggested that fowl plague virus was in fact a type A influenzavirus. The

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influenza isolates from swine were also identified as type A influenzaviruses. Since these early observations numerous isolations of type A influenzaviruses from swine and avian sources have been reported and, in addition, type A influenzaviruses have been isolated from horses with respiratory disease (Sovinova et al., 1956; Waddell et al., 1963). However, there are no confirmed reports of isolations type B or type C influenzaviruses from nonhuman sources.

Early studies on the antigenic relationships of the subtype-specific envelope analysis of type A influenzaviruses were largely confined to studies on the virus haemagglutinins. It is only comparatively recently that antigenic relationships specific to the neuraminidases of influenzaviruses have been studied. The first clear demonstration of the existence of antigenic relationships between the envelope antigens of type A influenzaviruses isolated from different species was between the human virus—A/Singapore/1/57 (H2N2)—and an influenzavirus A strain isolated from North American turkeys. Pereira et al. (1967) showed that these viruses contained antigenically identical neuraminidase, but distinct haemagglutinin antigens. Since this finding, numerous other antigenic relationships have been observed between the neuraminidase antigens of type A influenzaviruses from human, avian, porcine, and equine sources. This paper summarizes the available information on such antigenic relationships.

## ANTIGENIC RELATIONSHIPS OF HAEMAGGLUTININS

### *Relationships between strains isolated from the same host type*

Antigenic comparisons of influenzavirus haemagglutinins have usually been based on the results of haemagglutination inhibition (HI) tests with post-infection sera. In recent studies (Schild, 1970; Schild et al., 1972), antigenic comparisons have been carried out using precipitin tests with monospecific sera prepared against purified haemagglutinin subunits but such studies have so far been limited to a small number of strains. Strain specific complement fixation tests (Lief & Henle, 1959) have been used in antigenic comparisons but cross-reactions in such tests are observed with influenzaviruses containing related neuraminidases as well as related haemagglutinins and the interpretation of the results of such tests is difficult.

Type A influenzaviruses of human origin are divided into a number of subtypes on the basis of haemagglutination inhibition tests. The HO subtype was prevalent from 1933 to 1946, the H1 subtype from 1947 to 1957, and the H2 subtype from 1957 to 1968. In 1968 the A/Hong Kong/68 variant appeared and was found to contain a haemagglutinin (H3) antigenically distinct from that H2 of the formerly prevalent Asian virus (Coleman et al., 1968; Schild et al., 1972). In contrast to the results of HI tests, precipitin tests with monospecific sera prepared against purified H0 haemagglutinin have indicated the existence of antigenic determinants shared between human H0 and H1 haemagglutinins (Schild, 1970) but similar tests with antiserum against purified A/Hong Kong 68 haemagglutinin H3 failed to reveal antigenic relationships with that of the former Asian viruses (Schild et al., 1972).

Pereira et al. (1969) described the existence of six main subtypes of avian influenzavirus on the basis of the antigenic specificity of their haemagglutinins. Recently, two additional haemagglutinin subtypes have been described—namely, subtype 7, represented by duck/Ukraine/1/63 (Hav7Neq2) (Tumová et al., 1972), and subtype 8, represented by turkey/Ontario/6118/68 (Hav8Nav4) (Lang et al., 1972). However, the division of avian influenzaviruses with distinct haemagglutinin subtypes is complex since, when a large number of strains are included in antigenic comparisons, minor antigenic cross-reactions between some strains of different subtypes are observed. The division of avian influenzaviruses into haemagglutinin subtypes should therefore be regarded as an arbitrary and provisional one, which nevertheless serves a practical purpose in epidemiological and diagnostic work.

Equine influenzaviruses are clearly divided into two subtypes, one being represented by the strain A/equine/Prague/56 (Heq1Neq1), and the other being represented by A/equine/Miami/63 (Heq2Neq2). Viruses of " classical " swine influenza are regarded as belonging to a single subtype, the members of which are all related to the prototype swine influenzavirus A, swine/Iowa/15/30 (Hsw1N1) (Meier-Ewert et al., 1970). However, in 1969, the isolation from swine in Taiwan of virus strains antigenically identical to human A/Hong Kong/1/68 (H3N2) virus was described (Kundin, 1970). The epidemiological significance of these isolates is discussed in detail elsewhere (Harkness et al., 1972).

### *Relationships between strains from different hosts*

Although previous authors have described numerous examples of cross-reactions in haemagglutination inhibition tests between type A influenzaviruses from different hosts few of these have been confirmed in tests with monospecific antihaemagglutinin sera.

Some of the main antigenic relationships so far demonstrated in haemagglutination inhibition tests are summarized in Table 1. Cross-reactions have been demonstrated between swine/Iowa/15/30 and human A/WS/33 (H0N1) virus (Andrewes et al., 1935; Tumová, unpublished observations), between equine/Miami/63 and duck/Ukraine/1/63 and between equine/Miami/63 and A/Hong Kong/68. However, considerable caution is necessary in interpreting the results of haemagglutination inhibition tests, particularly where such tests are performed with hyperimmune sera. Under certain conditions antineuraminidase antibody may inhibit haemagglutination presumably by steric interference at the virus surface (Webster & Pereira, 1969; Schild et al., 1971). It therefore seems appropriate where possible to attempt to confirm the findings obtained with hyperimmune or postinfection sera in HI tests by the use of monospecific antihaemagglutinin sera in HI and precipitin tests. Attempts to confirm the relationship of swine/Iowa/15/30 and human A/WS/33 virus with antisera prepared against purified H0 haemagglutinin gave negative results (Schild, 1970). It therefore seems probable that the antigenic relationship demonstrated in conventional HI tests with postinfection sera (which contain both antihaemagglutinin and antineuraminidase antibodies) resulted from the fact that classical swine influenzaviruses and human viruses containing H0 and H1 haemagglutinins possess antigenically related neuraminidases (N1) (see Table 2). In contrast, it has been found that monospecific antiserum prepared against purified A/Hong Kong/68 haemagglutinin reacted both in HI tests and in precipitin tests with equine/Miami/63 virus (Schild et al., 1972), thus providing strong evidence that these two viruses contain antigenically related haemagglutinins. Similar evidence was obtained that certain strains of " classical " swine influenzavirus contain haemagglutinin antigenically related to that of human A/Hong Kong/68 virus (Schild et al., 1972).

Table 1. Antigenic relationships in haemagglutination inhibition tests

| | Antigens | Antisera | | | | | |
|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 4 | 5 | 6 |
| 1 | A/WS/33 | + | +[a] | | | | |
| 2 | swine/Iowa/15/30 | +[a] | + | | | | |
| 3 | equine/Miami/63 | | | + | + | | |
| 4 | duck/Ukraine/1/63 | | | | + | | |
| 5 | A/Hong Kong/68 | | | + | + | + | + |
| 6 | swine/Taiwan/69 | | | + | + | + | + |

[a] The existence of antigenic relationships between the haemagglutinins of human strain A/WS/33 and swine/Iowa/15/30 viruses could not be demonstrated in HI or immunodiffusion tests using monospecific antisera to purified haemagglutinin (Schild, 1970). In addition to the relationships shown in this table, antigenic relationships have been demonstrated between the haemagglutinins of human A/Hong Kong/68 virus and certain " classical " strains of swine influenza A virus (see Schild et al., 1972).

The swine/Taiwan/69 virus isolates (Kundin, 1970) were found to contain haemagglutinin and neuraminidase antigens (H3N2) identical to that of the human A/Hong Kong/68. This finding was confirmed by precipitin tests with monospecific antisera against purified A/Hong Kong/68 haemagglutinin and neuraminidase antigens (Schild et al., 1972). The isolation of the swine/Taiwan/69 virus is of particular interest as the first isolation from a nonhuman source of an influenzavirus showing complete antigenic identity with a human influenza A virus.

## ANTIGENIC RELATIONSHIPS OF NEURAMINIDASES

### *Relationships between strains from the same host and type*

Neuraminidase inhibition (NI) tests (Webster & Laver, 1966) with hyperimmune sera have been widely used in the study of antigenic relationships. However, some studies have employed NI and precipitin tests with monospecific sera prepared against purified neuraminidase subunits. Among the human type A influenzaviruses it has been shown that strains containing H0 and H1 heamagglutinins share antigenically related neuraminidases of subtype N1 (Paniker, 1968; Schild & Newman, 1969). Classical swine influenzaviruses also contain neuraminidase of subtype N1 (Schild et al., 1972). The neuraminidases (subtype N2) of the asian viruses isolated between 1957 and 1967 and of A/Hong Kong/68 virus show antigenic relationships that have been demonstrated in neuraminidase inhibition tests and also in precipitin tests with monospecific antisera (Schild & Newman, 1969). Antigenic comparisons of the neuraminidases of avian influenza viruses using NI tests have been carried out by a number of workers (Webster & Pereira, 1968; Kendal & Madley, 1969; Schild & Newman, 1969; Madley et al., 1971). The results obtained in the

Table 2. Antigenic relationships between th

| Host of origin | NA subtype[b] | HA subtype[b] | Strain | Antiserum to: | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | human strains | | | | swine strains | |
| | | | | A/34 | A/47 | A/57 (Asian) | A/68 (Hong Kong) | swine/Iowa/15/30 | swine/Taiwan/69 |
| man | N1 | H0 | PR8/34 | + | + | | | + | |
| | N1 | H1 | FM1/47 | + | + | | | + | |
| | N2 | H2 | Singapore/1/57 | | | + | + | | + |
| | N2 | H3 | Hong Kong/1/68 | | | + | + | | + |
| swine | N1 | Hsw1 | swine/Iowa/15/30 | + | + | | | + | |
| | N2 | H3 | swine/Taiwan/69 | | | + | + | | + |
| horses | Neq1 | Heq1 | equine/Prague/56 | | | | | | |
| | Heq2 | Heq2 | equine 2/Miami/63 | | | | | | |
| birds | N1 | Hav1 | FPV/Rostock/34 | + | + | | | + | |
| | | Hav6 | duck/Germany/68 | + | + | | | + | |
| | | Hav5 | chick/Scotland/59 | + | + | | | + | |
| | N2 | Hav2 | duck/Italy/574/66 | | | + | + | | NT |
| | | Hav6 | turkey/Mass/65 | | | + | + | | NT |
| | | Hav6 | turkey/Wisc/66 | | | + | + | | NT |
| | Neq1 | Hav1 | FPV/Dutch/27 | | | | | | |
| | | Hav2 | chick/Germany 'N'/49 | | | | | | |
| | Neq2 | Hav2 | quail/Italy/1117/65 | | | | | | |
| | | Hav6 | turkey/Canada/63 | | | | | | |
| | | Hav7 | duck/Ukraine/63 | | | | | | |
| | Nav1 | Hav3 | duck/England/56 | | | | | | |
| | | Hav4 | duck/Czechoslovakia/56 | | | | | | |
| | | Hav4 | duck/England/62 | | | | | | |
| | Nav2 | Hav5 | tern/South Africa/61[c] | | | | | | |
| | Nav3 | Hav1 | turkey/England/63[c] | | | | | | |
| | Nav4 | Hav8 | turkey/Ontario/6118/68 | | | | | | |

[a] + Indicates cross-reactions in NI tests at titres not less than 10% of the homologous titre of the antiserum. Blank spac

[b] Neuraminidase and haemagglutinin subtypes are numbered according to recent proposals for a revised system of influenza vir

[c] A minor cross-reaction (approx. 10% of the homologous titre) detected between turkey/England/63 and tern/South Africa/6

authors' laboratories (unpublished data) are summarized in Table 2 and are in general agreement with those obtained by other workers. It can be seen from this table that among avian influenza-viruses 8 antigenic varieties of neuraminidase exist and moreover that the neuraminidase antigenic groupings of these viruses do not correspond with the haemagglutinin antigenic groups. For example, although 3 avian virus strains, chicken/Scotland/59 (Hav5N1), duck/Germany/1868/68 (Hav6N1), and FPV/Rostock/34 (Hav1N1) contain unrelated haemagglutinins, they share antigenically closely related neuraminidase antigens. A similar heterogeneity of HA subtypes exists among avian viruses possessing the neuraminidases characterized by that of turkey/Massachusetts/65 (Hav6N2) virus, i.e., neuraminidase antigenically similar to that of human Asian viruses.

It should be stressed, however, that the results shown in Table 2 have largely been obtained with antisera prepared against whole (unfractionated) virus preparations and that several of the antigenic relationships, particularly in the case of avian virus strains, have not yet been fully studied with monospecific sera prepared against purified neuraminidase antigens. In addition, confirmatory evidence of antigenic relationships of neuraminidase antigens has been sought in precipitin tests in only a limited neuraminidases of type A influenzaviruses from various hosts [a]

| Antiserum to: | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| equine strains | | avian strains | | | | | | | |
| equine/ Prague/56 | equine/ Miami/63 | chicken/ Scotland/59 | turkey/ Mass./65 | FPV/ Dutch/27 | quail/Italy/ 1117/65 | duck/ England/56 | tern/ S. Africa/61 | turkey/ England/63 | turkey/ Ontario/68 |
| | | + | | | | | | | |
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ndicate the absence of NI reactions or reactions at titres less than 10 % of the homologous titre. NT indicates not tested.

nomenclature (*Bull. Wld. Hlth. Org.*, 1971).

number of strains (see Schild & Newman, 1969; Schild et al., 1972). The grouping of avian influenzavirus strains (Table 2) according to their neuraminidase antigens should therefore be regarded as provisional until the results of appropriate studies with monospecific sera are available.

### *Relationships between strains from different hosts*

In contrast to the relatively few antigenic relationships observed amongst the haemagglutinins of influenzavirus A from different hosts a considerable number of neuraminidase antigenic relationships have been observed (Webster & Pereira, 1968; Schild & Newman, 1969; Tumová & Easterday, 1969). These relationships are summarized in Table 2. It is seen that among the neuraminidases of avian influenza A viruses only those of the antigenic varieties contained in tern/South Africa/61 (Hav5-Nav2), turkey/England/63 (Hav1Nav3), turkey/Ontario/6118/68 (Hav8Nav4), duck/England/62 (Hav4Nav1) viruses are unique to viruses of avian origin. The four other antigenic varieties of neuraminidase of the avian influenzaviruses are antigenically closely related to that contained in human type A influenzaviruses isolated between 1933 and 1946 and in classical swine influenzaviruses (N1), to that of human Asian and Hong Kong viruses (N2), and to those of equine-1 (Neq1) and equine-2 viruses (Neq2).

## DISCUSSION

The studies summarized in the present paper indicate that there are a number of different types of antigenic relationship between type A influenzaviruses isolated from different hosts. However, this discussion will mainly concern the antigenic relationships between human and nonhuman influenzaviruses because of their possible significance in the origin of human influenza pandemics.

The antigenic identity of the ribonucleoprotein antigens of human and nonhuman type A influenzaviruses is well established. One significant aspect of the possession of a common ribonucleoprotein antigen is that type A influenzaviruses from different hosts have been shown to be capable of undergoing genetic interactions leading to the formation of recombinant strains sharing the antigenic characters of both parent viruses. The high degree of antigenic variation found among the type A influenzaviruses may be related to their ability to undergo genetic recombination. Recombinant influenzaviruses possessing envelope antigens derived from their human and avian influenzavirus parents have been produced experimentally *in vitro* (Tumová & Pereira, 1965; Easterday et al., 1970). In addition, Webster et al. (1971) have recently demonstrated that recombination may also occur *in vivo* between different type A influenzaviruses in a doubly infected host. It is tempting to postulate that recombination may play a role in the origin of new antigenic variants of influenza. The existence of influenzavirus strains sharing one envelope antigen (usually the neuraminidase) but not the other (the haemagglutinin), which have been isolated from natural infections of birds (A/turkey/Massachusetts/65 (Hav6N2) and others), appears to support the possibility that recombination leading to a reassortment of antigenic characteristics of the parent viruses may take place frequently in nature. However, other possible explanations for antigenic variation in the influenzavirus A cannot be disregarded including changes brought about by mutation and selection, and the suggestion put forward by Jensen & Francis (1953) that a finite number of antigenic varieties of haemagglutinin and neuraminidase antigens exist amongst type A influenzaviruses.

Few antigenic relationships have been detected between the haemagglutinins of human type A influenzaviruses and those of viruses so far isolated from nonhuman hosts. Furthermore, certain of the relationships that have been demonstrated between human and nonhuman influenza A strains are of doubtful significance since they have been observed only in tests with hyperimmune sera or, as is the case with the cross-reactions detected between A/Hong Kong/68 and A/Equine/Miami/63 virus, they are not reciprocal.

In contrast, studies on the neuraminidase antigens of type A influenzaviruses have revealed a considerable number of antigenic relationships between the neuraminidases of viruses of human and nonhuman origin. The neuraminidases (N1) of human influenzaviruses isolated between 1933 and 1946 are antigenically related to those of several swine and avian influenza strains, while neuraminidase of the same antigenic type as that of human Asian viruses has been detected in a number of avian influenzavirus A strains. Human and nonhuman viruses sharing neuraminidase antigens have been found to contain antigenically distinct haemagglutinins. On the appearance of a new subtype of influenzavirus A in man the previously prevalent subtype is rapidly replaced. In nonhuman hosts, however, antigenically distinct viruses have been frequently detected during the same period and in some cases antigenically distinct viruses have been isolated from the same epizootic in birds (Pereira et al., 1967) or in horses (Tumová et al., 1971). While type A influenzaviruses containing neuraminidase of subtype N1 have not been isolated from man since 1957, viruses containing this antigenic type of neuraminidase still exist in swine (" classical " swine influenzaviruses related to swine/Iowa/15/30) and were isolated from birds as recently as 1968 (Schild et al., 1969). Furthermore, neuraminidase of subtype N1 has been demonstrated in the Brescia strain of fowl plague virus isolated in 1902 (Schild, unpublished observation). Since the time of the first appearance of N1 neuraminidase in influenzaviruses infecting man is not known, it is not possible to state whether the date of isolation of a nonhuman virus containing N1 neuraminidase predated the appearance of viruses containing this subtype of neuraminidase in the human population. Neuraminidase related to that of human Asian viruses (N2) has been demonstrated in several avian influenzaviruses isolated in recent years (1965–71). There are no reports of the presence of this neuraminidase subtype among avian influenzavirus strains isolated before the appearance of Asian viruses in man in 1957. However, it should be mentioned that relatively few isolates of avian influenzavirus were made before 1957, presumably because relatively little attention was paid to the etiology of influenza in birds before that date.

The recent isolation of the swine/Taiwan/69 virus (Kundin, 1970), which is antigenically identical to A/Hong Kong/68 in both haemagglutinin and neuraminidase antigens, is the only isolation from a nonhuman source of an influenzavirus A identical to a human pandemic strain. Antibodies to A/Hong Kong/68 virus have been frequently demonstrated in sera from swine in several countries after the human pandemics of 1968–69 and 1969–70 (Romvary, personal communication; Styk et al., 1971; Harkness et al., 1972; Tumová et al., unpublished observation). Also, swine/Taiwan/69 virus has been shown to be capable of infecting human volunteers (Beare et al., 1971). These studies indicate that certain influenzaviruses might be capable of crossing species barriers. However, it has not yet been determined whether strains that are capable of crossing host barriers could become established in the new host and produce epidemics of disease.

That the type A influenzaviruses from a large and widely distributed group of agents containing at least four different antigenic types of neuraminidase that have not been demonstrated in human influenzavirus subtypes is of particular interest. If the hypothesis that recombination between two viruses of different hosts may occur is accepted, we might speculate that any of these antigenic types of neuraminidase might appear in future pandemic strains of human influenzavirus A. The possibility that the haemagglutinin antigens found amongst avian (and other nonhuman) influenzaviruses might appear in future pandemic strains of man should also be considered, but the results of current studies suggest that neuraminidase antigenic relationships are more frequent. The significance of these findings are at present not clear and their understanding requires further studies on the ecology of the influenzavirus.

## RÉSUMÉ

### RELATIONS ANTIGÉNIQUES ENTRE DES VIRUS GRIPPAUX DE TYPE A D'ORIGINE HUMAINE, PORCINE, ÉQUINE ET AVIAIRE

Le présent article résume les informations actuellement disponibles concernant les relations entre les antigènes d'enveloppe (hémagglutinine et neuraminidase) de virus grippaux isolés chez différents hôtes. Pour établir les liens entre les hémagglutinines, on a tenu compte des résultats des épreuves d'inhibition de l'hémagglutination portant sur des sérums prélevés après une infection grippale; les rapports entre les neuraminidases ont été déterminés à l'aide d'épreuves d'inhibition de la neuraminidase et de précipitation en gel utilisant des sérums hyperimmuns et monospécifiques.

Sur la base de la spécificité antigénique de l'hémagglutinine, on peut répartir les virus grippaux d'origine humaine en différents sous-types (H0, H1, H2) et les virus d'origine équine en deux sous-types (Heq1, Heq2). Les virus de la grippe porcine sont considérés comme appartenant à un sous-type unique, toutes les souches isolées étant apparentées à la souche prototype swine/Iowa/15/30. Pour les virus de la grippe aviaire, 6 sous-types antigéniques ont été décrits.

Des relations antigéniques entre hémagglutinines de souches isolées chez des hôtes différents ne sont pas fréquentes. On a démontré et confirmé l'existence de telles relations entre le virus humain A/Hong Kong/68 et des virus équins ainsi qu'entre le virus A/Hong Kong/68 et la souche swine/Taiwan/69. Cette dernière possède aussi une neuraminidase identique à celle du virus A/Hong Kong/68 et elle est donc la seule souche d'origine animale présentant une identité antigénique complète avec un virus humain A.

L'étude de la spécificité antigénique des neuraminidases met en évidence 8 variétés de cet antigène parmi les virus de la grippe aviaire. Leur répartition, au sein de ce groupe, est distincte de celle des hémagglutinines. Quatre de ces variétés de neuraminidases sont très proches de celles caractérisant les sous-types A0, A1 et A2 de la grippe humaine, les virus « classiques » de la grippe porcine et les virus équine-1 et équine-2. Les quatre autres variétés sont spécifiques des virus de la grippe aviaire.

Les auteurs insistent sur l'intérêt de ces relations entre virus de la grippe humaine et virus de la grippe animale pour l'étude de l'origine des pandémies grippales chez l'homme.

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