Table 1. Number of trials and errors to reach criterion.

Interval (seconds)	Number of dog	Preoperative			Postoperative		
		Trials	Omission errors	Commission errors	Trials	Omission errors	Commission errors
			Lateral lesion				
15	9	820	0	210	800	66	253
15	10	720	0	202	800	6	197
15	11	680	0	217	800	94	232
15	12	500	1	151	800	79	130
60	13	560	0	156	660	84	74
60	14	300	0	72	800	98	185
60	15	440	0	127	800	64	212
60	16	360	0	89	800	105	123
			Medial lesion				
15	1	1280	0	402	100	0	3
15	2	640	0	199	120	0	9
15	3	520	1	149	220	1	28
15	4	740	1	204	280	3	26
60	5	540	0	161	120	0	9
60	6	580	0	236	220	2	26
60	7	600	0	121	160	0	14
60	8	1320	54	225	120	0	7

almost unimpaired by medial lesions. Only three animals (Nos. 3, 4, and 6) did not reach criterion immediately. Histological verification showed that the lesions in these dogs invaded the white matter slightly.

Comparing two analogous series of experiments, one performed with the DAR procedure of the earlier study (*3*) and the other with the DSR procedure in this study, we find that with intertrial intervals lasting 60 seconds, medial and lateral lesions had quite opposite effects. Medial lesions produced impairment on the DAR test, but only very slight or no impairment on the DSR test; on the contrary, lateral lesions produced dramatic impairment on the DSR test, but no impairment on the DAR test. When the intervals between trials were very short (15 seconds), performance in the DAR test was impaired by both medial and lateral lesions, whereas performance on the DSR test was impaired after lateral lesions only.

These results seem to indicate that the DAR and DSR procedures measure two quite different physiological mechanisms. In fact, the DAR test may be regarded as a drive, no-drive differentiation because the no-go response is developed to a stimulus that is never followed by food. Consequently, the disinhibitory effect of the medial lesions in the DAR procedure was attributed to abnormal searching and sniffing activity and excessive conditioned response during intertrial intervals, which suggests that the retention loss of differential inhibition reflects the release of drive functions from cortical inhibitory control (*3*). On the other hand, in the DSR procedure both stimuli are followed by the presentation of food, but the animal must learn that to the positive CS it must perform the trained movement and to the negative CS it must not. Accordingly, the DSR procedure may be regarded as one requiring a differentiation between two movements, flexion of the leg to one CS and extension to the other one. In fact, it could be observed that in response to the negative CS the dogs actively restrained performance of flexion by performing antagonistic movements.

If this interpretation of the DSR test is correct, the lateral surface of the prefrontal cortex may be considered to be concerned with selection of the proper instrumental responses to the corresponding CS's.

In these experiments lateral lesions included both the dorsal aspect of the prefrontal cortex (gyrus proreus) and the lateral aspect (so-called gyrus orbitalis). In more recent experiments, we have found that performance on the DSR test is not impaired after purely proreal lesions, but that it is after orbital lesions. Since proreal lesions produce impairment in the delayed response test (*4*) whereas orbital lesions do not, the conclusion follows that the three tests—DAR, DSR, and delayed response—depend on different prefrontal structures.

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5. I thank Dr. J. Konorski for helping me in preparing this report and Dr. M. Mishkin for correcting its style. I am also indebted to Mrs. H. Kosmal for the histological analysis of the brains.

14 September 1970; revised 9 November 1970 ■

Development of Polysensory Responses in Association Cortex of Kitten

Abstract. *Sensory responsiveness of single neurons in posterior association cortex of kittens that were 7 to 50 days old was investigated. The percentage of trimodal cells (that is, cells that respond to visual, auditory, and somesthetic stimulation) increased gradually until day 50, when percentages of trimodally responsive cells approached the adult level. In the youngest kittens, cells were predominantly responsive to only visual stimulation. With maturation, responsiveness to auditory and then to somesthetic stimulation was observed in increasing percentages of cells.*

Although the immaturity of kitten cortex has been stressed in anatomical and physiological studies (*1*), several electrophysiological investigations have shown cortical activity in response to specific sensory stimuli. At the single neuron level, Hubel and Wiesel (*2*) have described cells that respond to complex visual stimuli in visual cortex of the 8-day kitten, and Rubel (*3*) reported somatotopic organization of unit cluster activity in sensorimotor cortex of the 1-day kitten. Gross evoked potentials have also been obtained from visual cortex (*4, 5*) and auditory cortex (*4, 6, 7*) in the neonate. Although these responses are characterized by long latencies and long recovery cycles, it appears that primary cortical areas are at least potentially capable of processing

sensory information in very young animals.

Less is known of the sensory responsiveness in cortical regions other than the primary receiving areas. Although gross evoked potential (*8, 9*) and unit (*10, 11*) studies have shown association cortex of the adult cat to be responsive to auditory, visual, and somesthetic stimuli, the ontogeny of evoked responses in these areas is unclear. Marty (*12*) noted the general difficulty with which gross evoked potentials in nonprimary cortex of kitten can be elicited. In this report we demonstrate that polysensory characteristics of neurons in an association area of the kitten develop between the postnatal ages of 8 and 50 days.

Single units were recorded in association response area PMSA (posterior middle suprasylvian area) of 34 acute kittens, which ranged in age from 7 to 50 days. After the animals had been anesthetized with chloralose (35 to 75 mg/kg), tracheotomy was performed, eyelids and auditory meatus were opened when necessary in the youngest animals, and a burr hole 1 to 3 mm in diameter was made in the overlying skull. Standard recording techniques were used to take extracellular records with glass-coated tungsten microelectrodes. Peripheral stimuli were binocular light flash to atropinized eyes, free field click, and single shock pulse to the ipsilateral forepaw. All stimuli were presented at intensities well above those necessary for eliciting responses in the primary sensory receiving areas. Control procedures ensured that any possible auditory stimulus associated with the flash of the photic stimulator was not effective in evoking unit discharge. Data were analyzed on line and recorded on film; poststimulus histograms were constructed with use of a Fabri-Tek 1062 laboratory computer.

A total of 150 cells from various cortical depths was studied. Units responsive to peripheral stimuli were observed no earlier than day 8 (six 7-day kittens were included in our sample). The modal response was a single discharge, although multiple discharges were also seen. Exceedingly long response latencies are typical for these cells. The median latency for cell discharge to a visual flash is 35 msec in PMSA of the adult cat, but it is 160 msec in the 8- to 16-day kitten. Corresponding values for response to auditory click are 130 msec in the 8- to 16-day kitten and 40 msec in the adult cat.

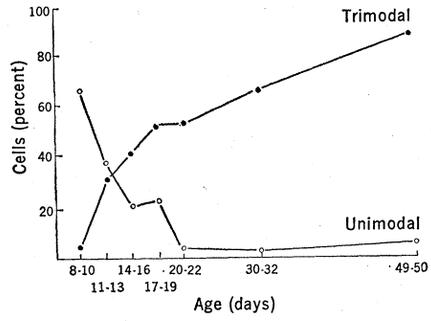

Fig. 1. Increase in percentage of cells that are trimodal (responsive to auditory, visual, and somesthetic stimuli) with increasing age. A corresponding decrease occurs in percentage of cells that are responsive to only one stimulus.

For forepaw shock, median response latency is 250 msec for the 8- to 16-day kitten and 60 msec for the adult cat (*13*).

In PMSA of the adult cat, 82 percent or more of cells respond to auditory, visual, and somesthetic stimuli (*13*). When the same stimuli are presented to kittens, the percentage of cells responsive to all three modalities of stimulation increases with age—from 6 percent in kittens 8 to 10 days of age, to 89 percent in kittens of 49 to 50 days of age (see Fig. 1). The earliest trimodal cell was observed in a 10-day kitten. The number of cells responsive to only one modality of stimulation decreases sharply from 67 percent in 8- to 10-day kittens to only 6 percent in 49- to 50-day animals, quite comparable to the 3 percent observed in the adult cat (*9*). The chi-square test indicates that the increase in the percentage of cells that show trimodal response characteristics is reliable ($\chi^2 = 30.86$, d.f. $= 6$, $P < .001$).

Responsiveness to the three modalities of stimuli appeared in this sequence: visual, auditory, somesthetic (see Table 1). Of the cells observed in this study over all ages from 8 to 50 days, 95 percent were responsive to visual stimuli as compared with 99 percent in the adult cat (*13*). Differences in responsivity between adult and infant cats to auditory and somesthetic stimuli are far more striking. The percentage of cells that respond to auditory stimuli increases from 33 percent at 8 to 10 days to 96 percent by 30 to 33 days. In the adult cat approximately 95 percent of cells were found to respond to auditory stimuli (*13*). Development of responsiveness to somesthetic stimuli occurs later than does responsiveness to visual or auditory stimuli. Only 6 percent of cells were found to respond to somesthetic stimulation at 8 to 10 days, increasing to 89 percent by 49 to 50 days. In the adult cat, 85 percent or more of cells respond to this somesthetic stimulus. The age-dependent changes in response tendencies were statistically reliable for auditory and somesthetic stimuli ($\chi^2 = 28.95$, d.f. $=$ 6, $P < .001$; and $\chi^2 = 32.61$, d.f. $= 6$, $P < .001$, respectively) but not for visual stimuli ($\chi^2 = 12.38$, d.f. $= 6$).

The data do not rule out the possibility that changes in visual responsiveness of PMSA neurons occur during the period under study but merely indicate that those neurons responsive to peripheral stimulation always exhibit a high degree of firing to visual stimulation. There may well be cells that respond to visual stimulation at day 50 that do not respond at day 8. Other response measures such as latency and length of recovery cycles indicate that response to visual input, as well as to auditory and somesthetic input, is changing during this period.

Several recent findings indicate that the data reported here cannot be explained by the maturation of receptor organs. At the time of birth, the kitten has complete receptive field organization of tactile pad receptors (*14*) and cortical somatotopic organization of sensorimotor cortex (*3*). The cochlea

Table 1. Percentage of cells responding to auditory, visual, and somesthetic stimulation as a function of age.

Age of kitten (days)	Percentage of cells responding to			Total No. of cells
	Auditory	Visual	Somesthetic	
8–10	33	100	6	18
11–13	74	85	35	34
14–16	73	95	50	22
17–19	65	100	59	17
20–22	88	100	63	17
30–33	96	100	67	24
49–50	94	100	89	18

appears to be functioning by day 2 or 3, as indicated by the presence of cortical evoked potentials to tone stimulation (*7*), and the electroretinogram, an index of functional maturity in the retina, appears at day 6 (*15*).

Neural pathways to association cortex may be different for each modality and may develop at different rates. Actual pathways of input to these areas are not yet known (*16*), but even if there is one common system, as has been suggested (*9, 17*), there must be a separate input for each modality at some point, possibly the reticular formation. Thus, the actual locus of differential development may be found at a subcortical level.

Our findings of this developmental sequence (visual, auditory, somesthetic) may seem puzzling in view of the fact that almost all sensory ontogenesis studies in mammals and birds—behavioral, anatomical, and physiological—reveal the maturational sequence of somesthetic, auditory, visual (*18*). Our data are, however, supported by Marty (*12*), who reports that gross evoked potentials to auditory and, especially, to somesthetic stimuli were difficult to record outside the primary sensory areas in his youngest kittens. Although it is unclear why the response sequence of association area PMSA development is different from that in other systems, the major import of these data is that response properties of single neurons of this area are maturing during the time when many behaviors in the cat's repertoire are developing, including visual exploratory behaviors, play, and predatory activities (*19*). Lesion and electrophysiological studies have suggested involvement of cortical association response areas in attentive aspects of behavior, stimulus integrative activities, and initiation of movement (*11, 20*). Thus, the maturation of the cortical association areas may be involved in the development of complex behavioral sequences in the cat. Furthermore, although these data may be a function of autonomous postnatal differentiation in the nervous system (*21*), the phenomena reported here may also provide a means whereby the growth and development of neural processes can be modulated by the sensory experience of the organism (*22*).

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23. Supported in part by NIH grant NS 07661 and NIMH research scientist award 06650 to R.F.T., NIMH research training grant 11095, NDEA Title 4 award to K.S.M., NIGMS award 42521 to R.T.R., and NIMH postdoctoral fellowship 31195 to E.W.R. We thank S. J. Adams, C. J. Patterson, and S. A. Beydler for technical assistance.

16 October 1970; revised 30 November 1970

Specialization of Rabbit Reticulocyte Transfer RNA Content for Hemoglobin Synthesis: Erratum

In the report by D. W. E. Smith and A. L. McNamara (12 February, p. 578) the lines of Table 2 were accidentally scrambled by the printers. The correct Table 2 follows.

Table 2. Acceptance of amino acids by preparations of tRNA from rabbit reticulocytes and livers.

Amino Acid	Residues/ hemoglobin molecule	Acceptance activity (pmole/ absorbancy unit)		Ratio of acceptance activity of reticulocyte tRNA to:	
		Reticulocyte tRNA	Liver tRNA	Residues per hemoglobin molecule	Acceptance activity of liver tRNA
Alanine	56	125	57	2.23	2.19
Arginine	12	41	52	3.41	0.79
Asparagine	24	31	36	1.29	0.86
Aspartic acid	22	52	48	2.36	1.08
Cysteine	4				
Glutamine	12	19	18	1.58	1.06
Glutamic acid	32	33	35	1.03	0.94
Glycine	40	99	48	2.48	2.06
Histidine	38	35	11	0.92	3.18
Isoleucine	8	14	31	1.75	0.45
Leucine	70	34	53	0.49	0.64
Lysine	48	60	61	1.25	0.98
Methionine	4	49	54	12.25	0.91
Phenylalanine	32	37	19	1.16	1.94
Proline	22	41	39	1.87	1.05
Serine	42	50	62	1.19	0.81
Threonine	32	58	49	1.81	1.18
Tryptophan	6	19	21	3.17	0.91
Tyrosine	12	16	15	1.33	1.07
Valine	58	95	38	1.64	2.50