Even if the validity of the results and conclusions presented here is accepted, these results do not afford proof of any similarity between the underlying mechanisms for color discrimination in the cat and the mechanisms for color discrimination in other animals for which the capability is widely acknowledged.

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Sound-Evoked Potentials in Neocortex of Unanesthetized Opossum

Abstract. *Short-latency potentials are evoked by auditory stimuli at all loci of neocortex recorded from, including points in orbital-frontal, visual, and somatosensory areas. These potentials are similar in latency and wave form to responses obtained from the primary auditory projection area in higher mammals, but occur in widely varying spatial patterns.*

In eutherian mammals, anatomical and electrophysiological studies have shown that the sensory projection nuclei of the dorsal thalamus (medial geniculate, lateral geniculate, and ventral basal) send their axons to well-defined and restricted portions of the neocortex. Anatomical (*1*, *2*) and electrophysiological studies (*3*) with a metatherian mammal, the Virginia opossum, also indicate differential specialization of the neocortical areas with respect to sensory modality; that is, visual, auditory, and somatic areas can be differentiated. Results reported here, obtained by using the method of evoked potentials in the unanesthetized opossum, do not confirm the existence of a localized cortical auditory projection area. Instead, short-latency activity evoked by auditory stimuli appears in widely varying patterns over extensive regions of the neocortex.

Chronic implants of Nichrome wire electrodes, insulated except at their tips, were made in the neocortex of four opossums. In each animal, surface-to-white-matter pairs of electrodes were implanted at loci evenly distributed over the entire lisencephalic neocortex of one hemisphere. Electrode positions were verified histologically.

After recovery from surgery (about 2 weeks), animals were adapted to the sound-treated recording room and small shielded cage. With the opossum apparently at ease and fully adapted to the situation, bursts of clicks were presented to elicit the evoked potentials, which were displayed on a four-beam oscilloscope. Several daily recording sessions were given for each opossum.

Short-latency evoked potentials were recorded from all electrode positions in all opossums. No recording site was active all the time, but evoked potentials could always be elicited from some loci. Figure 1 shows typical examples of the short-latency evoked potentials obtained from opossum No. P1. The region from which auditory evoked potentials were recorded from this opossum while anesthetized with sodium pentobarbital is also indicated on Fig. 1. This restricted "auditory" area has been described previously (*3*) and corresponds with cytoarchitectural (*2*) and retrograde-degeneration (*1*) delineations.

In the awake opossum the same types of short-latency evoked potentials appear in "non-auditory" and classically defined "auditory" neocortex.

Patterns of evoked activity varied (i) in the onset latencies of the evoked potentials and (ii) in the spatial distribution of activity. Table 1 shows the distribution of latencies falling in the range below 20 msec in opossum Pl, a typical case. Slow waves with latencies greater than 20 msec were often evoked, but only the shorter-latency, faster wave forms are under consideration here. Classically defined auditory cortex does not differ significantly from other cortex with respect to latencies of evoked potentials.

Table 1. Observed onset latencies of evoked potentials in opossum No. P1.

Electrode position	Onset latencies (msec)														
	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
1								x	x						
2						x		x	x	x		x			
3								x	x		x				
4							x	x							
5			x					x	x	x					
6								x	x						
7			x					x	x			x			
8			x				x	x	x	x		x			
9						x		x	x	x					
10						x		x							
11									x		x	x			
12								x	x	x					

Table 2. Observed dissociations of evoked potentials for electrode pairs in opossum No. P1.

Positions, potentials present	Positions, potentials not present											
	1	2	3	4	5	6	7	8	9	10	11	12
1					x			x		x	x	
2	x		x		x	x	x	x		x	x	
3	x			x				x			x	
4	x	x	x					x			x	
5						x				x		
6		x			x							
7		x	x		x	x		x			x	
8	x	x					x			x	x	
9					x		x	x		x	x	
10						x			x			
11		x	x		x	x				x		x
12			x			x				x	x	

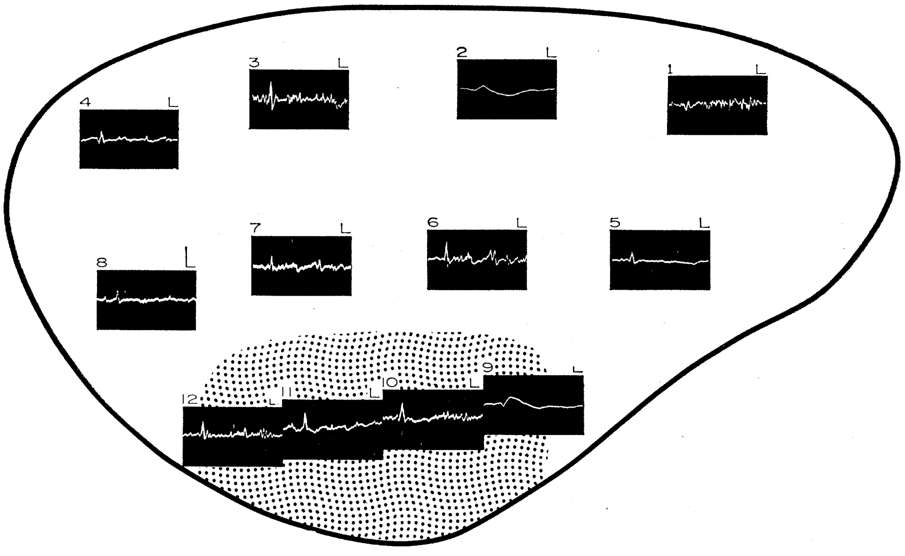

Fig. 1. Typical sound-evoked potentials at each electrode position in opposum Pl. The area from which evoked potentials could be elicited by sound stimuli in the Nembutal-anesthetized animal is stippled. Calibrations: horizontal, 10 msec; vertical, 100 μv. Onset of stimuli was at the beginning of the trace, and the animal was approximately 4 feet (1.2 m) from the speaker.

Some indication of the variability of spatial patterning can be obtained by constructing a table which shows the dissociation of evoked activity among the loci. Table 2 indicates this dissociation by showing (with *x*'s) the pairs of loci whose evoked activity did not at some time occur together. Table 2 indicates that there are 11 cases of double dissociation of evoked activity recorded from pairs of loci (for example, for loci 3 and 4 there were times when potentials were present at 3 and absent at 4, and vice versa). The loci in six of these double dissociation pairs are immediately adjacent positions within the electrode array, and two of these (9 and 10, 11 and 12) are in classically-defined-auditory cortex. Furthermore, the table indicates that for every locus there exists at least single dissociation from an adjacent locus, that is, potentials were elicited at the given locus while an adjacent locus was inactive.

Most likely the data of Table 2 could have been extended; even more variety of spatial patterning of evoked potentials in the unanesthetized opossum may be expected. Also, the minimum possible spacing between evoked potentials may be smaller than the interelectrode spacing used. Thus, the total number of possible patterns of active loci—presumably related to the total possible number of input-output functions—is probably larger than our data indicate.

A pathway for the short-latency evoked response is suggested by the work of Diamond and Utley (*1*). They found that cortical lesions restricted to the temporal area produced only small retrograde changes in the medial geniculate body; severe degeneration was produced only by greatly extending the area of cortical destruction. It is thought that results like these depend on the existence of axon collaterals—sustaining projections—which terminate outside of primary projection cortex. Presumably, thalamic cells with uncut axon collaterals do not degenerate (*4*). The sustaining projections found in the opossum could constitute the pathway to cortex for the evoked potentials found in this study. Wave forms and latencies of responses in opossum cortex are similar to those in projection areas of higher mammals in which also areas receiving diffuse sustaining projections are silent under pentobarbital anesthesia.

Other pathways, however, are possible. It has been reported that single units in the region between the medial geniculate nucleus and the ventral anterior nucleus respond to auditory stimuli (*5*). According to Erickson such units are also found in the ventral posterior nucleus itself (*6*). Both of these regions project to cortex (*1*).

Since auditory potentials are recorded from known visual and somatosensory receiving areas (*3*) these areas of opossum cortex are polysensory in nature. Thus, the principle of segregation of sensory projection areas is not an essential mammalian characteristic. The opossum does represent a step in the direction of specialization of sensory cortical areas: (i) these areas are cytoarchitectonically definable, (ii) the results of Diamond and Utley indicate some specialization of thalamic connections, and (iii) responses are evoked only from the temporal area in the anesthetized animal.

A similar type of transitional cortical organization in opossum and wallaby has been reported by Linde (*3*), who demonstrated complete overlapping of cortical somatosensory and motor areas.

A polysensory condition is considered essential for the evolutionary development of neocortex (*7*). According to Herrick, the evolutionary progression to neocortex requires the penetration of a diversity of nonolfactory fiber systems into olfactory cortex. Our results suggest that the transition from polysensory to higher mammalian cortex may involve either the movement of sensory collaterals to restricted loci, their selective loss, or both.

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