Summary of neuraminidase (NA) amino acid substitutions assessed for their effects on inhibition by NA inhibitors (NAIs) among avian influenza viruses of Group 1 (N1, N4, N5, N8 subtypes) and Group 2 (N2, N3, N6, N7, N9 subtypes) NAs.

NA subtype	Amino acid substitution[a]	N2 numbering[b]	Susceptibility assessed by NA inhibition assays (IC_{50} fold change)[c]				Source of viruses/ selection with[d]	References
			Oseltamivir	Zanamivir	Peramivir	Laninamivir		
Group 1								
H5N1	V96A	116	**RI (11–18)**	**RI (10–63)**	NI (4)	?[e]	Sur	(1, 2)
	I97T	117	**RI (19)**	**RI (12)**	?	?	Sur	(3)
	I117T[f]	117	NI (1)	NI (1)	NI (1)	NI (1)	Sur	(4)
	I97V	117	NI (5–9)	NI (2–4)	?	?	RG; Sur	(3, 5, 6)
	E99A	119	**RI (10–35)**	**HRI (51–1254)**	NI (7)	?	RG	(5, 7)
	E99D	119	**RI (87)**	**HRI (132)**	**HRI (1436)**	?	RG	(7)
	E99G	119	NI (3–6)	**HRI (438–1485)**	**RI/HRI (12–164)**	?	RG; in vitro/Zan	(7, 8)
	Q116L	136	**RI (26)**	**HRI (350)**	?	?	In vivo/Zan	(9)
	V129A	149	NI (4)	NI (8)	?	?	Sur	(10)
	D179G	198	**RI (32)**	**RI (44)**	NI (4)	?	RG; in vitro/Zan	(8)
	I203M	222	**RI (36)**	NI (1)	NI (1)	?	RG; in vitro/Zan	(8)
	I203V	222	NI (7)	NI (1)	NI (1)	?	RG; in vitro/Zan	(8)
	S227N	246	**RI (24)**	NI (2)	?	?	Sur	(1)
	S247N[f]	246	NI (6)	NI (1)	NI (4)	NI (2)	Sur	(4)
	H255Y	274	**RI/HRI (44–2502)**	NI (1–3)	**RI/HRI (23–533)**	NI (6)	Sur; Clin/Ose; RG; in vitro/Zan	(5, 7, 8, 11, 12)
	N275S	294	**RI/HRI (12–138)**	NI/**RI** (1–**27**)	NI/**RI/HRI** (1–**130**)	?	Clin/Ose; RG	(5, 7, 11, 13)
	N295D[f]	294	NI (1)	NI (4)	NI (2)	NI (2)	Sur	(4)
	N295S[f]	294	**RI (14)**	NI (4)	NI (6)	NI (3)	Sur	(4)
	K412T	432	NI (9)	**RI (12)**	NI (5)	?	Sur; in vitro	(14)
	T438I[f]	439	NI (1–8)	**RI/HRI (17–98)**	NI/**RI** (6–**23**)	?	RG, Sur	(15)
	T438N[f]	439	NI (2)	**RI (12)**	NI (2)	NI (2)	Sur	(4)
	I97V+I294V	117+314	**RI (16)**	NI (1)	NI (1)	?	Sur	(2)
	E99A+H255Y	119+274	**HRI (1530)**	**RI (50)**	**HRI (2686)**	?	RG	(7)
	E99D+H255Y	119+274	**HRI (160)**	**RI (65)**	**HRI (1629)**	?	RG	(7)
	E99G+H255Y	119+274	**HRI (801)**	**RI (76)**	**HRI (>7692)**	?	RG	(7)
	I203L+ S227N	222+246	**RI (14)**	NI (1)	NI (5)	?	Sur; in vitro	(14)
	I203M+H255Y	222+274	**HRI (8024)**	NI (3)	**HRI (3340)**	?	RG; in vitro/Zan	(8)
	I203V+H255Y	222+274	**HRI (1925)**	NI (2)	**HRI (2106)**	?	RG; in vitro/Zan	(8)
	N295S+T438N[f]	294+439	**HRI (51–74)**	**HRI (76–86)**	**HRI (73–90)**	**RI (16-19)**	Sur	(4)

	K130N+I203L+S227N	150+222+246	**RI (77)**	NI (1)	?	?	Sur	(1)
N4	H274Y	274	**HRI (318)**	NI (2)	**HRI (115)**	NI (5)	in vitro; RG	(16, 17)
	E276D	276	**RI (11)**	**HRI (249)**	**RI (18)**	**RI (81)**	in vitro; RG/Zan	(16, 17)
	R292K	292	**HRI (52862135)**	**HRI (465)**	**HRI (30252)**	**HRI (293)**	in vitro; RG	(16, 17)
	I428L	427	**RI (19)**	**RI (76)**	NI (9)	**RI (21)**	in vitro; RG/Zan	(16, 17)
N5	E116V	119	**RI (59)**	**HRI (737)**	**RI (64)**	**HRI (386)**	in vitro; RG/Ose	(16, 17)
	N143I	147	NI (1)	**RI (31)**	NI (3)	NI (1)	in vitro; RG/Zan	(16, 17)
	H271Y	274	**HRI (1082)**	NI (3)	**HRI (312)**	NI (2)	in vitro; RG	(16, 17)
	R289K	292	**HRI (964)**	NI (4)	**HRI (284)**	NI (3)	in vitro; RG	(16, 17)
	L87I+E116V	91+119	**RI (43)**	**HRI (556)**	**RI (87)**	**HRI (274)**	in vitro; RG/Ose	(16, 17)
N8	E117V	119	**RI (30)**	**HRI (255)**	**HRI (130)**	?	RG	(18)
	Q134K	136	NI (1)	**HRI (263)**	**HRI (185)**	**HRI (550)**	in vitro; RG/Zan	(16, 17)
	G145V	147	NI (2)	**RI (25)**	NI (5)	**RI (22)**	in vitro; RG/Zan	(16, 17)
	H273Y	274	**HRI (202–425)**	NI (1–2)	**HRI (103–244)**	NI (3)	in vitro; RG	(16−18)
	R291K	292	**HRI (50636336)**	**RI (93)**	**HRI (8540)**	**HRI (152)**	in vitro; RG	(16, 17)
	N293S	294	**RI (62−79)**	NI (3)	**RI (15)**	?	RG, Sur	(18, 19)
Group 2								
N2	E119A	119	NI (9)	**HRI (100–600)**	NI (1)	?	in vitro/Zan	(20, 21)
	E119D	119	NI (4–5)	**HRI (323– 500)**	**RI (33)**	?	in ovo; in vitro/Zan	(20−22)
	E119G	119	**RI (2–87)**	**HRI (71–700)**	NI (2)	?	in vivo; in vitro/Zan	(20, 21, 23)
	E119V	119	**RI (48)**	NI (3)	NI (1)	?	RG	(18)
	H274Y	274	NI (1)	NI (5)	NI (2)	?	RG	(18)
	R292K	292	**HRI (1268– >2900)**	NI/**RI (4–26)**	**RI (43–100)**	?	in vivo, in ovo; in vitro/Zan; RG	(18–22, 24, 25)
	N294S	294	NI (3)	**RI (14)**	NI (1)	?	RG	(18)
N3	E119G	119	**RI (25)**	**HRI (523)**	**RI (14)**	**RI (24)**	in vitro; RG/Zan	(17, 26)
	H276Y	274	**HRI (12229)**	NI (2)	NI (1)	NI (0.5)	in vitro; RG	(17, 26)
	R293K	292	**HRI (17960)**	**RI (23)**	**RI (41)**	NI (2)	in vitro; RG/Ose	(17, 26)
N6	E119D	119	NI (2)	**HRI (249)**	**RI (31)**	**HRI (370)**	in vitro; RG/Zan	(17, 26)
	E119V	119	**RI (75)**	NI (4)	NI (4)	?	RG	(18)
	A247V	246	NI (3)	**RI (17)**	NI (5)	**RI (14)**	in vitro; RG/Zan	(17, 26)
	H275Y	274	**RI (13)**	NI (3)	NI (3)	?	RG	(18)
	R293K	292	**HRI (15068)**	**RI/HRI (46)**	**HRI (844)**	**HRI (126)**	in vitro; RG/Ose	(17, 26)
	N295S	294	NI (1)	**RI (18)**	NI (3)	?	RG	(18)

	R372K	371	**RI (23)**	**RI (53)**	**RI (12)**	**RI (95)**	in vitro; RG/Zan	(17, 26)
N7	E118D	119	NI (3)	**HRI (101)**	NI (1)	**RI (60)**	in vitro; RG/Zan	(17, 26)
	E118G	119	NI (1)	**RI (67)**	NI (1)	**RI (42)**	in vitro; RG/Zan	(17, 26)
	E118V	119	**RI (55)**	NI (1)	NI (2)	NI (0.5)	in vitro; RG/Ose	(17, 26)
	R151W	152	**RI (14)**	**RI (11)**	NI (1)	NI (4)	in vitro; RG/Ose	(17, 26)
	H274Y	274	**RI (17)**	NI (2)	NI (2)	NI (1)	in vitro; RG	(17, 26)
	E276D	276	NI (7)	**RI (26)**	NI (5)	NI (3)	in vitro; RG/Zan	(17, 26)
	R292K	292	**HRI (44326)**	**RI (21)**	**HRI (415)**	**RI (11)**	in vitro; RG/Ose	(17, 26)
	D293N	293	**RI (14)**	**RI (57)**	NI (5)	**RI (31)**	in vitro; RG/Zan	(17, 26)
	S110N+E119D	111+119	NI (4)	**HRI (116)**	NI (1)	**RI (79)**	in vitro; RG/Zan	(17, 26)
	I275T+E276D	275+276	NI (6)	**RI (14)**	NI (5)	NI (0.4)	in vitro; RG/Zan	(17, 26)
H7N9	E115A	119	**RI (19)**	**HRI (228)**	**RI (20)**	**RI (62)**	in vitro; recNA	(27)
	E115D	119	**RI (14)**	**HRI (1436)**	**HRI (411)**	**HRI (383)**	in vitro; recNA	(27)
	E115G	119	NI (2)	**HRI (419)**	**RI (48)**	**HRI (124)**	in vitro; recNA	(27)
	E115V	119	**RI/HRI (84−169)**	NI (6−9)	NI (1−2)	NI (2−5)	Sur; P-p; in vitro; recNA; RG	(27−29)
	Q132K	136	NI (1)	**HRI (702)**	**HRI (131)**	**HRI (313)**	in vitro; recNA	(27)
	R148K	152	NI (1)	NI (5)	NI (3)	**RI (16)**	in vitro; recNA	(27)
	I219K	222	**RI (32−46)**	NI/**RI (8−17)**	NI/**RI (6−11)**	**RI (13−27)**	in vitro; recNA; Sur; P-p	(27, 28)
	I219L	222	NI (5)	NI (2)	NI (1)	NI (2)	RG	(29)
	I219R	222	**RI/HRI (37−143)**	**RI (12−38)**	**RI (12−44)**	**RI (14−63)**	In vitro; recNA; sur; P-p	(27, 28)
	T244P	247	**RI (27)**	**RI (69)**	NI (4)	NI (9)	in vitro; recNA	(27)
	H271Y	274	**HRI (105)**	NI (2)	NI (9)	NI (2)	in vitro; Sur	(27)
	E273D	276	**RI (13)**	**HRI (427)**	**RI (25)**	**RI (90)**	in vitro; recNA	(27)
	R289K	292	**HRI (>4600)**	**RI (11–67)**	**HRI (405–2487)**	**RI (16–35)**	in vitro; recNA; Sur; P-p	(27, 28, 30, 31)
	N291S	294	NI (2)	**RI (10)**	NI (1)	NI (3)	in vitro; recNA	(27)
	R367K	371	**RI (70)**	**RI (64)**	**RI (29)**	**RI (19)**	in vitro; recNA	(27)
	E115V+I219L	119+222	**HRI (306)**	NI (8)	NI (2)	NI (4)	RG	(29)
N9	*E120V*	119	**RI (50)**	NI (3)	NI (1)	NI (3)	in vitro; RG/Ose	(17, 26)
	Q137K	136	NI (0.5)	**HRI (121)**	**RI (54)**	**RI (63)**	in vitro; RG/Zan	(17, 26)
	R153K	152	NI (2)	**RI (10)**	?	?	RG	(29)
	I224M	222	**RI (18)**	NI (4)	NI (4)	NI (1)	in vitro; RG/Ose	(17, 26)
	A248T	246	NI (6)	**RI (25)**	NI (7)	NI (2)	in vitro; RG/Zan	(17, 26)
	H276Y	274	**RI (80–90)**	NI (2–3)	**RI (11)**	NI (2)	in vitro; RG	(17, 26, 32)
	R294K	292	**HRI (10000–68891)**	**RI (32–51)**	**HRI (2068)**	**RI (35)**	in vitro; RG/Ose	(17, 26, 32)

[a] Numbering is based on the neuraminidase subtype of influenza A viruses.
[b] Equivalent N2 numbering is based on an alignment of neuraminidases from A/turkey/Turkey/1/2005 (H5N1), A/goose/Taiwan/01031/2015 (H5N2), A/turkey/Minnesota/916/80 (H7N3), A/environment/South Korea/W140/2006 (H10N4), A/aquatic bird/Korea/W69/2005 (H6N5), A/environment/South Korea/W20/2005 (H4N6), A/chicken/Jiangxi/02.05 YGYXG023-P/2015 (H5N6), A/duck/Germany/62-4/81 (H7N7), A/environment/Korea/W468/2014 (H5N8), A/scarlet ibis/Germany/AR44-L01279/2015 (H5N8), and A/duck/Memphis/546/74 (H11N9 – N9 numbers shown in *italics*) influenza viruses.
[c] Assessed by NA inhibition (NI) assays: chemiluminescent (NA-Star), fluorescent (MUNANA) and/or colorimetric (fetuin). NAI results are shown according to the referenced studies: NI, normal inhibition; **RI**, reduced inhibition; **HRI**, highly reduced inhibition as defined in (31). Fold-changes in IC_{50} (half maximal inhibitory concentration) relative to wild-type viruses or subtype- or clade-specific median IC_{50}s, are shown in parentheses.
[d] Clin, clinical detection; Ose, oseltamivir used; Zan, zanamivir used; P-p, Plaque purification; RG, reverse genetics; recNA, recombinant NA; Sur, surveillance studies.
[e] ? signifies that the NAI(s) indicated were not studied.
[f] Equivalent N1 numbering is based on an alignment of neuraminidase from A/bald eagle/Florida/W22-134-OP/2022 (H5N1) clade 2.3.4.4b influenza virus that does not carry a 20 amino acid deletion in the neuraminidase stalk region.

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