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CORRIGENDA

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C. L. Cleland, L. Hayward, and W. Z. Rymer, page 1319, the title of the article should read: "Neural Mechanisms Underlying the Clasp-Knife Reflex in the Cat. II. Stretch-Sensitive **Muscular Free Nerve Endings.**" The running head should read: "PROPERTIES OF MUSCULAR FREE NERVE ENDINGS."

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Excitatory Postsynaptic Potentials in Rat Neocortical Neurons In Vitro. III. Effects of a Quinoxalinedione Non-NMDA Receptor Antagonist

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SUMMARY AND CONCLUSIONS

1. Intracellular microelectrodes were used to obtain recordings from neurons in layer II/III of rat frontal cortex. A bipolar electrode positioned in layer IV of the neocortex was used to evoke postsynaptic potentials. Graded series of stimulation were employed to selectively activate different classes of postsynaptic responses. The sensitivity of postsynaptic potentials and iontophoretically applied neurotransmitters to the non-*N*-methyl-D-asparate (NMDA) antagonist 6-cyano-7-nitroquinoxaline-2,3-dione (CNQX) was examined.

2. As reported previously, low-intensity electrical stimulation of cortical layer IV evoked short-latency early excitatory postsynaptic potentials (eEPSPs) in layer II/III neurons. CNQX reversibly antagonized eEPSPs in a dose-dependent manner. Stimulation at intensities just subthreshold for activation of inhibitory postsynaptic potentials (IPSPs) produced long-latency (10 to 40-ms) EPSPs (late EPSPs or lEPSPs). CNQX was effective in blocking lEPSPs.

3. With the use of stimulus intensities at or just below threshold for evoking an action potential, complex synaptic potentials consisting of EPSP-IPSP sequences were observed. Both early, Cl^--dependent and late, K^+-dependent IPSPs were reduced by CNQX. This effect was reversible on washing. This disinhibition could lead to enhanced excitability in the presence of CNQX.

4. Iontophoretic application of quisqualate produced a membrane depolarization with superimposed action potentials, whereas NMDA depolarized the membrane potential and evoked bursts of action potentials. At concentrations up to 5 μM, CNQX selectively antagonized quisqualate responses. NMDA responses were reduced by 10 μM CNQX. D-Serine (0.5–2 mM), an agonist at the glycine regulatory site on the NMDA receptor, reversed the CNQX depression of NMDA responses.

5. These experiments provide evidence that CNQX, at appropriate concentrations, is a selective non-NMDA receptor antagonist in the neocortex. Non-NMDA receptors play an important role in both excitatory and inhibitory neurotransmission in the rat frontal neocortex.

INTRODUCTION

Excitatory amino acids (EAAs) are prominent neurotransmitter candidates in a variety of neocortical areas (Streit 1984). Glutamate and aspartate are accumulated by neocortical cells (Baughman and Gilbert 1981; Matute and Streit 1985), released on depolarization in a calcium-dependent manner (Baughman and Gilbert 1981), and excite cortical cells when exogenously applied (Krnjevic and Phillis 1963). Immunocytochemical studies have identified glutamate-positive neurons (Giuffrida and Rustioni 1989; Ottersen and Storm-Mathisen 1984) and glutamate-positive axon terminals forming asymmetric synapses in the neocortex (DeFelipe et al. 1988). Although the evidence pointing toward an EAA as a neurotransmitter in the neocortex is strong, the nature of the receptor mediating various types of synaptic responses is less clear. From electrophysiological and receptor binding studies, there appear to be at least three major EAA-receptor subtypes (Mayer and Westbrook 1988; Watkins and Evans 1981). Named after the specific agonists that bind to them, these are the kainate, quisqualate and *N*-methyl-D-aspartate (NMDA) receptors (Foster and Fagg 1984; Watkins and Evans 1981). NMDA receptor antagonists block certain synaptic responses in the neocortex, but the role of kainate and quisqualate receptors is unknown.

Complex synaptic responses have been observed in neocortical slices after stimulation of the white matter (Thomson 1986) or corpus callosum (Vogt and Gorman 1982). Our electrophysiological studies of layer II/III pyramidal neurons in the rat neocortex in vitro have demonstrated the existence of two types of excitatory postsynaptic potentials (EPSPs) (Sutor and Hablitz 1989a,b). Electrical stimulation of neuronal elements in layer IV at low intensities produces a short-latency EPSP (early EPSP or eEPSP); higher stimulus strengths evoke a delayed or late EPSP (lEPSP). The short latency and lack of decrement with increases in stimulus frequency suggest involvement of a monosynaptic pathway in generation of the eEPSP (Sutor and Hablitz 1989a,b). In contrast, lEPSPs fail completely at a stimulus rate of 1 Hz, suggesting a polysynaptic origin. The eEPSP was not affected by the NMDA receptor antagonist D-2-amino-5-phosphonovaleric acid (D-APV), whereas the lEPSP was effectively suppressed.

Investigations of inhibitory postsynaptic potentials (IPSPs) in the neocortex have shown that both early and late IPSPs are present (Connors et al. 1988; Howe et al. 1987). The early IPSP is a $GABA_A$-receptor–mediated, chloride-dependent event (Connors et al. 1988; Howe et al. 1987; Weiss and Hablitz 1984), whereas the late IPSP is potassium-dependent and thought to be mediated by $GABA_B$-receptors (Connors et al. 1988; Howe et al. 1987). The pathways responsible for IPSP generation are unclear but may involve activation of inhibitory interneurons by

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recurrent collaterals (Stefanis and Jasper 1964). Presumably synapses onto interneurons would involve an EAA neurotransmitter (Stone 1973).

An important question is the relative contribution of NMDA and non-NMDA receptors in generation of synaptic potentials in the neocortex. The availability of specific competitive antagonists for NMDA receptors has helped delineate the role of this receptor type in excitatory neurotransmission. An NMDA-receptor–mediated component of EPSPs in cortical neurons has been reported by several investigators (Fletcher et al. 1988; Jones and Baughman 1988; Sutor and Hablitz 1989a,b; Thomson 1986). Non-NMDA receptor–mediated synaptic potentials have not been well characterized because of the lack of potent and/or specific antagonists. The broad-spectrum antagonist kynurenic acid does, however, greatly reduce synaptic potentials in the neocortex (Jones and Baughman 1988), suggesting that an EAA receptor is involved. Development of quinoxalinediones as antagonists of kainate and quisqualate receptors (Honore et al. 1988) has provided an opportunity for further analysis of the role of non-NMDA receptors in the neocortex.

In this study we have examined the effect of the non-NMDA receptor antagonist 6-cyano-7-nitroquinoxaline-2,3-dione (CNQX) on synaptic potentials in layer II/III neocortical pyramidal neurons. The goal of these studies was to determine the effect of blocking non-NMDA receptors on the overall excitability of the complex synaptic network present in the cortex. We have found that both excitatory and inhibitory neurotransmission are reduced. The effect of CNQX on responses to iontophoretically applied EAAs was also examined to establish the selectivity of this compound in this preparation. At concentrations up to 5 μM, CNQX is a selective non-NMDA antagonist and at higher doses reduces NMDA responses via an effect at the glycine regulatory site.

METHODS

Neocortical slices were prepared from Sprague-Dawley rats (120–160 g) with the use of standard techniques (Sutor and Hablitz 1989a). Animals were decapitated under ether anesthesia. After rapid removal, the brain was placed in ice-cold saline and blocked for cutting on a Vibroslicer (Camden Instruments). Four to six coronal slices (500 μM thick) were taken from each hemisphere starting 1 mm caudal to the frontal pole and stored in oxygenated saline for 1 h at room temperature. Slices were then transferred to the recording chamber where they were continuously perfused with a saline containing (in mM) 125 NaCl, 3.5 KCl, 1.25 NaH_2PO_4, 2.5 $CaCl_2$, 1.3 $MgSO_4$, 25 $NaHCO_3$, and 10 glucose. The saline was gassed with a mixture of 95% O_2-5% CO_2; the pH was 7.4 at the maintained temperature of 33–35°C.

For electrophysiological studies, layer II/III neurons were impaled with glass microelectrodes filled with either 4 M potassium acetate or 3 M KCl. These electrodes had resistances of 40–90 MΩ. All recordings were made with the use of a single-electrode current- and voltage-clamp amplifier, as described previously (Sutor and Hablitz 1989a). Recordings were made in the current-clamp mode and stored on tape for subsequent computer analysis.

Synaptic potentials were evoked by means of a bipolar stimulating electrode placed in cortical layer IV, 0.5–1.0 mm lateral to the recording electrode. Graded series of stimulations were given in each neuron, and responses to hyperpolarizing and depolarizing current pulses (100 ms; 0.1–0.5 nA) were obtained. Similar measurements were made after bath application of CNQX (2–10 μM); each neuron served as its own control.

Responses to iontophoretically applied inhibitory and excitatory amino acid receptor agonists were examined before and after bath application of CNQX and D-serine (0.5–2 mM). Double-barreled iontophoresis electrodes were prepared from glass capillaries. The balance barrel contained 1 M NaCl, whereas the ejection barrel contained either NMDA (25 mM, pH 8), kainate (20 mM, pH 8), quisqualate (10 mM, pH 8), or γ-aminobutyric acid (GABA) (1 M, pH 4.5). In some experiments tetrodotoxin (TTX) was added to block sodium-dependent action potentials.

Intracellular injection of Lucifer yellow or horseradish peroxidase (HRP) was carried out in some cases to allow identification of the recorded cells. For Lucifer yellow, the electrodes were filled with a 5% solution of the dye in 1 M lithium chloride and had resistances of 70–120 MΩ. Hyperpolarizing current (150- to 300-ms pulses of 1–1.5 nA for 5–10 min) were used to eject the dye. Slices containing injected neurons were processed as described previously (Weiss and Hablitz 1984). HRP was injected from electrodes containing a 4% solution of the enzyme in 0.5 M KCl/Tris buffer (pH 7.6). The electrode resistance ranged between 160 and 250 MΩ. The injection was carried out with the use of 500- to 1,000-ms depolarizing current pulses (0.5–1 nA at 1–2 Hz for 30–45 min). After fixation in 1% paraformaldehyde and 1.25% glutaraldehyde, serial sections (50 μm) of the slices were made and reacted with diaminobenzidine. The neurons were visualized under a light microscope and camera lucida drawings made.

RESULTS

In several experiments neurons were intracellularly injected with HRP (n = 5) or Lucifer yellow (n = 4). As reported previously (Weiss and Hablitz 1984; Sutor and Zieglgansberger 1987), intracellular staining indicated that recordings were obtained exclusively from pyramidal-type neurons. Depolarizing current pulses elicited, in all neurons tested, repetitive action potentials with no sign of burst discharges. This behavior is typical of so-called regular spiking pyramidal cells (McCormick et al. 1985). The neurons recorded in this series of experiments had an average resting potential of −82 ± 3.7 (SD) mV and input resistance of 27 ± 10.8 MΩ (mean ± SD; n = 41). These parameters were not affected by application of 2–10 μM CNQX.

Effect of CNQX on EPSPs

As reported previously, the first response to stimulation of layer IV was a small, short-latency EPSP (Sutor and Hablitz 1989a). Examples of eEPSPs under control conditions are shown in Fig. 1, *A* and *D*. Such EPSPs were stable in amplitude and latency over time and were observed in all cells tested. Bath application of the non-NMDA antagonist CNQX produced a dose-dependent reduction in the amplitude of the eEPSP (Fig. 1, *B* and *E*). This effect was reversible on washing (Fig. 1*C*). Increasing the stimulus strength in the presence of CNQX could partially restore responses (Fig. 1*F*). The effect of CNQX was quantified by determining the percent decrease in eEPSP observed after drug exposure. The result of CNQX application was dose dependent producing 53, 80, and 84% decreases at concentrations of 1–3, 4–5, and 10 μM, respectively (n = 15, 8, and 5 for each concentration, respectively).

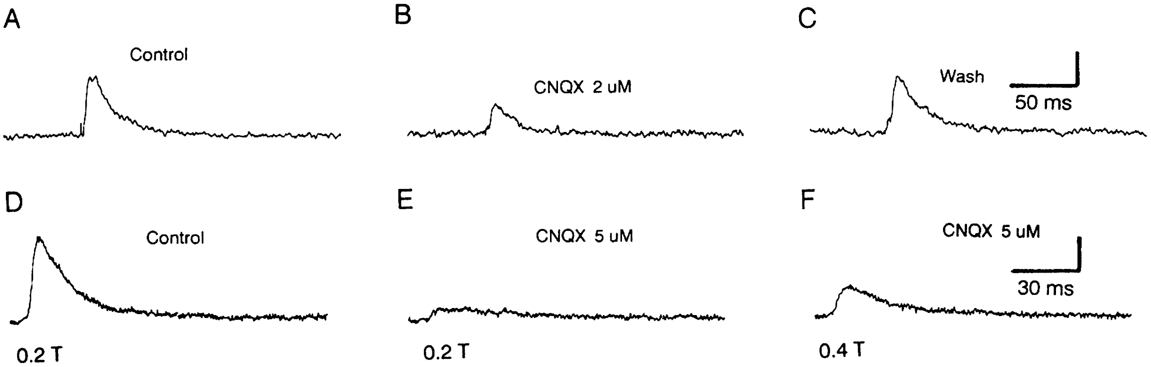

FIG. 1. Reduction of eEPSPs by the non-NMDA antagonist CNQX. *A*: control recording of an eEPSP in a layer II neuron in response to intracortical stimulation. *B*: response obtained 10 min after bath application of 2 μM CNQX. *C*: recovery of eEPSP after washout of CNQX. Resting membrane potential (RMP), −84 mV. *D*: eEPSP recorded in another neuron. Stimulus strength was 0.2 of threshold (T) value needed for evoking an action potential. *E*: marked reduction in eEPSP after exposure to 5 μM CNQX. *F*: increasing stimulus strength to 0.4 T results in increase in response amplitude. RMP = −80 mV. Vertical bar indicates 2 mV.

Higher stimulus intensities evoked, in addition to the eEPSP, a delayed or lEPSP. An example of a robust lEPSP is shown in Fig. 2*A*. The lEPSP was reversibly blocked by the NMDA receptor antagonist D-APV (10 μM) (Fig. 2, *B* and *C*) indicating involvement of NMDA receptors. Application of CNQX reduced the amplitude of the eEPSP (Fig. 2*D*) and abolished the lEPSP. Increasing the stimulus strength in the presence of CNQX did not restore the lEPSP (Fig. 2*E*) but did increase the amplitude of the eEPSP. When CNQX was removed, responses similar to those observed during control periods were recorded (Fig. 2*F*). Similar results were obtained in all neurons tested (*n* = 12). Given our findings that the NMDA receptors involved in generation of the lEPSP reside on interneurons making non-NMDA synapses onto pyramidal cells (Sutor and Hablitz 1989b), the lEPSP's sensitivity to both NMDA and non-NMDA antagonists is not unexpected.

Alterations in IPSPs

When stimulus intensities at, or just below, those needed for triggering an action potential are employed, complex synaptic potentials consisting of an EPSP-IPSP composite are evoked (Connors et al. 1988; Howe et al. 1987; Sutor and Hablitz 1989a). A typical example is shown in Fig. 3*A*. At the resting membrane potential (*middle* trace), there is an initial depolarizing potential that is rapidly terminated, a second depolarizing potential, and a final hyperpolarizing response. Depolarization of the cell via current passed through the microelectrode results in the appearance of an early hyperpolarization. Membrane hyperpolarization produces a large increase in amplitude of the peak depolarization and a decrease in the late hyperpolarization. Such recordings indicate that early IPSPs are depolarizing at rest in neocortical neurons, and the sensitivity to current injection suggests a somatic origin. After bath application of CNQX, it can be seen that synaptic potentials are reduced. Synaptic potentials at rest consist of a monophasic depolarization (Fig. 3*B*). In the presence of CNQX, alterations in membrane potential failed to reveal the presence of IPSPs. The enhanced synaptic response seen on depolarization in Fig. 3*B* is due to activation of voltage-dependent currents (Sutor and Hablitz 1989a,b). The amplitude of early and late IPSPs were measured at fixed latencies corresponding to the peak hyperpolarization observed at depolarized levels under control conditions. Measurements were then obtained at the same latency after CNQX exposure. Plots of measurements at the early time point versus membrane potential are shown in Fig. 3*C*. Under control conditions a

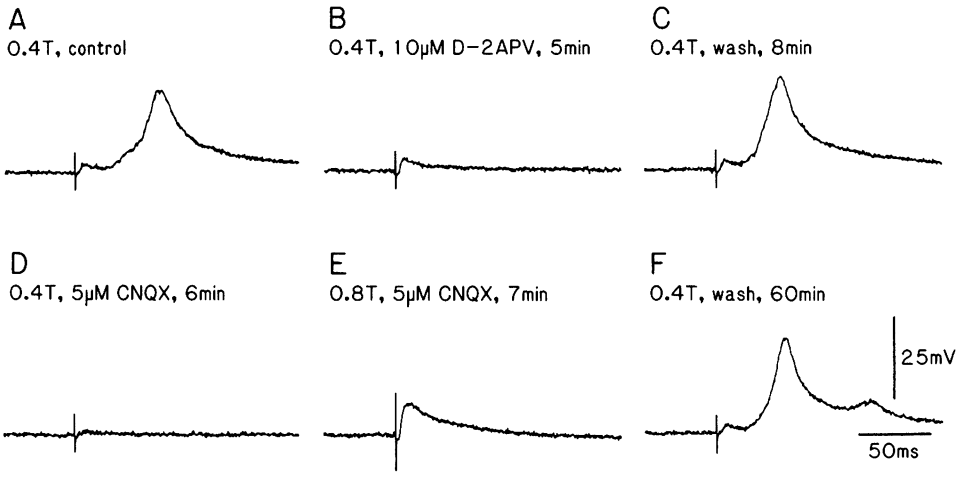

FIG. 2. Effect of NMDA and non-NMDA antagonists on lEPSPs. *A*: lEPSP recorded under control conditions. *B*: suppression of lEPSP by the NMDA antagonist D-APV. Note preservation of eEPSP. *C*: recovery of lEPSP on D-APV washout. *D*: reduction of eEPSP and lEPSP by CNQX. *E*: increasing stimulus strength results in increase in eEPSP amplitude; lEPSP still not seen. *F*: return of lEPSP with washout of CNQX. RMP = −84 mV.

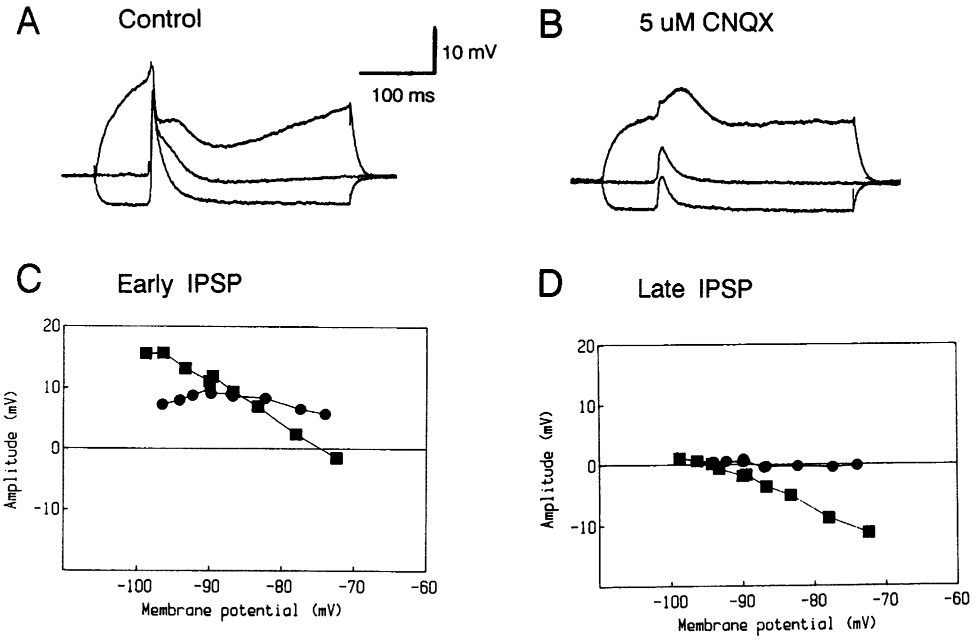

FIG. 3. Alterations in IPSPs after bath application of CNQX. *A*: control recordings of EPSP-IPSP complex after stimulation at 0.8 T. Stimulation was given at RMP (−82 mV) and after changing the membrane potential with current pulses. *B*: responses to the same stimulation after 5 μM CNQX. *C*: plot of response amplitude as a function of membrane potential before (■) and after (●) CNQX. Measurement was made 20 ms after stimulation, corresponding to the peak of the early IPSP under control conditions. *D*: similar plot as in *C* but measurements taken at peak of late IPSP (120 mS after stimulus).

reversal potential of −73 mV was obtained, suggesting a Cl$^-$-dependent IPSP was present. After CNQX a voltage-insensitive response was obtained, suggesting that the falling phase of an EPSP was measured. At longer latencies (Fig. 3*D*), a response with a reversal potential of −92 mV was observed under control conditions, suggesting a K$^+$-dependent IPSP. Such responses were virtually unmeasurable after CNQX, being reduced by 82% by 1–5 μM CNQX ($n = 8$).

It has been previously shown that inhibition effectively controls excitability in neocortical neurons (Sutor and Hablitz 1989a–c). If CNQX is affecting inhibition in the neocortex, it is possible that such disinhibition may lead to increases in excitability under some circumstances. This was examined by examining synaptic responses at different membrane potentials before and after application of non-NMDA antagonists. Figure 4 shows an example of a EPSP-IPSP sequence recorded at rest (Fig. 4*A*) and on depolarization (Fig. 4*B*). After application of CNQX (2 μM), the EPSP was reduced and IPSPs abolished when measured at rest (Fig. 4*C*). However, on depolarization, the reduced EPSP was capable of triggering an action potential (Fig. 4*D*). This is due to EPSP activation of voltage-dependent currents, an effect previously curtailed by IPSPs. These results indicate that the net excitability of a cell after synaptic activation is a product of intrinsic membrane currents and inhibitory and excitatory conductances.

Specificity of CNQX

The results with synaptic activation indicate that a non-NMDA receptor makes a significant contribution to neurotransmission in the neocortex. To elucidate the nature of the non-NMDA receptor involved and establish the selec-

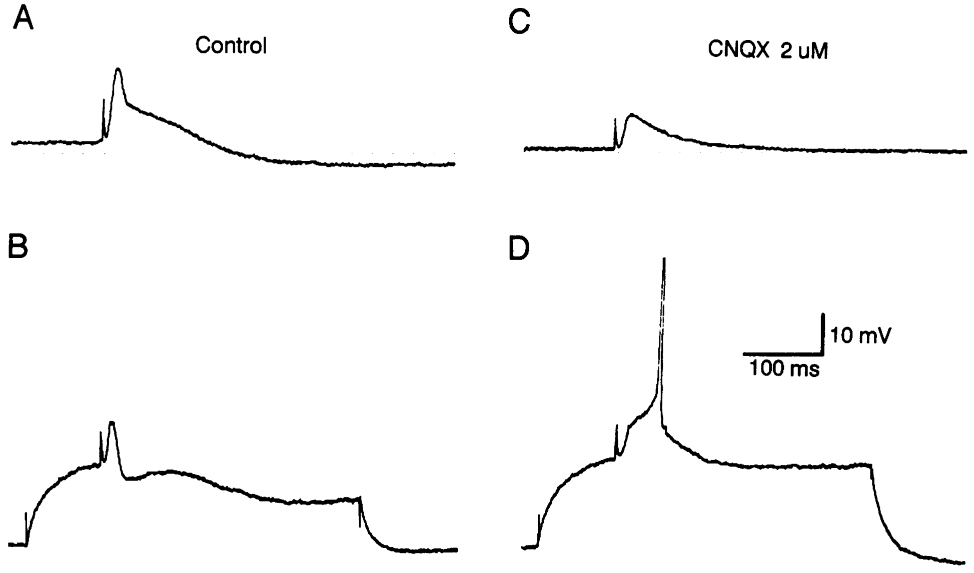

FIG. 4. Disinhibitory effect of CNQX seen on depolarization. *A*: EPSP-IPSP sequence seen in response to stimulation at the RMP (−79 mV). *B*: depolarization of the membrane potential discloses the presence of an early IPSP. *C*: after application of CNQX synaptic response consists of a smoothly decaying depolarization. *D*: EPSP triggers a spike when evoked at depolarized levels. No indication of an IPSP is seen.

tivity of CNQX under our recording conditions, responses to iontophoretically applied EAA agonists were examined. Typical results with quisqualate responses are shown in Fig. 5. Under control conditions (Fig. 5*A*, *left* trace), quisqualate produced a large membrane depolarization that reached threshold for spike initiation. This response was reversibly reduced by CNQX (5 μM) (Fig. 5*A*, *2nd* trace). An increase in the iontophoretic current partially restored the magnitude of quisqualate response (Fig. 5*A*, *3rd* trace). CNQX's antagonist action was reversible on washing (Fig. 5*A*, *right* trace). Bath application of 2–5 μM CNQX for periods of 5–20 min reduced quisqualate responses by 40–70%. In no cell was the response abolished ($n = 8$). At 5 μM, CNQX selectively reduced quisqualate responses without affecting response to iontophoretically applied NMDA (Fig. 5*B*). However, significant reductions in NMDA responses were observed at higher CNQX concentrations. Control responses to two doses of NMDA are shown in Fig. 6, *A* and *B* (*left* trace). Application of 5 μM CNQX had no effect on NMDA responses (Fig. 6, *A* and *B*, *2nd* trace); increasing the CNQX concentration to 10 μM (*3rd* trace) reduced responses to both low and high doses of NMDA. Responses recovered toward control values on washout of CNQX (*right* traces). This was a consistent effect in all neurons tested ($n = 6$); at concentrations of 10 μM or greater, CNQX reversibly reduced NMDA responses by 70–80%.

The inhibitory effect of CNQX on the quisqualate response was dose dependent, and, as shown above, increasing the dose could overcome the block. Analysis of log iontophoretic-charge-response curves indicated that CNQX caused a parallel rightward shift, suggesting a competitive antagonism. In one neuron exposed to 5- and 10-μM concentrations of the antagonist, EC_{50}s were 18.6 nA under control conditions and 27.1 nA and 35.8 nA after 5 and 10 μM CNQX, respectively. The corresponding dose ratios were 8.5 (5 μM) and 17.2 (10 μM). From these values it was possible to estimate an apparent pA_2 value of 6.1. This value is in agreement with the more detailed estimates obtained by Fletcher et al. (1988).

Quinoxaline derivatives have been shown to be antagonists of the NMDA-receptor–associated glycine site (Harris and Miller 1989; Kemp et al. 1988; Kessler et al. 1989). To test whether the observed CNQX-induced decreases in NMDA responses could be attributed to an effect at the glycine site, we tested the ability of D-serine to reverse the effect of CNQX. D-Serine mimicks the effect of glycine on NMDA receptors (Snell et al. 1987) but is a poor substrate for uptake systems. Examples of NMDA-induced responses before and after 10 μM CNQX are shown in Fig. 7,

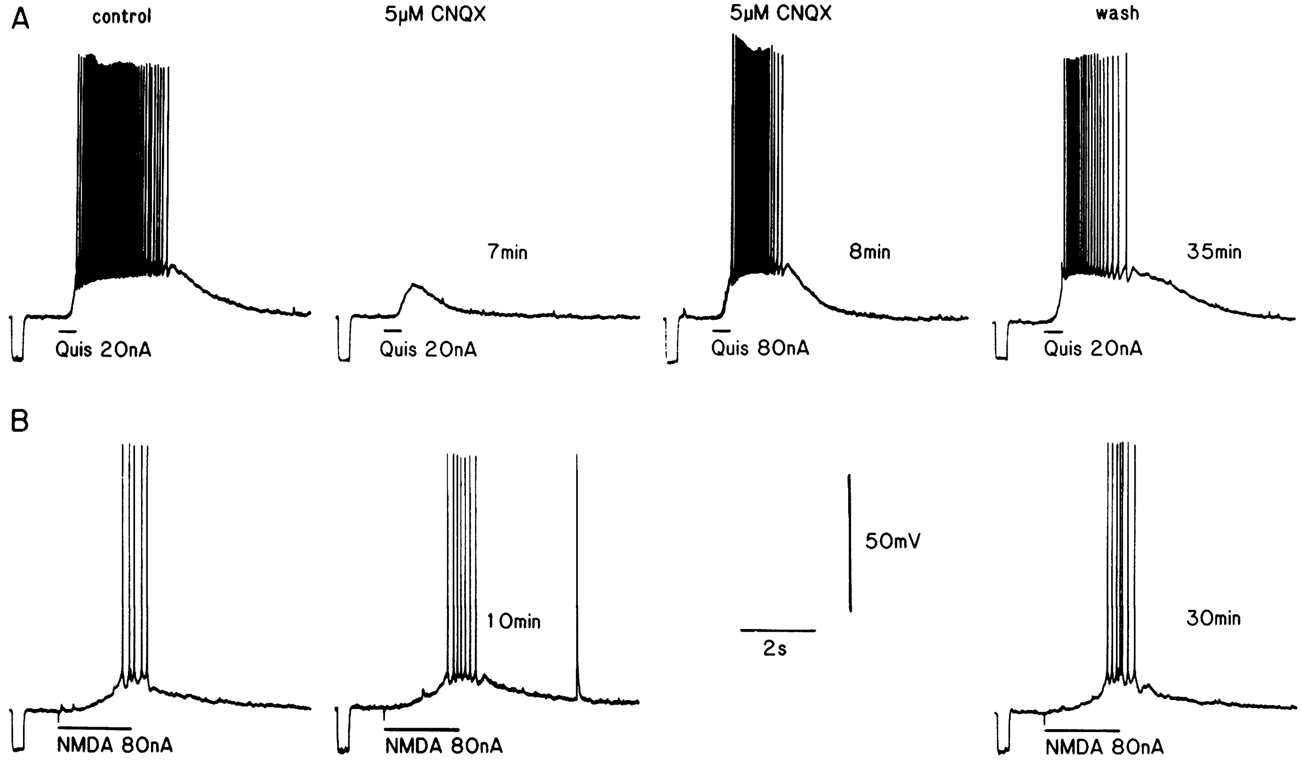

FIG. 5. Effect of the non-NMDA antagonist CNQX on iontophoretic responses to quisqualate and NMDA. Recording was obtained from a layer II/III neuron, and iontophoretic electrode was positioned near site of intracellular electrode. Negative-going potential before iontophoretic response is in response to a 0.3-nA current pulse. *A*: *left* trace, under control conditions, quisqualate (20 nA, 500 ms) produces a membrane depolarization with superimposed repetitive discharges. *Second* trace, after exposure to 5 μM CNQX, same quisqualate application produces only a small membrane depolarization. *Third* trace, increasing the ejection current to 80 nA in the continued presence of the antagonist partially restores the response. *Right* trace, after washout of CNQX, ejection of quisqualate at the original current strength (20 nA) evokes a response similar to that seen in control. *B*: response of the same neuron to iontophoresis of NMDA. No effect of CNQX was observed. RMP = −83 mV.

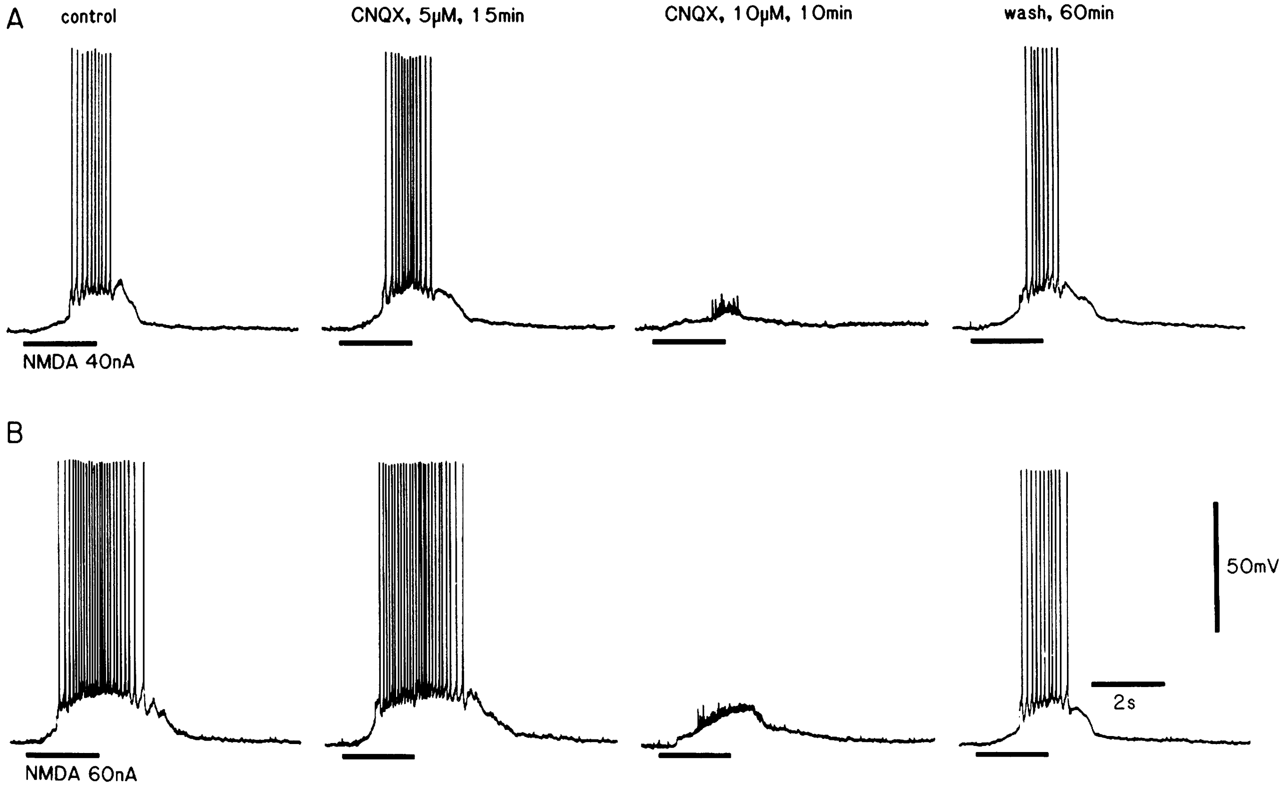

FIG. 6. High concentrations of CNQX can antagonize NMDA responses. *A*: NMDA was applied with the use of an ejection current of 40 nA for 2 s. Application of 5 μM CNQX did not affect the NMDA response, but a marked reduction was seen after application of 10 M. *B*: response of the same neuron to a larger dose of NMDA (60 nA; 2s). High concentrations of CNQX also antagonized this response. These effects were partially reversible on washing. RMP = −84 mV.

A and *B*, respectively. The non-NMDA antagonist reduced the underlying depolarization and inhibited burst firing. Addition of D-serine in the presence of CNQX resulted in a restoration of the response. Firing was enhanced over that seen under control conditions. Similar results were obtained with all neurons tested (n = 4).

To further examine the role of the glycine regulatory site in controlling responsiveness to NMDA, the effect of D-serine was studied in neurons not exposed to CNQX. Figure 8*A* shows an NMDA-evoked depolarization with superimposed action potentials obtained under control conditions. To rule out possible indirect synaptically mediated effects of NMDA, TTX was added to the bathing medium. TTX did not affect the underlying NMDA-evoked depolarization and slow, presumably calcium-dependent, action potentials were seen riding on the depolarization (Fig. 8*B*). Eight minutes after starting bath application of D-serine an enhancement of the response to NMDA was observed (Fig. 8*C*). Further exposure resulted in a further increase in the NMDA response and a decreased latency to onset of the

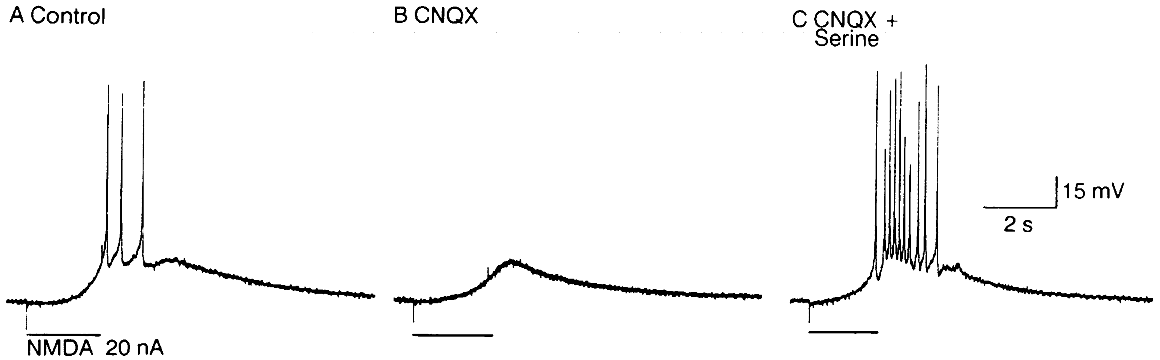

FIG. 7. Reversal of CNQX-induced depression of NMDA responses by D-serine in a neocortical neuron. *A*: response to NMDA under control conditions consisted of a membrane depolarization and repetitive bursts of action potentials. NMDA was ejected with a 20-nA current for the period indicated by the horizontal line. *B*: 2 superimposed responses obtained 20 min after starting 10 μM CNQX. *C*: 15 min after adding 1 mM D-serine in the presence of CNQX; the NMDA response is restored and augmented above control levels. Action potentials are truncated in these digitized records. RMP = −82 mV.

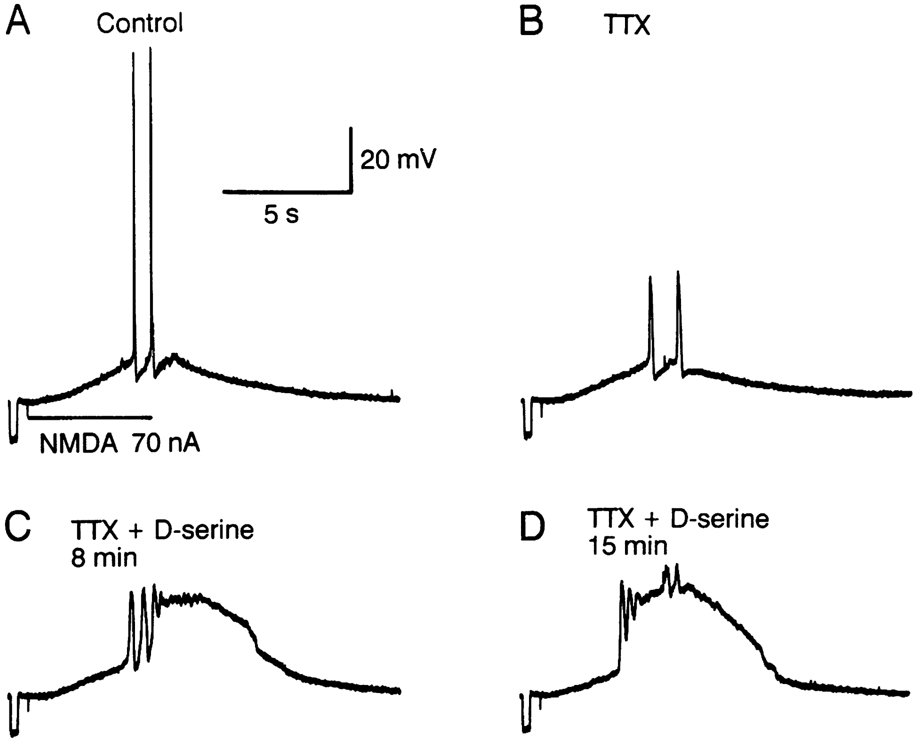

FIG. 8. Enhancement of NMDA responses by D-serine. *A*: example of membrane depolarization and actions potentials evoked by NMDA under control conditions. NMDA was applied for 5 s at 70 nA as indicated by the horizontal line. *B*: response to same dose of NMDA after bath application of TTX. This was done to block sodium-dependent action potentials and evoked synaptic potentials. Remaining regenerative responses are presumed calcium spikes. *C*: 8 min after starting bath application of 500 μM D-serine, regenerative response is enhanced. *D*: after 15 min of exposure to D-serine, NMDA response is further enhanced and occurs at a shorter latency. Negative deflection at beginning of each trace is voltage response to a 0.3-nA, 300-ms hyperpolarizing current pulse. RMP = −84 mV.

regenerative response (Fig. 8*D*). These effects were reversible on washing and seen in all neurons tested ($n = 5$).

Reliable responses to iontophoretically applied kainate were difficult to obtain. Brief applications of kainate produced depolarizations that were small in amplitude and persisted for long periods. Such responses were consistent only when sufficient time (>5 min) elapsed between applications. Larger doses of kainate were often toxic, producing irreversible depolarizations. Such behavior is atypical for a receptor mediating synaptic responses, and the effects of CNQX on kainate responses were not further evaluated.

The pronounced effects of CNQX on IPSPs raised the possibility that this was due to a direct effect on GABA receptors. To test this hypothesis, responses to iontophoretically applied GABA were examined. When responses to iontophoretically applied GABA before, during, and after bath application of CNQX were examined no effect was seen, indicating that postsynaptic responses to GABA are not affected by CNQX.

DISCUSSION

This study has shown that the quinoxalinedione compound CNQX can be used as a selective non-NMDA antagonist in rat neocortical slices in vitro. At concentrations up to 5 μM, CNQX reduced responses to iontophoretically applied quisqualate without affecting NMDA responses. CNQX effectively antagonized synaptic potentials in the neocortical slice and reduced both inhibitory and excitatory responses. This dual effect suggests the presence of EAA receptors on intrinsic interneurons in the cortex and points to a complex role for EAAs in controlling neuronal excitability.

Until recently specific and potent antagonists have been available only for NMDA receptors. Analysis of the effects of one such antagonist, D-APV, has had a significant impact on our understanding of the basic mechanisms underlying epileptiform discharges (Dingledine et al. 1986) and induction of long-term potentiation (Sutor and Hablitz 1989c). The advent of the quinoxalinedione group of glutamate receptor antagonists (Honore et al. 1988) provides a pharmacologic tool for the study of non-NMDA receptor–mediated responses. In the CA1 region of the hippocampus, these non-NMDA receptor antagonists have been shown to completely block synaptic responses (Andreasen et al. 1989; Blake et al. 1988, 1989; Fletcher et al. 1988). Blockade of excitatory synaptic transmission in the CA3 region with sparing of intracellularly recorded IPSPs has also been reported (Neuman et al. 1988). Investigation of the involvement of non-NMDA receptors in epileptiform activity in hippocampal pyramidal neurons has indicated that, in both CA1 and CA3 regions, CNQX is capable of completely suppressing picrotoxin-induced epileptiform activity (Lee and Hablitz 1989). Similar findings have been reported in organotypic cultures of rat hippocampus (McBain et al. 1988) indicating a significant contribution from non-NMDA receptors in paroxysmal bursting. The present results indicate that a substantial component of normal synaptic excitation in the neocortex is mediated by non-NMDA receptors (see also Jones and Baughmann 1988).

Our results in the neocortex have confirmed the selectivity of CNQX for non-NMDA over NMDA activated channels (Honore et al. 1988) but indicate that, at the background level of glycine present in brain slices, it is selective only at concentrations up to 5 μM. This is in keeping with previous studies of the neocortex (Fletcher et al. 1988) but stands in contrast to hippocampal investigations showing that 10 μM CNQX does not affect NMDA responses

(Blake et al. 1988, 1989). The reason for these differences is presently unclear but underscores the need for establishing the selectivity of CNQX in each brain region investigated. The mechanism whereby CNQX reduces NMDA responses in the neocortex appears to be due to an action at the glycine modulatory site (Harris and Miller 1989; Kessler et al. 1989). Our results indicate that D-serine, a glycine-site agonist, can reverse the effect of CNQX and even potentiate NMDA responses under normal conditions. Potentiation of NMDA responses by glycine has been reported in neocortical and hippocampal brain slices (Minota et al. 1989; Thomsen et al. 1989). Thus despite the suggestion that endogenous levels of glycine in brain slices is high (Hegsted et al. 1989), modulation via the glycine site may be significant.

Establishing the nature of the non-NMDA receptor (i.e., quisqualate or kainate) involved in synaptic transmission in the neocortex was not feasible. Reproducible, graded responses to kainate were difficult to obtain, and comparison of CNQXs' effect on kainate and quisqualate responses was not possible. The atypical responses to iontophoretically applied kainate are not those expected of a transmitter responsible for rapid neurotransmission and may indicate that fast excitatory responses in the neocortex are mediated by a quisqualate receptor. Studies with local iontophoresis (Trussel et al. 1988) or rapid perfusion of quisqualate (Tang et al. 1989) onto cultured neurons have been able to mimic many features of synaptic responses. It seems reasonable, although as yet unproven, that quisqualate receptors mediate fast neurotransmission.

In these experiments, both IPSPs and EPSPs were diminished after CNQX application. Because responses to iontophoretically applied GABA were not altered by the antagonist, it is unlikely that a direct effect on postsynaptic receptors mediating IPSPs is involved. The pathways involved in elaboration of IPSPs in the neocortex probably consist of both feedforward and recurrent circuits. Thalamocortical afferents terminate on both pyramidal cells and presumably inhibitory aspiny neurons (White 1978). These inhibitory neurons synapse on pyramidal neurons, providing the pathway for feedforward inhibition (Peters and Fairen 1978). Although the elements involved are not established, feedback inhibition mediated by axon collaterals of pyramidal cells has been demonstrated in the neocortex (Stefanis and Jasper 1964). Because there is evidence that corticofugal and efferent fibers use an EAA as a neurotransmitter, it is reasonable to assume that the collaterals of these fibers making synapses onto interneurons also release EAAs. We therefore interpret the decreases in IPSPs observed after CNQX application to a loss of non-NMDA receptor-mediated input to inhibitory interneurons.

Decreases in inhibition were often the first observable change. It is not clear whether this relates to the polysynaptic nature of inhibitory pathways, differences in convergence of afferents onto pyramidal cells versus inhibitory neurons, or different antagonist sensitivity. However, this disinhibitory action could give rise to both transient and sustained increases in excitability. Inhibition effectively controls the expression of lEPSPs in the neocortex (Sutor and Hablitz 1989a,c). During the wash-in of CNQX, lEPSPs were sometimes observed at stimulus strengths that were previously ineffective in evoking such responses, an effect attributable to decreased inhibitory control of the polysynaptic pathways generating the lEPSP. A more long-lasting increase in excitability was observed when cells were depolarized via current injection. EPSPs, although reduced in amplitude by CNQX, were more effectively amplified by voltage-dependent currents activated by synaptically evoked depolarization. This is presumably due to a decreased shunting by IPSPs. These studies with the non-NMDA antagonist CNQX underscore the complexity of circuits utilizing EAAs in the neocortex and illustrate the multiplicity of factors involved in controlling neuronal excitability.

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REFERENCES

ANDREASEN, M., LAMBERT, J. D. C., AND JENSEN, M. S. Effects of new non-*N*-methyl-D-aspartate antagonists on synaptic transmission in the in vitro rat hippocampus. *J. Physiol. Lond.* 414: 317–336, 1989.

BAUGHMAN, R. W. AND GILBERT, C. D. Aspartate and glutamate as possible neurotransmitters in the visual cortex. *J. Neurosci.* 1: 427–439, 1981.

BLAKE, J. F., BROWN, M. W., AND COLLINGRIDGE, G. L. CNQX blocks acidic amino acid induced depolarizations and synaptic components mediated by non-NMDA receptors in rat hippocampal slices. *Neurosci. Lett.* 89: 182–186, 1988.

BLAKE, J. J., YATES, R. G., BROWN, M. W., AND COLLINGRIDGE, G. L. 6-Cyano-7-nitroquinoxaline-2,3-dione as an excitatory amino acid antagonist in area CA1 of rat hippocampus. *Br. J. Pharmacol.* 97: 71–75, 1989.

CONNORS, B. W., MALENKA, R. C., AND SILVA, L. R. Two inhibitory postsynaptic potentials and $GABA_A$ and $GABA_B$ receptor-mediated responses in neocortex of rat and cat. *J. Physiol. Lond.* 406: 443–468, 1988.

DEFELIPE, J., CONTI, F., VAN EYCK, S. L., AND MANZONI, T. Demonstration of glutamate-positive axon terminals forming asymmetric synapses in cat neocortex. *Brain Res.* 455: 162–165, 1988.

DINGLEDINE, R., HYNES, M. A., AND KING, G. L. Involvement of *N*-methyl-D-aspartate receptors in epileptiform bursting in the rat hippocampal slice. *J. Physiol. Lond.* 380: 175–189, 1986.

FLETCHER, E. J., MARTIN, D., ARAM, J. A., LODGE, D., AND HONORE, T. Quinoxalinediones selectively block quisqualate and kainate receptors and synaptic events in rat neocortex and hippocampus and frog spinal cord in vitro. *Br. J. Pharmacol.* 95: 585–597, 1988.

FOSTER, A. C. AND FAGG, G. E. Acidic amino acid binding sites in mammalian neuronal membranes: their characteristics and relationship to synaptic responses. *Brain Res. Rev.* 7: 103–164, 1984.

GIUFFRIDA, R. AND RUSTIONI, A. Glutamate and aspartate immunoreactivity in cortico-cortical neurons of the sensorimotor cortex of rats. *Exp. Brain Res.* 74: 41–46, 1989.

HARRIS, K. M. AND MILLER, R. J. CNQX (6-cyano-7-nitroquinoxaline-2,3-dione) antagonizes NMDA-evoked [^{3}H] GABA release from cultured cortical neurons via an inhibitory action at the strychnine-insensitive glycine site. *Brain Res.* 489: 185–189, 1989.

HEGSTED, E., LANGMOEN, I. A., AND HABLITZ, J. J. Zinc and glycine do not modify low-magnesium-induced epileptiform activity in the immature neocortex in vitro. *Epilepsy Res.* 3: 174–177, 1989.

HONORE, T., DAVIES, S. N., DREJER, J., FLETCHER, E. J., JACOBSEN, P., LODGE, D., AND NIELSEN, F. E. Quinoxalinediones: potent competitive non-NMDA glutamate receptor antagonists. *Science Wash. DC* 241: 701–704, 1988.

HOWE, J. R., SUTOR, B., AND ZIEGLGANSBERGER, W. Characteristics of long-duration inhibitory postsynaptic potentials in rat neocortical neurons in vitro. *Cell. Mol. Neurobiol.* 7: 1–18, 1987.

JONES, K. A. AND BAUGHMAN, R. W. NMDA- and non-NMDA-receptor components of excitatory synaptic potentials recorded from cells in layer V of rat visual cortex. *J. Neurosci.* 8: 3522–3534, 1988.

KEMP, J. A., FOSTER, A. C., LEESON, P. D., PRIESTLY, T., TRIDGETT, R., IVERSEN, L. L., AND WOODRUFF, G. N. 7-Chlorokynurenic acid is a selective antagonist at the glycine modulatory site of the *N*-methyl-D-aspartate receptor complex. *Proc. Natl. Acad. Sci. USA* 85: 6547–6550, 1988.

KESSLER, M., BAUDRY, M., AND LYNCH, G. Quinoxaline derivatives are high-affinity antagonists of the NMDA receptor-associated glycine sites. *Brain Res.* 489: 377–382, 1989.

KRNJEVIC, K. AND PHILLIS, J. W. Iontophoretic studies of neurones in the mammalian cerebral cortex. *J. Physiol. Lond.* 165: 274–304, 1963.

LEE, W. L. AND HABLITZ, J. J. Involvement of non-NMDA receptors in picrotoxin-induced epileptiform activity in the hippocampus. *Neurosci. Lett.* 107: 129–134, 1989.

MATUTE, C. AND STREIT, P. Selective retrograde labelling with [^{3}H]-D-aspartate in afferents to the mammalian superior colliculus. *J. Comp. Neurol.* 241: 34–49, 1985.

MAYER, M. L. AND WESTBROOK, G. L. The physiology of excitatory amino acids in the vertebrate central nervous system. *Prog. Neurobiol.* 28: 197–276, 1988.

MCBAIN, C. J., BODEN, P., AND HILL, R. G. The kainate/quisqualate receptor antagonist, CNQX, blocks the fast component of spontaneous epileptform activity in organotypic cultures of rat hippocampus. *Neurosci. Lett.* 93: 341–345, 1988.

MCCORMICK, D. A., CONNORS, B. W., LIGHTHALL, J. W., AND PRINCE, D. A. Comparative electrophysiology of pyramidal and sparsely spiny stellate neurons of the neocortex. *J. Neurophysiol.* 54: 782–806, 1985.

MINOTA, S., MIYAZAKI, T., WANG, M. Y., READ, H. L., AND DUN, N. Glycine potentiates NMDA responses in rat hippocampal CA1 neurons. *Neurosci. Lett.* 100: 237–242, 1989.

NEUMAN, R. S., BEN-ARI, Y., GHO, M., AND CHERUBINI, E. Blockade of excitatory synaptic transmission by 6-cyano-7-nitroquinoxaline-2,3-dione (CNQX) in the hippocampus in vitro. *Neurosci. Lett.* 92: 64–68, 1988.

OTTERSON, O. P. AND STORM-MATHIESEN, J. Glutamate- and GABA-containing neurons in the mouse and rat brain, as demonstrated with a new immunocytochemical technique. *J. Comp. Neurol.* 229: 374–392, 1984.

PETERS, A. AND FARIEN, A. Smooth and sparsely-spined stellate cells in the visual cortex of the rat: a study using a combined Golgi-electron microscope technique. *J. Comp. Neurol.* 181: 129–172, 1978.

SNELL, L. D., MORTER, R. S., AND JOHNSON, K. M. Glycine potentiates *N*-methyl-D-aspartate-induced [^{3}H]TCP binding to rat cortical membranes. *Neurosci. Lett.* 83: 313–317, 1987.

STEFANIS, C. N. AND JASPER, H. H. Recurrent collateral inhibition in pyramidal tract neurones. *J. Neurophysiol.* 27: 855–877, 1964.

STONE, T. W. Cortical pyramidal tract interneurones and their sensitivity to L-glutamic acid. *J. Physiol. Lond.* 233: 211–225, 1973.

STREIT, P. Glutamate and aspartate as transmitter candidates for systems of the cerebral cortex. In: *Cerebral Cortex. Functional Properties of Cortical Cells,* edited by E. G. Jones and A. Petters. New York: Plenum, 1984, vol. 2, p. 119–143.

SUTOR, B. AND HABLITZ, J. J. Excitatory postsynaptic potentials in rat neocortical neurons in vitro. I. Electrophysiological evidence for two distinct EPSPs. *J. Neurophysiol.* 61: 607–620, 1989a.

SUTOR, B. AND HABLITZ, J. J. Excitatory postsynaptic potentials in rat neocortical neurons in vitro. II. Involvement of *N*-methyl-D-aspartate receptors in the generation of EPSPs. *J. Neurophysiol.* 61: 621–634, 1989b.

SUTOR, B. AND HABLITZ, J. J. Long-term potentiation in frontal cortex:role of NMDA-modulated polysynaptic excitatory pathways. *Neurosci. Lett.* 97: 111–117, 1989c.

SUTOR, B. AND ZIEGLGANSBERGER, W. A low-voltage activated, transient calcium current is responsible for the time-dependent depolarizing inward rectification of rat neocortical neurons in vitro. *Pfluegers Arch.* 410: 102–111, 1987.

TANG, C., DICHTER, M., AND MORAD, M. Quisqualate activates a rapidly inactivating high conductance ionic channel in hippocampal neurons. *Science Wash. DC* 243: 1474–1477, 1989.

THOMSON, A. M. A magnesium-sensitive post-synaptic potential in rat cerebral cortex resembles neuronal responses to *N*-methylaspartate. *J. Physiol. Lond.* 370: 531–549, 1986.

THOMSON, A. M., WALKER, V. E., AND FLYNN, D. M. Glycine enhances NMDA-receptor mediated synaptic potentials in neocortical slices. *Nature Lond.* 338: 422–424, 1989.

TRUSSEL, L. O., THIO, L. L., ZORUMSKI, C. F., AND FISCHBACH, G. D. Rapid desensitization of glutamate receptors in vertebrate central neurons. *Proc. Natl. Acad. Sci. USA* 85: 2834–2838, 1988.

VOGT, B. A. AND GORMAN, A. L. F. Responses of cortical neurons to stimulation of corpus callosum in vitro. *J. Neurophysiol.* 48: 1257–1273, 1982.

WATKINS, J. C. AND EVANS, R. H. Excitatory amino acid transmitters. *Annu. Rev. Pharmacol. Toxicol.* 21: 165–204, 1981.

WEISS, D. S. AND HABLITZ, J. J. Interaction of penicillin and pentobarbital with inhibitory synaptic mechanisms in neocortex. *Cell. Mol. Neurobiol.* 4: 301–317, 1984.

WHITE, E. L. Identified neurons in mouse SmI cortex which are postsynaptic to thalamocortical axon terminals: a combined Golgi-electronmicroscope and degeneration study. *J. Comp. Neurol.* 181: 627–662, 1978.

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