

Ionotropic glutamate receptors (version 2019.4) in the IUPHAR/BPS Guide to Pharmacology Database

Bernhard Bettler¹, Graham L. Collingridge², Ray Dingledine³, Stephen F. Heinemann⁴, Michael Hollmann⁵, Juan Lerma⁶, David Lodge², Mark Mayer⁷, Masayoshi Mishina⁸, Christophe Mulle⁹, Shigetada Nakanishi¹⁰, Richard Olsen¹¹, Stephane Peigneur², John A. Peters¹², Peter Seeburg¹³, Michael Spedding¹⁴ and Jeffrey C. Watkins²

1. University of Basel, Switzerland
2. University of Bristol, UK
3. Emory University, USA
4. Salk Institute, USA
5. Ruhr University Bochum, Germany
6. Universidad Miguel Hernández, Spain
7. National Institutes of Health, USA
8. University of Tokyo, Japan
9. Université Bordeaux 2, France
10. Kyoto University Faculty of Medicine, Japan
11. University of California Los Angeles, USA
12. University of Dundee, UK
13. Max Planck Institute for Medical Research, Germany
14. Spedding Research Solutions SARL, France

Abstract

The ionotropic glutamate receptors comprise members of the NMDA (N-methyl-D-aspartate), AMPA (α -amino-3-hydroxy-5-methyl-4-isoxazolepropionic acid) and kainate receptor classes, named originally according to their preferred, synthetic, agonist [34, 87, 147]. Receptor heterogeneity within each class arises from the homo-oligomeric, or hetero-oligomeric, assembly of distinct subunits into cation-selective tetramers. Each subunit of the tetrameric complex comprises an extracellular amino terminal domain (ATD), an extracellular ligand binding domain (LBD), three transmembrane domains composed of three membrane spans (M1, M3 and M4), a channel lining re-entrant 'p-loop' (M2) located between M1 and M3 and an intracellular carboxy-terminal domain (CTD) [94, 66, 102, 147, 77]. The X-ray structure of a homomeric ionotropic glutamate receptor (GluA2 – see below) has recently been solved at 3.6Å resolution [135] and although providing the most complete structural information currently available may not be representative of the subunit arrangement of, for example, the heteromeric

ionotropic glutamate receptor isoforms in detail; such information can be gleaned from [34, 65, 30, 73, 41, 108, 23, 64, 147, 106, 107, 152]. Agents that discriminate between subunit isoforms are, where appropriate, noted in the tables and additional compounds that distinguish between receptor isoforms are indicated in the text below.

The classification of glutamate receptor subunits has been re-addressed by NC-IUPHAR [27]. The scheme developed recommends a nomenclature for ionotropic glutamate receptor subunits that is adopted here.

NMDA receptors

NMDA receptors assemble as obligate heteromers that may be drawn from GluN1, GluN2A, GluN2B, GluN2C, GluN2D, GluN3A and GluN3B subunits. Alternative splicing can generate eight isoforms of GluN1 with differing pharmacological properties. Various splice variants of GluN2B, 2C, 2D and GluN3A have also been reported. Activation of NMDA receptors containing GluN1 and GluN2 subunits requires the binding of two agonists, glutamate to the S1 and S2 regions of the GluN2 subunit and glycine to S1 and S2 regions of the GluN1 subunit [40, 24]. The minimal requirement for efficient functional expression of NMDA receptors *in vitro* is a di-heteromeric assembly of GluN1 and at least one GluN2 subunit variant, as a dimer of heterodimers arrangement in the extracellular domain [47, 94, 69]. However, more complex tri-heteromeric assemblies, incorporating multiple subtypes of GluN2 subunit, or GluN3 subunits, can be generated *in vitro* and occur *in vivo*. The NMDA receptor channel commonly has a high relative permeability to Ca^{2+} and is blocked, in a voltage-dependent manner, by Mg^{2+} such that at resting potentials the response is substantially inhibited.

AMPA and Kainate receptors

AMPA receptors assemble as homomers, or heteromers, that may be drawn from GluA1, GluA2, GluA3 and GluA4 subunits. Transmembrane AMPA receptor regulatory proteins (TARPs) of class I (i.e. $\gamma 2$, $\gamma 3$, $\gamma 4$ and $\gamma 8$) act, with variable stoichiometry, as auxiliary subunits to AMPA receptors and influence their trafficking, single channel conductance gating and pharmacology (reviewed in [42, 98, 145, 63]). Functional kainate receptors can be expressed as homomers of GluK1, GluK2 or GluK3 subunits. GluK1-3 subunits are also capable of assembling into heterotetramers (e.g. GluK1/K2; [82, 113, 112]). Two additional kainate receptor subunits, GluK4 and GluK5, when expressed individually, form high affinity binding sites for [kainate](#), but lack function, but can form heteromers when expressed with GluK1-3 subunits (e.g. GluK2/K5; reviewed in [113, 64, 112]). Kainate receptors may also exhibit 'metabotropic' functions [82, 123]. As found for AMPA receptors, kainate receptors are modulated by auxiliary subunits (Neto proteins, [112, 83]). An important function difference between AMPA and kainate receptors is that the latter require extracellular Na^+ and Cl^- for their activation [11, 114]. RNA encoding the GluA2 subunit undergoes extensive RNA editing in which the codon encoding a p-loop glutamine residue (Q) is converted to one encoding arginine (R). This Q/R site strongly influences the biophysical properties of the receptor. Recombinant AMPA receptors lacking RNA edited GluA2 subunits are: (1) permeable to Ca^{2+} ; (2) blocked by intracellular polyamines at depolarized potentials causing inward rectification (the latter being reduced by TARPs); (3) blocked by extracellular argitoxin and Joro spider toxins and (4) demonstrate higher channel conductances than receptors containing the edited form of GluA2 [131, 62]. GluK1 and GluK2, but not other kainate receptor subunits, are similarly edited and broadly similar functional characteristics apply to kainate receptors lacking either an RNA edited GluK1, or GluK2, subunit [82, 112]. Native AMPA and kainate receptors displaying differential channel conductances, Ca^{2+} permeabilities and sensitivity to block by intracellular polyamines have been identified [29, 62, 86]. GluA1-4 can exist as two variants generated by alternative splicing (termed 'flip' and 'flop') that differ in their desensitization kinetics and their desensitization in the presence of cyclothiazide which stabilises the nondesensitized state. TARPs also stabilise the non-desensitized conformation of AMPA receptors and facilitate the action of [cyclothiazide](#) [98]. Splice variants of GluK1-3 also exist which affects their trafficking [82, 112].

Contents

This is a citation summary for Ionotropic glutamate receptors in the [Guide to Pharmacology](#) database (GtoPdb). It exists purely as an adjunct to the database to facilitate the recognition of citations to and from the database by citation analyzers. Readers will almost certainly want to visit the relevant sections of the database which are given here under database links.

[GtoPdb](#) is an expert-driven guide to pharmacological targets and the substances that act on them. GtoPdb is a reference work which is most usefully represented as an on-line database. As in any publication this work should be appropriately cited, and the papers it cites should also be recognized. This document provides a citation for the relevant parts of the database, and also provides a reference list for the research cited by those

parts.

Please note that the database version for the citations given in GtoPdb are to the most recent preceding version in which the family or its subfamilies and targets were substantially changed. The links below are to the current version. If you need to consult the cited version, rather than the most recent version, please contact the GtoPdb curators.

Database links

Ionotropic glutamate receptors

<http://www.guidetopharmacology.org/GRAC/FamilyDisplayForward?familyId=75>

Channels and Subunits

GluA1

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=444>

GluA2

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=445>

GluA3

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=446>

GluA4

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=447>

GluD1

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=448>

GluD2

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=449>

GluK1

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=450>

GluK2

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=451>

GluK3

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=452>

GluK4

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=453>

GluK5

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=454>

GluN1

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=455>

GluN2A

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=456>

GluN2B

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=457>

GluN2C

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=458>

GluN2D

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=459>

GluN3A

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=460>

GluN3B

<http://www.guidetopharmacology.org/GRAC/ObjectDisplayForward?objectId=461>

References

1. Acker TM, Yuan H, Hansen KB, Vance KM, Ogden KK, Jensen HS, Burger PB, Mullasseril P, Snyder JP and Liotta DC *et al.*. (2011) Mechanism for noncompetitive inhibition by novel GluN2C/D N-methyl-D-aspartate receptor subunit-selective modulators. *Mol. Pharmacol.* **80**: 782-95 [PMID:21807990]
2. Aicher SA, Sharma S and Mitchell JL. (2002) Co-localization of AMPA receptor subunits in the nucleus of the solitary tract in the rat. *Brain Res.* **958**: 454-8 [PMID:12470884]
3. Antal M, Fukazawa Y, Eördögh M, Muszil D, Molnár E, Itakura M, Takahashi M and Shigemoto R. (2008) Numbers, densities, and colocalization of AMPA- and NMDA-type glutamate receptors at individual synapses in the superficial spinal dorsal horn of rats. *J. Neurosci.* **28**: 9692-701 [PMID:18815255]
4. Atlason PT, Scholefield CL, Eaves RJ, Mayo-Martin MB, Jane DE and Molnár E. (2010) Mapping the ligand binding sites of kainate receptors: molecular determinants of subunit-selective binding of the antagonist [3H]UBP310. *Mol. Pharmacol.* **78**: 1036-45 [PMID:20837679]
5. Auberson YP, Allgeier H, Bischoff S, Lingenhoehl K, Moretti R and Schmutz M. (2002) 5-Phosphonomethylquinolalinediones as competitive NMDA receptor antagonists with a preference for the human 1A/2A, rather than 1A/2B receptor composition. *Bioorg. Med. Chem. Lett.* **12**: 1099-102 [PMID:11909726]
6. Bassani S, Valnegri P, Beretta F and Passafaro M. (2009) The GLUR2 subunit of AMPA receptors: synaptic role. *Neuroscience* **158**: 55-61 [PMID:18977416]
7. Beneyto M, Kristiansen LV, Oni-Orisan A, McCullumsmith RE and Meador-Woodruff JH. (2007) Abnormal glutamate receptor expression in the medial temporal lobe in schizophrenia and mood disorders. *Neuropsychopharmacology* **32**: 1888-902 [PMID:17299517]
8. Bettini E, Sava A, Griffante C, Carignani C, Buson A, Capelli AM, Negri M, Andreetta F, Senar-Sancho SA and Guiral L *et al.*. (2010) Identification and characterization of novel NMDA receptor antagonists selective for NR2A- over NR2B-containing receptors. *J. Pharmacol. Exp. Ther.* **335**: 636-44 [PMID:20810618]
9. Bochet P, Audinat E, Lambolez B, Crépel F, Rossier J, Iino M, Tsuzuki K and Ozawa S. (1994) Subunit composition at the single-cell level explains functional properties of a glutamate-gated channel. *Neuron* **12**: 383-8 [PMID:7509161]
10. Boulter J, Hollmann M, O'Shea-Greenfield A, Hartley M, Deneris E, Maron C and Heinemann S. (1990) Molecular cloning and functional expression of glutamate receptor subunit genes. *Science* **249**: 1033-7 [PMID:2168579]
11. Bowie D. (2010) Ion-dependent gating of kainate receptors. *J. Physiol. (Lond.)* **588**: 67-81 [PMID:19822544]
12. Brand-Schieber E, Lowery SL and Werner P. (2004) Select ionotropic glutamate AMPA/kainate receptors are expressed at the astrocyte-vessel interface. *Brain Res.* **1007**: 178-82 [PMID:15064149]
13. Brand-Schieber E and Werner P. (2003) (+/-)-Alpha-amino-3-hydroxy-5-methylisoxazole-4-propionic acid and kainate receptor subunit expression in mouse versus rat spinal cord white matter: similarities in astrocytes but differences in oligodendrocytes. *Neurosci. Lett.* **345**: 126-30 [PMID:12821187]
14. Brand-Schieber E and Werner P. (2003) AMPA/kainate receptors in mouse spinal cord cell-specific display of receptor subunits by oligodendrocytes and astrocytes and at the nodes of Ranvier. *Glia* **42**: 12-24 [PMID:12594733]
15. Brusa R, Zimmermann F, Koh DS, Feldmeyer D, Gass P, Seeburg PH and Sprengel R. (1995) Early-onset epilepsy and postnatal lethality associated with an editing-deficient GluR-B allele in mice. *Science* **270**: 1677-80 [PMID:7502080]
16. Burnashev N, Monyer H, Seeburg PH and Sakmann B. (1992) Divalent ion permeability of AMPA receptor channels is dominated by the edited form of a single subunit. *Neuron* **8**: 189-98 [PMID:1370372]
17. Caicedo A, Zucchi B, Pereira E and Roper SD. (2004) Rat gustatory neurons in the geniculate ganglion express glutamate receptor subunits. *Chem. Senses* **29**: 463-71 [PMID:15269118]
18. Cantrell BE, Zimmerman DM, Monn JA, Kamboj RK, Hoo KH, Tizzano JP, Pullar IA, Farrell LN and Bleakman D. (1996) Synthesis of a series of aryl kainic acid analogs and evaluation in cells stably expressing the kainate receptor humGluR6. *J. Med. Chem.* **39**: 3617-24 [PMID:8809152]
19. Cavara NA and Hollmann M. (2008) Shuffling the deck anew: how NR3 tweaks NMDA receptor function.

- Mol. Neurobiol.* **38**: 16-26 [PMID:18654865]
20. Chatterton JE, Awobuluyi M, Premkumar LS, Takahashi H, Talantova M, Shin Y, Cui J, Tu S, Sevarino KA and Nakanishi N *et al.*. (2002) Excitatory glycine receptors containing the NR3 family of NMDA receptor subunits. *Nature* **415**: 793-8 [PMID:11823786]
 21. Chazot PL, Reiss C, Chopra B and Stephenson FA. (1998) [3H]MDL 105,519 binds with equal high affinity to both assembled and unassembled NR1 subunits of the NMDA receptor. *Eur. J. Pharmacol.* **353**: 137-40 [PMID:9721050]
 22. Chen LW, Tse YC, Li C, Guan ZL, Lai CH, Yung KK, Shum DK and Chan YS. (2006) Differential expression of NMDA and AMPA/KA receptor subunits in the inferior olive of postnatal rats. *Brain Res.* **1067**: 103-14 [PMID:16376317]
 23. Chen PE, Geballe MT, Katz E, Erreger K, Livesey MR, O'Toole KK, Le P, Lee CJ, Snyder JP and Traynelis SF *et al.*. (2008) Modulation of glycine potency in rat recombinant NMDA receptors containing chimeric NR2A/2D subunits expressed in *Xenopus laevis* oocytes. *J. Physiol. (Lond.)* **586**: 227-45 [PMID:17962328]
 24. Chen PE and Wyllie DJ. (2006) Pharmacological insights obtained from structure-function studies of ionotropic glutamate receptors. *Br. J. Pharmacol.* **147**: 839-53 [PMID:16474411]
 25. Chopra B, Chazot PL and Stephenson FA. (2000) Characterization of the binding of two novel glycine site antagonists to cloned NMDA receptors: evidence for two pharmacological classes of antagonists. *Br. J. Pharmacol.* **130**: 65-72 [PMID:10780999]
 26. Chun YH, Frank D, Lee JS, Zhang Y, Auh QS and Ro JY. (2008) Peripheral AMPA receptors contribute to muscle nociception and c-fos activation. *Neurosci. Res.* **62**: 97-104 [PMID:18655811]
 27. Collingridge GL, Olsen RW, Peters J and Spedding M. (2009) A nomenclature for ligand-gated ion channels. *Neuropharmacology* **56**: 2-5 [PMID:18655795]
 28. Corbett EK, Saha S, Deuchars J, McWilliam PN and Batten TF. (2003) Ionotropic glutamate receptor subunit immunoreactivity of vagal preganglionic neurones projecting to the rat heart. *Auton Neurosci* **105**: 105-17 [PMID:12798207]
 29. Cull-Candy S, Kelly L and Farrant M. (2006) Regulation of Ca²⁺-permeable AMPA receptors: synaptic plasticity and beyond. *Curr. Opin. Neurobiol.* **16**: 288-97 [PMID:16713244]
 30. Cull-Candy SG and Leszkiewicz DN. (2004) Role of distinct NMDA receptor subtypes at central synapses. *Sci. STKE* **2004**: re16 [PMID:15494561]
 31. Deng YP, Xie JP, Wang HB, Lei WL, Chen Q and Reiner A. (2007) Differential localization of the GluR1 and GluR2 subunits of the AMPA-type glutamate receptor among striatal neuron types in rats. *J. Chem. Neuroanat.* **33**: 167-92 [PMID:17446041]
 32. Deur C, Agrawal AK, Baum H, Booth J, Bove S, Brieland J, Bunker A, Connolly C, Cornicelli J and Dumin J *et al.*. (2007) N-(6,7-dichloro-2,3-dioxo-1,2,3,4-tetrahydroquinoxalin-5-yl)-N-alkylsulfonamides as peripherally restricted N-methyl-D-aspartate receptor antagonists for the treatment of pain. *Bioorg. Med. Chem. Lett.* **17**: 4599-603 [PMID:17562362]
 33. Dijk F and Kamphuis W. (2004) Ischemia-induced alterations of AMPA-type glutamate receptor subunit. Expression patterns in the rat retina--an immunocytochemical study. *Brain Res.* **997**: 207-21 [PMID:14706873]
 34. Dingledine R, Borges K, Bowie D and Traynelis SF. (1999) The glutamate receptor ion channels. *Pharmacol. Rev.* **51**: 7-61 [PMID:10049997]
 35. Douyard J, Shen L, Haganir RL and Rubio ME. (2007) Differential neuronal and glial expression of GluR1 AMPA receptor subunit and the scaffolding proteins SAP97 and 4.1N during rat cerebellar development. *J. Comp. Neurol.* **502**: 141-56 [PMID:17335044]
 36. Dracheva S, Byne W, Chin B and Haroutunian V. (2008) Ionotropic glutamate receptor mRNA expression in the human thalamus: absence of change in schizophrenia. *Brain Res.* **1214**: 23-34 [PMID:18462708]
 37. Dracheva S, McGurk SR and Haroutunian V. (2005) mRNA expression of AMPA receptors and AMPA receptor binding proteins in the cerebral cortex of elderly schizophrenics. *J. Neurosci. Res.* **79**: 868-78 [PMID:15696539]

38. Dravid SM, Erreger K, Yuan H, Nicholson K, Le P, Lyuboslavsky P, Almonte A, Murray E, Mosely C and Barber J *et al.*. (2007) Subunit-specific mechanisms and proton sensitivity of NMDA receptor channel block. *J. Physiol. (Lond.)* **581**: 107-28 [PMID:17303642]
39. Edman S, McKay S, Macdonald LJ, Samadi M, Livesey MR, Hardingham GE and Wyllie DJ. (2012) TCN 201 selectively blocks GluN2A-containing NMDARs in a GluN1 co-agonist dependent but non-competitive manner. *Neuropharmacology* **63**: 441-9 [PMID:22579927]
40. Erreger K, Chen PE, Wyllie DJ and Traynelis SF. (2004) Glutamate receptor gating. *Crit Rev Neurobiol* **16**: 187-224 [PMID:15701057]
41. Erreger K, Geballe MT, Kristensen A, Chen PE, Hansen KB, Lee CJ, Yuan H, Le P, Lyuboslavsky PN and Micale N *et al.*. (2007) Subunit-specific agonist activity at NR2A-, NR2B-, NR2C-, and NR2D-containing N-methyl-D-aspartate glutamate receptors. *Mol. Pharmacol.* **72**: 907-20 [PMID:17622578]
42. Esteban JA. (2008) Intracellular machinery for the transport of AMPA receptors. *Br. J. Pharmacol.* **153 Suppl 1**: S35-43 [PMID:18026130]
43. Feng B, Tse HW, Skifter DA, Morley R, Jane DE and Monaghan DT. (2004) Structure-activity analysis of a novel NR2C/NR2D-preferring NMDA receptor antagonist: 1-(phenanthrene-2-carbonyl) piperazine-2,3-dicarboxylic acid. *Br. J. Pharmacol.* **141**: 508-16 [PMID:14718249]
44. Fletcher EJ, Nutt SL, Hoo KH, Elliott CE, Korczak B, McWhinnie EA and Kamboj RK. (1995) Cloning, expression and pharmacological characterization of a human glutamate receptor: hGluR4. *Recept. Channels* **3**: 21-31 [PMID:8589990]
45. Frizelle PA, Chen PE and Wyllie DJ. (2006) Equilibrium constants for (R)-[(S)-1-(4-bromo-phenyl)-ethylamino]-(2,3-dioxo-1,2,3,4-tetrahydroquinoxalin-5-yl)-methyl]-phosphonic acid (NVP-AAM077) acting at recombinant NR1/NR2A and NR1/NR2B N-methyl-D-aspartate receptors: Implications for studies of synaptic transmission. *Mol. Pharmacol.* **70**: 1022-32 [PMID:16778008]
46. Fujiyama F, Kuramoto E, Okamoto K, Hioki H, Furuta T, Zhou L, Nomura S and Kaneko T. (2004) Presynaptic localization of an AMPA-type glutamate receptor in corticostriatal and thalamostriatal axon terminals. *Eur. J. Neurosci.* **20**: 3322-30 [PMID:15610164]
47. Furukawa H, Singh SK, Mancusso R and Gouaux E. (2005) Subunit arrangement and function in NMDA receptors. *Nature* **438**: 185-92 [PMID:16281028]
48. Fux CM, Krug M, Dityatev A, Schuster T and Schachner M. (2003) NCAM180 and glutamate receptor subtypes in potentiated spine synapses: an immunogold electron microscopic study. *Mol. Cell. Neurosci.* **24**: 939-50 [PMID:14697660]
49. Gallo V, Upson LM, Hayes WP, Vyklicky L, Winters CA and Buonanno A. (1992) Molecular cloning and development analysis of a new glutamate receptor subunit isoform in cerebellum. *J. Neurosci.* **12**: 1010-23 [PMID:1372042]
50. Gielen M, Siegler Retchless B, Mony L, Johnson JW and Paoletti P. (2009) Mechanism of differential control of NMDA receptor activity by NR2 subunits. *Nature* **459**: 703-7 [PMID:19404260]
51. Greger IH, Khatri L, Kong X and Ziff EB. (2003) AMPA receptor tetramerization is mediated by Q/R editing. *Neuron* **40**: 763-74 [PMID:14622580]
52. Gryder DS, Castaneda DC and Rogawski MA. (2005) Evidence for low GluR2 AMPA receptor subunit expression at synapses in the rat basolateral amygdala. *J. Neurochem.* **94**: 1728-38 [PMID:16045445]
53. Hansen KB, Ogden KK and Traynelis SF. (2012) Subunit-selective allosteric inhibition of glycine binding to NMDA receptors. *J. Neurosci.* **32**: 6197-208 [PMID:22553026]
54. Hansen KB and Traynelis SF. (2011) Structural and mechanistic determinants of a novel site for noncompetitive inhibition of GluN2D-containing NMDA receptors. *J. Neurosci.* **31**: 3650-61 [PMID:21389220]
55. Henson MA, Roberts AC, Pérez-Otaño I and Philpot BD. (2010) Influence of the NR3A subunit on NMDA receptor functions. *Prog. Neurobiol.* **91**: 23-37 [PMID:20097255]
56. Hollmann M, Hartley M and Heinemann S. (1991) Ca²⁺ permeability of KA-AMPA-gated glutamate receptor channels depends on subunit composition. *Science* **252**: 851-3 [PMID:1709304]
57. Hollmann M, O'Shea-Greenfield A, Rogers SW and Heinemann S. (1989) Cloning by functional

- expression of a member of the glutamate receptor family. *Nature* **342**: 643-8 [PMID:2480522]
58. Horak M, Vlcek K, Choudounska H and Vyklicky L. (2006) Subtype-dependence of N-methyl-D-aspartate receptor modulation by pregnenolone sulfate. *Neuroscience* **137**: 93-102 [PMID:16257494]
 59. Horning MS, Kwon B, Blakemore LJ, Spencer CM, Goltz M, Houpt TA and Trombley PQ. (2004) Alpha-amino-3-hydroxy-5-methyl-4-isoxazolepropionate receptor subunit expression in rat olfactory bulb. *Neurosci. Lett.* **372**: 230-4 [PMID:15542246]
 60. Hume RI, Dingledine R and Heinemann SF. (1991) Identification of a site in glutamate receptor subunits that controls calcium permeability. *Science* **253**: 1028-31 [PMID:1653450]
 61. Iino M, Koike M, Isa T and Ozawa S. (1996) Voltage-dependent blockage of Ca²⁺-permeable AMPA receptors by joro spider toxin in cultured rat hippocampal neurones. *J. Physiol. (Lond.)* **496 (Pt 2)**: 431-7 [PMID:8910227]
 62. Isaac JT, Ashby M and McBain CJ. (2007) The role of the GluR2 subunit in AMPA receptor function and synaptic plasticity. *Neuron* **54**: 859-71 [PMID:17582328]
 63. Jackson AC and Nicoll RA. (2011) The expanding social network of ionotropic glutamate receptors: TARPs and other transmembrane auxiliary subunits. *Neuron* **70**: 178-99 [PMID:21521608]
 64. Jane DE, Lodge D and Collingridge GL. (2009) Kainate receptors: pharmacology, function and therapeutic potential. *Neuropharmacology* **56**: 90-113 [PMID:18793656]
 65. Jane DE, Tse H-W, Skifter DA, Christie JM and Monaghan DT. (2000) Glutamate receptor ion channels: activators and inhibitors. In *Handbook of Experimental Pharmacology, Pharmacology of Ionic Channel Function: Activators and Inhibitors* Edited by Endo M, Kurachi Y, Mishina M: Springer: 415-478
 66. Kaczor AA and Matosiuk D. (2010) Molecular structure of ionotropic glutamate receptors. *Curr. Med. Chem.* **17**: 2608-35 [PMID:20491632]
 67. Kamphuis W, Klooster J and Dijk F. (2003) Expression of AMPA-type glutamate receptor subunit (GluR2) in ON-bipolar neurons in the rat retina. *J. Comp. Neurol.* **455**: 172-86 [PMID:12454983]
 68. Karakas E and Furukawa H. (2014) Crystal structure of a heterotetrameric NMDA receptor ion channel. *Science* **344**: 992-7 [PMID:24876489]
 69. Karakas E, Simorowski N and Furukawa H. (2011) Subunit arrangement and phenylethanolamine binding in GluN1/GluN2B NMDA receptors. *Nature* **475**: 249-53 [PMID:21677647]
 70. Kaur C, Sivakumar V and Ling EA. (2005) Expression of N-methyl-D-aspartate (NMDA) and alpha-amino-3-hydroxy-5-methyl-4-isoxazolepropionate (AMPA) GluR2/3 receptors in the developing rat pineal gland. *J. Pineal Res.* **39**: 294-301 [PMID:16150111]
 71. Kawahara Y, Kwak S, Sun H, Ito K, Hashida H, Aizawa H, Jeong SY and Kanazawa I. (2003) Human spinal motoneurons express low relative abundance of GluR2 mRNA: an implication for excitotoxicity in ALS. *J. Neurochem.* **85**: 680-9 [PMID:12694394]
 72. Keinänen K, Wisden W, Sommer B, Werner P, Herb A, Verdoorn TA, Sakmann B and Seeburg PH. (1990) A family of AMPA-selective glutamate receptors. *Science* **249**: 556-60 [PMID:2166337]
 73. Kew JN and Kemp JA. (2005) Ionotropic and metabotropic glutamate receptor structure and pharmacology. *Psychopharmacology (Berl.)* **179**: 4-29 [PMID:15731895]
 74. Kim M, Chiego DJ and Bradley RM. (2008) Ionotropic glutamate receptor expression in preganglionic neurons of the rat inferior salivatory nucleus. *Auton Neurosci* **138**: 83-90 [PMID:18096442]
 75. Koike M, Tsukada S, Tsuzuki K, Kijima H and Ozawa S. (2000) Regulation of kinetic properties of GluR2 AMPA receptor channels by alternative splicing. *J. Neurosci.* **20**: 2166-74 [PMID:10704491]
 76. Kulagowski JJ, Baker R, Curtis NR, Leeson PD, Mawer IM, Moseley AM, Ridgill MP, Rowley M, Stansfield I and Foster AC *et al.* (1994) 3'-(Arylmethyl)- and 3'-(aryloxy)-3-phenyl-4-hydroxyquinolin-2(1H)-ones: orally active antagonists of the glycine site on the NMDA receptor. *J. Med. Chem.* **37**: 1402-5 [PMID:8182696]
 77. Kumar J and Mayer ML. (2013) Functional insights from glutamate receptor ion channel structures. *Annu. Rev. Physiol.* **75**: 313-37 [PMID:22974439]
 78. Kuner T and Schoepfer R. (1996) Multiple structural elements determine subunit specificity of Mg²⁺ block in NMDA receptor channels. *J. Neurosci.* **16**: 3549-58 [PMID:8642401]

79. Köhler M, Kornau HC and Seeburg PH. (1994) The organization of the gene for the functionally dominant alpha-amino-3-hydroxy-5-methylisoxazole-4-propionic acid receptor subunit GluR-B. *J. Biol. Chem.* **269**: 17367-70 [PMID:7545935]
80. Lachamp P, Balland B, Tell F, Crest M and Kessler JP. (2003) Synaptic localization of the glutamate receptor subunit GluR2 in the rat nucleus tractus solitarii. *Eur. J. Neurosci.* **17**: 892-6 [PMID:12603280]
81. Leeson PD, Carling RW, Moore KW, Moseley AM, Smith JD, Stevenson G, Chan T, Baker R, Foster AC and Grimwood S *et al.*. (1992) 4-Amido-2-carboxytetrahydroquinolines. Structure-activity relationships for antagonism at the glycine site of the NMDA receptor. *J. Med. Chem.* **35**: 1954-68 [PMID:1534584]
82. Lerma J. (2006) Kainate receptor physiology. *Curr Opin Pharmacol* **6**: 89-97 [PMID:16361114]
83. Lerma J. (2011) Net(o) excitement for kainate receptors. *Nat. Neurosci.* **14**: 808-10 [PMID:21709676]
84. Linja MJ and Visakorpi T. (2004) Alterations of androgen receptor in prostate cancer. *J. Steroid Biochem. Mol. Biol.* **92**: 255-64 [PMID:15663988]
85. Liu Q and Wong-Riley MT. (2005) Postnatal developmental expressions of neurotransmitters and receptors in various brain stem nuclei of rats. *J. Appl. Physiol.* **98**: 1442-57 [PMID:15618314]
86. Liu SJ and Zukin RS. (2007) Ca²⁺-permeable AMPA receptors in synaptic plasticity and neuronal death. *Trends Neurosci.* **30**: 126-34 [PMID:17275103]
87. Lodge D. (2009) The history of the pharmacology and cloning of ionotropic glutamate receptors and the development of idiosyncratic nomenclature. *Neuropharmacology* **56**: 6-21 [PMID:18765242]
88. Lomeli H, Mosbacher J, Melcher T, Höger T, Geiger JR, Kuner T, Monyer H, Higuchi M, Bach A and Seeburg PH. (1994) Control of kinetic properties of AMPA receptor channels by nuclear RNA editing. *Science* **266**: 1709-13 [PMID:7992055]
89. Lu CR, Hwang SJ, Phend KD, Rustioni A and Valtchanoff JG. (2002) Primary afferent terminals in spinal cord express presynaptic AMPA receptors. *J. Neurosci.* **22**: 9522-9 [PMID:12417676]
90. Lu CR, Willcockson HH, Phend KD, Lucifora S, Darstein M, Valtchanoff JG and Rustioni A. (2005) Ionotropic glutamate receptors are expressed in GABAergic terminals in the rat superficial dorsal horn. *J. Comp. Neurol.* **486**: 169-78 [PMID:15844209]
91. Madry C, Betz H, Geiger JR and Laube B. (2008) Supralinear potentiation of NR1/NR3A excitatory glycine receptors by Zn²⁺ and NR1 antagonist. *Proc. Natl. Acad. Sci. U.S.A.* **105**: 12563-8 [PMID:18711142]
92. Malayev A, Gibbs TT and Farb DH. (2002) Inhibition of the NMDA response by pregnenolone sulphate reveals subtype selective modulation of NMDA receptors by sulphated steroids. *Br. J. Pharmacol.* **135**: 901-9 [PMID:11861317]
93. Martínez L, Nascimento AS, Nunes FM, Phillips K, Aparicio R, Dias SM, Figueira AC, Lin JH, Nguyen P, Apriletti JW, Neves FA, Baxter JD, Webb P, Skaf MS and Polikarpov I. (2009) Gaining ligand selectivity in thyroid hormone receptors via entropy. *Proc. Natl. Acad. Sci. U.S.A.* [PMID:19926848]
94. Mayer ML. (2006) Glutamate receptors at atomic resolution. *Nature* **440**: 456-62 [PMID:16554805]
95. McKay S, Griffiths NH, Butters PA, Thubron EB, Hardingham GE and Wyllie DJ. (2012) Direct pharmacological monitoring of the developmental switch in NMDA receptor subunit composition using TCN 213, a GluN2A-selective, glycine-dependent antagonist. *Br. J. Pharmacol.* **166**: 924-37 [PMID:22022974]
96. McNamara JO, Eubanks JH, McPherson JD, Wasmuth JJ, Evans GA and Heinemann SF. (1992) Chromosomal localization of human glutamate receptor genes. *J. Neurosci.* **12**: 2555-62 [PMID:1319477]
97. Meyerson JR, Kumar J, Chittori S, Rao P, Pierson J, Bartesaghi A, Mayer ML and Subramaniam S. (2014) Structural mechanism of glutamate receptor activation and desensitization. *Nature* **514**: 328-34 [PMID:25119039]
98. Milstein AD and Nicoll RA. (2008) Regulation of AMPA receptor gating and pharmacology by TARP auxiliary subunits. *Trends Pharmacol. Sci.* **29**: 333-9 [PMID:18514334]
99. Miu P, Jarvie KR, Radhakrishnan V, Gates MR, Ogden A, Ornstein PL, Zarrinmayeh H, Ho K, Peters D and Grabell J *et al.*. (2001) Novel AMPA receptor potentiators LY392098 and LY404187: effects on recombinant human AMPA receptors in vitro. *Neuropharmacology* **40**: 976-83 [PMID:11406188]
100. Morley RM, Tse HW, Feng B, Miller JC, Monaghan DT and Jane DE. (2005) Synthesis and pharmacology of N1-substituted piperazine-2,3-dicarboxylic acid derivatives acting as NMDA receptor antagonists. *J.*

- Med. Chem.* **48**: 2627-37 [PMID:15801853]
101. Mosbacher J, Schoepfer R, Monyer H, Burnashev N, Seeburg PH and Ruppertsberg JP. (1994) A molecular determinant for submillisecond desensitization in glutamate receptors. *Science* **266**: 1059-62 [PMID:7973663]
 102. Nakagawa T. (2010) The biochemistry, ultrastructure, and subunit assembly mechanism of AMPA receptors. *Mol. Neurobiol.* **42**: 161-84 [PMID:21080238]
 103. Nakanishi N, Shneider NA and Axel R. (1990) A family of glutamate receptor genes: evidence for the formation of heteromultimeric receptors with distinct channel properties. *Neuron* **5**: 569-81 [PMID:1699567]
 104. Naur P, Hansen KB, Kristensen AS, Dravid SM, Pickering DS, Olsen L, Vestergaard B, Egebjerg J, Gajhede M and Traynelis SF *et al.*. (2007) Ionotropic glutamate-like receptor delta2 binds D-serine and glycine. *Proc. Natl. Acad. Sci. U.S.A.* **104**: 14116-21 [PMID:17715062]
 105. Neyton J and Paoletti P. (2006) Relating NMDA receptor function to receptor subunit composition: limitations of the pharmacological approach. *J. Neurosci.* **26**: 1331-3 [PMID:16452656]
 106. Paoletti P. (2011) Molecular basis of NMDA receptor functional diversity. *Eur. J. Neurosci.* **33**: 1351-65 [PMID:21395862]
 107. Paoletti P, Bellone C and Zhou Q. (2013) NMDA receptor subunit diversity: impact on receptor properties, synaptic plasticity and disease. *Nat. Rev. Neurosci.* **14**: 383-400 [PMID:23686171]
 108. Paoletti P and Neyton J. (2007) NMDA receptor subunits: function and pharmacology. *Curr Opin Pharmacol* **7**: 39-47 [PMID:17088105]
 109. Peddie CJ, Davies HA, Colyer FM, Stewart MG and Rodríguez JJ. (2008) Colocalisation of serotonin2A receptors with the glutamate receptor subunits NR1 and GluR2 in the dentate gyrus: an ultrastructural study of a modulatory role. *Exp. Neurol.* **211**: 561-73 [PMID:18439999]
 110. Pedregal C, Collado I, Escribano A, Ezquerra J, Domínguez C, Mateo AI, Rubio A, Baker SR, Goldsworthy J and Kamboj RK *et al.*. (2000) 4-Alkyl- and 4-cinnamylglutamic acid analogues are potent GluR5 kainate receptor agonists. *J. Med. Chem.* **43**: 1958-68 [PMID:10821708]
 111. Perrais D, Pinheiro PS, Jane DE and Mulle C. (2009) Antagonism of recombinant and native GluK3-containing kainate receptors. *Neuropharmacology* **56**: 131-40 [PMID:18761361]
 112. Perrais D, Veran J and Mulle C. (2010) Gating and permeation of kainate receptors: differences unveiled. *Trends Pharmacol. Sci.* **31**: 516-22 [PMID:20850188]
 113. Pinheiro P and Mulle C. (2006) Kainate receptors. *Cell Tissue Res.* **326**: 457-82 [PMID:16847640]
 114. Plested AJ. (2011) Kainate receptor modulation by sodium and chloride. *Adv. Exp. Med. Biol.* **717**: 93-113 [PMID:21713670]
 115. Polgár E, Watanabe M, Hartmann B, Grant SG and Todd AJ. (2008) Expression of AMPA receptor subunits at synapses in laminae I-III of the rodent spinal dorsal horn. *Mol Pain* **4**: 5 [PMID:18215271]
 116. Potier MC, Spillantini MG and Carter NP. (1992) The human glutamate receptor cDNA GluR1: cloning, sequencing, expression and localization to chromosome 5. *DNA Seq.* **2**: 211-8 [PMID:1320959]
 117. Puckett C, Gomez CM, Korenberg JR, Tung H, Meier TJ, Chen XN and Hood L. (1991) Molecular cloning and chromosomal localization of one of the human glutamate receptor genes. *Proc. Natl. Acad. Sci. U.S.A.* **88**: 7557-61 [PMID:1652753]
 118. Puyal J, Sage C, Demêmes D and Dechesne CJ. (2002) Distribution of alpha-amino-3-hydroxy-5-methyl-4-isoazolepropionic acid and N-methyl-D-aspartate receptor subunits in the vestibular and spiral ganglia of the mouse during early development. *Brain Res. Dev. Brain Res.* **139**: 51-7 [PMID:12414093]
 119. Radley JJ, Farb CR, He Y, Janssen WG, Rodrigues SM, Johnson LR, Hof PR, LeDoux JE and Morrison JH. (2007) Distribution of NMDA and AMPA receptor subunits at thalamo-amygdaloid dendritic spines. *Brain Res.* **1134**: 87-94 [PMID:17207780]
 120. Ragnarson B, Ornung G, Grant G, Ottersen OP and Ulfhake B. (2003) Glutamate and AMPA receptor immunoreactivity in Ia synapses with motoneurons and neurons of the central cervical nucleus. *Exp Brain Res* **149**: 447-57 [PMID:12677325]
 121. Rampersad V, Elliott CE, Nutt SL, Foldes RL and Kamboj RK. (1994) Human glutamate receptor hGluR3 flip and flop isoforms: cloning and sequencing of the cDNAs and primary structure of the proteins. *Biochim.*

- Biophys. Acta* **1219**: 563-6 [PMID:7918660]
122. Ritter LM, Vazquez DM and Meador-Woodruff JH. (2002) Ontogeny of ionotropic glutamate receptor subunit expression in the rat hippocampus. *Brain Res. Dev. Brain Res.* **139**: 227-36 [PMID:12480137]
 123. Rodríguez-Moreno A and Sihra TS. (2007) Kainate receptors with a metabotropic modus operandi. *Trends Neurosci.* **30**: 630-7 [PMID:17981346]
 124. Rubio ME. (2006) Redistribution of synaptic AMPA receptors at glutamatergic synapses in the dorsal cochlear nucleus as an early response to cochlear ablation in rats. *Hear. Res.* **216-217**: 154-67 [PMID:16644159]
 125. Sagot E, Pickering DS, Pu X, Umberti M, Stensbøl TB, Nielsen B, Chapelet M, Bolte J, Gefflaut T and Bunch L. (2008) Chemo-enzymatic synthesis of a series of 2,4-syn-functionalized (S)-glutamate analogues: new insight into the structure-activity relation of ionotropic glutamate receptor subtypes 5, 6, and 7. *J. Med. Chem.* **51**: 4093-103 [PMID:18578478]
 126. Sakai R, Swanson GT, Shimamoto K, Green T, Contractor A, Ghetti A, Tamura-Horikawa Y, Oiwa C and Kamiya H. (2001) Pharmacological properties of the potent epileptogenic amino acid dysiherbaine, a novel glutamate receptor agonist isolated from the marine sponge *Dysidea herbacea*. *J. Pharmacol. Exp. Ther.* **296**: 650-8 [PMID:11160654]
 127. Sakimura K, Bujo H, Kushiya E, Araki K, Yamazaki M, Yamazaki M, Meguro H, Warashina A, Numa S and Mishina M. (1990) Functional expression from cloned cDNAs of glutamate receptor species responsive to kainate and quisqualate. *FEBS Lett.* **272**: 73-80 [PMID:1699805]
 128. Sakimura K, Morita T, Kushiya E and Mishina M. (1992) Primary structure and expression of the gamma 2 subunit of the glutamate receptor channel selective for kainate. *Neuron* **8**: 267-74 [PMID:1310861]
 129. Santiago AR, Hughes JM, Kamphuis W, Schlingemann RO and Ambrósio AF. (2008) Diabetes changes ionotropic glutamate receptor subunit expression level in the human retina. *Brain Res.* **1198**: 153-9 [PMID:18258217]
 130. Schauwecker PE. (2003) Differences in ionotropic glutamate receptor subunit expression are not responsible for strain-dependent susceptibility to excitotoxin-induced injury. *Brain Res. Mol. Brain Res.* **112**: 70-81 [PMID:12670704]
 131. Seeburg PH and Hartner J. (2003) Regulation of ion channel/neurotransmitter receptor function by RNA editing. *Curr. Opin. Neurobiol.* **13**: 279-83 [PMID:12850211]
 132. Semkova I, Huemmeke M, Ho MS, Merkl B, Abari E, Paulsson M, Jousen AM and Plomann M. (2010) Retinal localization of the glutamate receptor GluR2 and GluR2-regulating proteins in diabetic rats. *Exp. Eye Res.* **90**: 244-53 [PMID:19878674]
 133. Small B, Thomas J, Kemp M, Hoo K, Ballyk B, Deverill M, Ogden AM, Rubio A, Pedregal C and Bleakman D. (1998) LY339434, a GluR5 kainate receptor agonist. *Neuropharmacology* **37**: 1261-7 [PMID:9849663]
 134. Smothers CT and Woodward JJ. (2007) Pharmacological characterization of glycine-activated currents in HEK 293 cells expressing N-methyl-D-aspartate NR1 and NR3 subunits. *J. Pharmacol. Exp. Ther.* **322**: 739-48 [PMID:17502428]
 135. Sobolevsky AI, Rosconi MP and Gouaux E. (2009) X-ray structure, symmetry and mechanism of an AMPA-subtype glutamate receptor. *Nature* **462**: 745-56 [PMID:19946266]
 136. Sommer B, Keinänen K, Verdoorn TA, Wisden W, Burnashev N, Herb A, Köhler M, Takagi T, Sakmann B and Seeburg PH. (1990) Flip and flop: a cell-specific functional switch in glutamate-operated channels of the CNS. *Science* **249**: 1580-5 [PMID:1699275]
 137. Sommer B, Köhler M, Sprengel R and Seeburg PH. (1991) RNA editing in brain controls a determinant of ion flow in glutamate-gated channels. *Cell* **67**: 11-9 [PMID:1717158]
 138. Sun H, Kawahara Y, Ito K, Kanazawa I and Kwak S. (2005) Expression profile of AMPA receptor subunit mRNA in single adult rat brain and spinal cord neurons in situ. *Neurosci. Res.* **52**: 228-34 [PMID:15927724]
 139. Sun W, Ferrer-Montiel AV, Schinder AF, McPherson JP, Evans GA and Montal M. (1992) Molecular cloning, chromosomal mapping, and functional expression of human brain glutamate receptors. *Proc. Natl. Acad. Sci. U.S.A.* **89**: 1443-7 [PMID:1311100]
 140. Szczesniak AM, Gilbert RW, Mukhida M and Anderson GI. (2005) Mechanical loading modulates

- glutamate receptor subunit expression in bone. *Bone* **37**: 63-73 [PMID:15922681]
141. Talos DM, Fishman RE, Park H, Folkerth RD, Follett PL, Volpe JJ and Jensen FE. (2006) Developmental regulation of alpha-amino-3-hydroxy-5-methyl-4-isoxazole-propionic acid receptor subunit expression in forebrain and relationship to regional susceptibility to hypoxic/ischemic injury. I. Rodent cerebral white matter and cortex. *J. Comp. Neurol.* **497**: 42-60 [PMID:16680782]
 142. Talos DM, Follett PL, Folkerth RD, Fishman RE, Trachtenberg FL, Volpe JJ and Jensen FE. (2006) Developmental regulation of alpha-amino-3-hydroxy-5-methyl-4-isoxazole-propionic acid receptor subunit expression in forebrain and relationship to regional susceptibility to hypoxic/ischemic injury. II. Human cerebral white matter and cortex. *J. Comp. Neurol.* **497**: 61-77 [PMID:16680761]
 143. Tan PH, Yang LC, Chiang PT, Jang JS, Chung HC and Kuo CH. (2008) Inflammation-induced up-regulation of ionotropic glutamate receptor expression in human skin. *Br J Anaesth* **100**: 380-4 [PMID:18238837]
 144. Todd AJ, Polgár E, Watt C, Bailey ME and Watanabe M. (2009) Neurokinin 1 receptor-expressing projection neurons in laminae III and IV of the rat spinal cord have synaptic AMPA receptors that contain GluR2, GluR3 and GluR4 subunits. *Eur. J. Neurosci.* **29**: 718-26 [PMID:19200070]
 145. Tomita S. (2010) Regulation of ionotropic glutamate receptors by their auxiliary subunits. *Physiology (Bethesda)* **25**: 41-9 [PMID:20134027]
 146. Traynelis SF, Burgess MF, Zheng F, Lyuboslavsky P and Powers JL. (1998) Control of voltage-independent zinc inhibition of NMDA receptors by the NR1 subunit. *J. Neurosci.* **18**: 6163-75 [PMID:9698310]
 147. Traynelis SF, Wollmuth LP, McBain CJ, Menniti FS, Vance KM, Ogden KK, Hansen KB, Yuan H, Myers SJ and Dingledine R. (2010) Glutamate receptor ion channels: structure, regulation, and function. *Pharmacol. Rev.* **62**: 405-96 [PMID:20716669]
 148. Tse YC, Lai CH, Lai SK, Liu JX, Yung KK, Shum DK and Chan YS. (2008) Developmental expression of NMDA and AMPA receptor subunits in vestibular nuclear neurons that encode gravity-related horizontal orientations. *J. Comp. Neurol.* **508**: 343-64 [PMID:18335497]
 149. Wang C and Niu L. (2013) Mechanism of inhibition of the GluA2 AMPA receptor channel opening by talampanel and its enantiomer: the stereochemistry of the 4-methyl group on the diazepine ring of 2,3-benzodiazepine derivatives. *ACS Chem Neurosci* **4**: 635-44 [PMID:23402301]
 150. Wang YQ, Hu HJ, Cao R and Chen LW. (2005) Differential co-localization of neurokinin-3 receptor and NMDA/AMPA receptor subunits in neurons of the substantia nigra of C57/BL mice. *Brain Res.* **1053**: 207-12 [PMID:16038885]
 151. Willcockson H and Valtschanoff J. (2008) AMPA and NMDA glutamate receptors are found in both peptidergic and non-peptidergic primary afferent neurons in the rat. *Cell Tissue Res.* **334**: 17-23 [PMID:18679721]
 152. Wyllie DJ, Livesey MR and Hardingham GE. (2013) Influence of GluN2 subunit identity on NMDA receptor function. *Neuropharmacology* **74**: 4-17 [PMID:23376022]
 153. Yoneyama M, Kitayama T, Taniura H and Yoneda Y. (2004) Immunohistochemical detection by immersion fixation with Carnoy solution of particular non-N-methyl-D-aspartate receptor subunits in murine hippocampus. *Neurochem. Int.* **44**: 413-22 [PMID:14687606]
 154. Yuzaki M. (2003) The delta2 glutamate receptor: 10 years later. *Neurosci. Res.* **46**: 11-22 [PMID:12725908]
 155. Zhang JP, Wei LC, Cao R and Chen LW. (2006) Differential co-expression of AMPA receptor subunits in substance P receptor-containing neurons of basal forebrain regions of C57/BL mice. *Neurochem. Int.* **49**: 319-26 [PMID:16580093]
 156. Zhou LM, Gu ZQ, Costa AM, Yamada KA, Mansson PE, Giordano T, Skolnick P and Jones KA. (1997) (2S,4R)-4-methylglutamic acid (SYM 2081): a selective, high-affinity ligand for kainate receptors. *J. Pharmacol. Exp. Ther.* **280**: 422-7 [PMID:8996224]