plement components (C5–C9). Complement may act by inducing specific alterations in membrane structure, making these polypeptides susceptible to enzyme action. However, simple rupture of membranes by mechanical means does not cause these changes to occur.

Protein alterations induced by complement may vary in different cells. In sheep erythrocyte membranes as noted by Knüfermann *et al.* (*16*) the slight diminution in high-molecular-weight polypeptides that occurs after complement action is in contrast to the total deletion we have reported here. Similar studies of other cell types known to be functionally altered by complement may also reveal characteristic changes.

Complement and thrombin trigger platelet aggregation, release reactions, and the development of coagulant activity. Both induce similar changes in platelet polypeptides. Thus, these deletions may reflect occurrences common to different mechanisms of platelet activation. Their description here provides an initial step in delineation of the molecular events underlying complement platelet reactions.

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Development of Rabbit Visual Cortex: Late Appearance of a Class of Receptive Fields

Abstract. *In young rabbits before the age at which the eyes open, only three of the seven receptive field types described in the adult visual cortex are detectable. The remaining four receptive field types—which share the property of having radially asymmetric fields—appear later, coincident with a decline in the percentage of cells that are visually responsive but not classifiable as to receptive field type.*

Increasing attention has been paid to the receptive field organization of central neurons in neonatal and perinatal organisms. Cases in which the development of adult receptive field organization continues postnatally are of special interest for the following reasons: (i) Analysis of a developmental sequence may be expected to provide clues as to the neuronal circuitry underlying receptive field properties. (ii) Such analyses should provide information about the mechanisms by which this circuitry is established. (iii) Additionally, normative data on the ontogeny of receptive field organization may be used as a basis for study of developmental alterations produced by environmental manipulation.

All of the visual receptive field types found in the superior colliculus of the adult rabbit are present in the superior colliculus of the neonatal rabbit with apparently adult-like organization before the time at which the eyes open (eye opening) (*1*). The same appears to be true for the cat visual cortex (*2*, *3*) although the responses of the cells to stimulus orientation are not as selective as in the adult. Superior colliculus cells of the cat, on the other hand, do not develop motion and directional selectivity until eye opening (*4*). Of the seven receptive field types found in the striate cortex of the adult rabbit (*5*), three—those with more or less radially symmetric fields (*6*)—are present before eye opening, which occurs at about 10 days postnatal. The other four receptive field types—those with radially asymmetric fields—do not appear until 2 to 8 days after eye opening. The appearance of these latter receptive field types is correlated with a decline in the percentage of cells classified as indefinite—cells which, while clearly responsive to light, are so unpredictable in their behavior that they cannot be identified as one of the seven adult receptive field types.

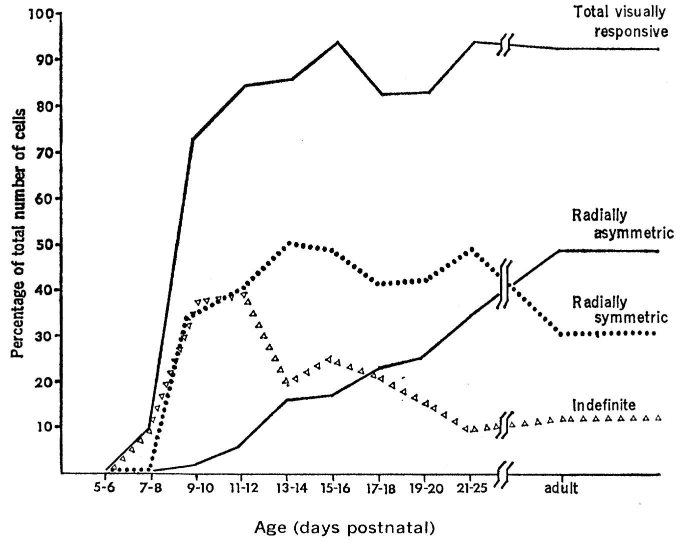

Fig. 1. Time course of percentage of units encountered that had radially symmetric and radially asymmetric receptive fields in rabbit striate cortex. Also shown are the percentages of units encountered that were responsive to visual stimuli and the percentage of units that could not be classified as to receptive field type. Eyes usually opened on day 10 or day 11.

Table 1. A summary of receptive classifications of 598 cells studied in 50 neonatal rabbits. Parallel data from an earlier study of the adult rabbit striate cortex are presented for comparison (*5*). Column 12 shows the percentage of total units which, while light responsive, could not be classed in one of the seven categories. These indefinite units, which are also present in the adult striate cortex (*5*), have poor receptive field boundaries and give unpredictable responses to stationary or moving light. In the case of neonatal rabbits, we found it necessary to subdivide the previously described category of directionally receptive fields. A directionally selective cell in the adult is defined as one which has a true null direction (*5*); the percentage of such cells is indicated to the left of the slash in column 8. To the right is given the percentage of a class of "atypical directional" cells not found in the adult. These cells give an excitatory response to a movement in any direction across their field, but clearly have a favored direction as defined by number of spikes per response.

Age (days)	*N*	Total units (No.)	Cells visually responsive (%)	Receptive field types: Concentric (%)	Uniform (%)	Motion (%)	Direction (%)	Simple (%)	Complex (%)	Oriented direction-selective (%)	Indefinite (%)
5–6	2	12									
7–8	6	79	10			1					9
9–10	8	97	73	4	4	25	0/2				38
11–12	7	95	84	15	4	20	0/3			2	40
13–14	6	68	86	15	6	28	8/2		4	4	19
15–16	5	56	93	13	10	23	9/2		9		27
17–18	5	61	82	10	2	26	11/0	5	2	5	21
19–20	4	54	83	13		28	10/0	7	5	5	15
21–25	5	76	93	21	11	16	11/0	12	7	5	10
Adult	27	213	92	12	3	15	19/0	17	8	5	12

Tungsten microelectrodes were used to sample striate cortical neurons in 50 Dutch-belted rabbits ranging in postnatal age from 5 to 25 days. Animals were prepared for recording under Fluothane (Ayerst) anesthesia, paralyzed with gallamine triethiodide (Flaxedil, Abbott), and artificially ventilated through a tracheal tube. Long-lasting local anesthetic (Zyljectin, Abbott) was applied to all wounds. A small bolt was cemented to the skull for purposes of supporting the animal in the stereotaxic frame (no eye, ear, or pressure bars of any kind were employed). Body temperature was maintained with a heating pad, and heart rate was continuously monitored. Constancy of heart rate was taken as a sign that the animal was experiencing no discomfort. Units encountered during electrode penetrations were accepted as cortical neurons only if they met the wave-form criteria given in (*5*), although in very young animals spike duration was 2 to 8 msec. Each neuron was classified as to receptive field type according to descriptions of adult cortex (*5*).

The first light responsive neurons, observed at 8 days, tended to exhibit low spontaneous activity, to respond somewhat weakly and sluggishly, and to adapt quickly to repeated stimulation, properties characteristic of neonatal neurons (*1, 2, 7*). The properties became less marked with age, and by about 18 days postnatal most neurons responded as they do in the adult. In spite of these considerations, receptive field classification was possible in all cases, with the reservations discussed below. Details of the experimental method and a fuller account of the properties of neonatal cortex will be reported elsewhere (*8*).

Table 1 shows that there is a clear dichotomy in the development of two classes of receptive field types. The earlier group, with symmetric receptive fields (concentric, uniform, motion), all appear before eye opening and are present in adult percentages or higher shortly thereafter. Adult-like directional cells, as well as simple, complex, and oriented direction-selective cells, on the other hand, do not appear until well after eye opening and seem to attain adult levels somewhat more slowly.

These results indicate that asymmetric receptive fields are retarded in their development relative to symmetric receptive fields, and, indeed, retarded in such a way as to make their initial appearance follow the first potential for visual experience of the young rabbit. They were not detected prior to eye opening. We are confident that asymmetric receptive fields are not missed in the younger animals because poor optics prevent their detection while permitting detection of symmetric receptive fields. Two lines of evidence support this: (i) receptive field sizes and the sharpness of excitatory-inhibitory zone boundaries of the cells present before eye opening resemble those observed in the adult (*8*), whereas larger receptive field sizes would be expected if the image were blurred; and (ii) the optics at the early ages are known to be sufficient to permit detection of asymmetric fields, since both directionally selective and oriented direction-selective cells have been observed with the same techniques in the rabbit superior colliculus before eye opening (*1*). We conclude, therefore, that the development of the neural circuits necessary to support asymmetric receptive fields in the rabbit striate cortex continues until well after eye opening.

We do not believe that the late appearance of asymmetric cells represents the addition to the cortex of new visually responsive cells. Rather, it appears that cells already responsive to light acquire more selective response properties. In Fig. 1, the total percentage of cells that is responsive to light, the percentage of indefinite units, the percentage of units with symmetric fields, and the percentage of units with asymmetric fields are plotted as a function of age. The percentage of light-responsive units behaves in a manner similar to that of units with symmetric fields, rising to near-adult levels prior to eye opening. However, until 11 to 12 days postnatal, a large fraction of these units falls into the indefinite category, which is elevated to three times the adult level at this point. Coincident with the first appearance and increase in percentage of cells with asymmetric fields, the percentage of indefinite cells begins to fall to adult levels. The fact that the total percentage of responsive cells does not increase greatly between 11 to 13 days and adulthood suggests that cells with asymmetric fields are developing out of initially diffusely responsive, indefinite cells. The same initial elevation in percentage and subsequent diminution to adult levels can be seen in the category of movement-selective cells, although to a lesser extent (Table 1, column 7).

Special note should be made of the development of directionally selective cells. These cells, like others with asymmetric fields, appear later in the developmental sequence, rising to adult levels over the span of 11 to 20 days postnatal. From 9 to 16 days, we were able to detect the presence of cells we called atypical directional, that responded best to movement in one direction, but did not have the null direction found in adult directionally selective cells (*5*). After 16 days postnatal, all directional cells met the criteria for adult directional selectivity. We suggest that a progression from movement selective (initially elevated, see below) to atypical directional to complete directional selectivity may be taking place, as an example of the increasing specificity of receptive field organization alluded to above. It should not be too hastily concluded, however, that the movement-selective category is the only source of what will ultimately be directionally selective cells, and that the indefinite category is the only source of what will be simple, complex, or oriented direction-selective cells. Either of the categories that exceed adult percentages in the early period of light responsiveness may well serve as a source for any of the receptive field types which are delayed in their appearance.

Our data suggest that, in the rabbit, receptive field organization of many striate cortical neurons is not like that of the adult until at least 3 weeks after birth. At eye opening, approximately the adult percentage of cells is responsive to light, and approximate adult percentages of cells with symmetric fields are present. However, a large number of the responsive cells exhibit poor specificity and reliability in their response, and asymmetric fields are lacking entirely. Over the next 10 days, these indefinite cells (and perhaps some of the symmetric ones) probably become cells with asymmetric fields.

The neuronal changes responsible for the transition from diffuse to specific receptive fields remains a matter for future research. It is worth noting, however, that the adult asymmetric fields are at least logically derivable from the presumptive "protofields" by the addition of inhibition. This leads to the hypothesis that a major part of the transition from diffuse to specific receptive fields may involve the late addition of synapses from inhibitory interneurons intrinsic to the cortex (*10*). Such a hypothesis is consistent with speculation about the late development of intrinsic interneurons (*11*), and with the work of Lund and Lund (*12*) showing a late wave of synaptogenesis from inhibitory interneurons during ontogenesis of the superior colliculus in the rat. The fact that indefinite receptive fields persist into adulthood in the rabbit striate cortex (*5*) raises the possibility that a reservoir of unspecified cells may remain even in the adult (*13*).

Our results are also of interest with respect to the question of a possible role of sensory input in the elaboration of receptive field circuitry. A number of studies have shown that the receptive field organization of the cat cortex is profoundly sensitive to visual input (*9, 13, 14*). This has not been accepted as conclusive evidence of a normal role for sensory input in the elaboration of neural connections because of the belief that the neonatal cat visual cortex is already organized like that in the adult (*2*). This view would suggest that any changes brought about by sensory input must be destructive or atrophic (*14*). However, experiments suggest that this conclusion may have been too hastily drawn (*3*). In any case, it clearly does not apply to rabbit striate cortex. A significant amount of development, the appearance of asymmetric receptive fields, takes place after the time when patterned visual experience begins. Therefore, the opportunity for interaction of genetic and ontogenetic information in the elaboration of neural connections is clearly present in the rabbit cortex (*15*).

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6. Cells with radially symmetric fields are those for which the best stimulus has no preferred orientation or direction of movement. Cells with asymmetric fields are those for which the best stimulus has a particular orientation or direction of movement, or both. The former group includes concentric, uniform, and movement-selective cells; the latter consists of simple, complex, oriented direction-selective, and directionally selective cells.
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10. Striate cortical neurons with concentric receptive fields also involve inhibitory processes, but appear early in development. If inhibitory processes are added later to some cortical neurons, to produce cells with asymmetric fields, and concentric cells are present early in development, then it may be that two phases of inhibitory interneural growth occur. However, since concentric cells are also present in the lateral geniculate nucleus, the inhibitory mechanisms necessary to produce cells with concentric receptive fields in the striate cortex may actually lie in the lateral geniculate nucleus. Thus, it would not be necessary to postulate two phases of inhibitory interneuronal growth in the cortex.
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