Development of Inferior Temporal Cortex in the Monkey

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Inferior temporal (IT) cortex is critical for visual pattern recognition in adult primates. However, the functional development of IT cortex appears to be incomplete until late in the first year of life in monkeys and probably beyond. Responses of neurons in IT are substantially weaker, of longer latency, and more susceptible to anesthesia within at least the first half year of life. In addition, refinement of connections of IT, particularly those with regions in the opposite hemisphere and with regions related to memory and attention, continues for at least several months after birth. Moreover, many of the pattern recognition functions that IT supports in adulthood themselves show a very protracted period of development, and damage to IT cortex in infancy appears to have relatively little effect on pattern recognition abilities, despite the pronounced effects of comparable damage in adulthood. These findings all suggest that IT undergoes an extended period of postnatal development, during which both visual experience and the maturation of other brain structures may contribute to the emergence of mechanisms of pattern recognition within IT.

In other respects, fundamental characteristics of IT emerge quite early. For example, despite their weaker responses, IT neurons have adult-like patterns of responsiveness—including pronounced form selectivity and large bilateral receptive fields—as early as we were able to test (~6 weeks). Thus, IT cortex appears to be prewired with (or predisposed to develop rapidly) neural circuitry sufficient to produce basic properties remarkably similar to those found in the adult animal. Future studies of IT cortex will need to address the development of signals related to perceptual constancies and to formation and retrieval of visual object memories, the development of interactions with other regions involved in visual recognition (particularly frontal cortex), and the specific mechanisms underlying various types of plasticity present in IT cortex in both developing and mature primates.

Inferior temporal (IT) cortex[1] is a region of "high-order" visual cortex occupying the inferior temporal gyrus and adjacent portions of the lower bank of the superior temporal sulcus (Fig. 1). This region of cortex has a number of unique characteristics that have made it of special interest to those studying cortical mechanisms of visual cognition. As has been known for many years, damage to this region or to equivalent cortex in humans produces an agnosic-type syndrome in which recognition of previously familiar visual objects—or learning about new ones—is impaired in the absence of any purely "sensory" deficits (reviewed in Gross, 1973, 1992). Moreover, this functional role is reflected in the intriguing visual response properties of its neurons. IT cells often discharge preferentially to the sight of particular objects or classes of objects and, occasionally, show highly selective responses to specific images including faces and even particular face views (e.g., Desimone et al., 1984; reviewed in Perrett et al., 1992; Gross et al., 1993). Finally, a plethora of recent experiments have demonstrated that IT neurons exhibit considerable plasticity in adulthood and appear to carry explicit information about stimulus recency and familiarity—visual memory traces (reviewed in Desimone, 1992).

Despite all these findings, relatively little study has been devoted to understanding the maturation of this region of cortex and the processes by which its properties are acquired or expressed in ontogeny. The relative lack of developmental work on IT cortex is also surprising given that developmental studies have historically proven an invaluable approach in the earlier stages of understanding the workings of a given cortical region. Such was the case in striate cortex, where Hubel and Wiesel's groundbreaking developmental studies were begun very early in the history of our understanding of striate organization and physiology (e.g., Hubel and Wiesel, 1963; Hubel et al., 1977). Such was also the case in frontal cortex, where studies of early lesions (e.g., Akert et al., 1960; Goldman, 1971; Goldman et al., 1974) produced highly influential data both on frontal lobe function and on basic mechanisms of cortical development. This article attempts to describe what is known of the functional, physiological, and structural development of IT cortex in the macaque monkey, to suggest ways, *en passant*, in which such developmental studies complement other approaches to cortical function, and to define critical directions for future studies of the development of temporal lobe neocortex.

Development of Visual Functions That Draw on Inferior Temporal Cortex in Adulthood

Not surprisingly, as in adult monkeys, the extent of visual pattern recognition performance achieved by infant macaques is dependent on the type of task used to probe these capacities. Even discounting the complication of the task difficulty inherent in more complex recognition tasks, the overall picture of development of macaque visual recognition processes is one of primitive early capacity, followed by a long period of gradual emergence of adult levels of performance.

One early line of research using primarily observational techniques focused on inherent preferences of infant monkeys for stimulus attributes, and, as in humans, the results have been used to infer both the ability of infants of a given age to discriminate among stimuli and innate predispositions to specific stimulus types. Much as newborn human infants are preferentially attentive to face shapes (e.g., Goren et al., 1975), infant monkeys raised in partial isolation exhibit visual preferences for conspecifics (Sackett, 1970), and infant monkeys reared in complete isolation are most reactive to pictures of other infant monkeys or of threat faces (Sackett, 1966a). They also come to prefer to view increasingly more complex (i.e., more highly textured) patterns in the course of the first month of life (Sackett, 1966b). More recently, a modification of the preferential viewing familiarization-novelty technique introduced by Fantz (e.g., Fantz, 1965) for the study of human infant perception has been applied successfully to infant monkeys. Using this paradigm, both Gunderson and Sackett (1984) and Bachevalier (1990) found a visual preference for novel patterns or objects within the first month of life. Older infant monkeys (6 weeks or more) showed more robust visual memory, in that they required less study time to show a significant preference for the novel stimulus (Gunderson and Swartz, 1986).

Other studies of visual discrimination ability in infant monkeys have used operant techniques similar to those routinely used for testing visual recognition in adult animals. Using a feeding-booth or home-cage choice apparatus designed specifically for infant monkeys, Zimmermann (1961) found, for example, that simple form discriminations (horizontal vs vertical stripes, or circle vs triangle) could be solved by 3 weeks of age, whereas color discrimination was possible by 10 days of age. Employing a Wisconsin General Test Apparatus (WGTA), using methods more or less identical to those used for adults, Harlow et al. (1960) studied the ability of monkeys ranging from 2 months to 1 year to discriminate among small, multidimensional objects and found that all age groups could solve the problem, with progressively older infants taking progressively fewer trials to reach criterion performance. Using a reduced WGTA, Bachevalier and Mishkin (see Bachevalier, 1990) further found that 3-4-month-old infant monkeys could learn long lists of object-pair discriminations (in their parlance, visual "habits") nearly as quickly as adult monkeys even with 24 hr delays between successive presentations of a given object pair. However, they also found that infant monkeys do not even begin to be able to learn a more complex form of visual recognition task, namely, delayed nonmatch to sample (DNMS), until they are about 4 months, and do not reach adult levels of ability until 2 years.

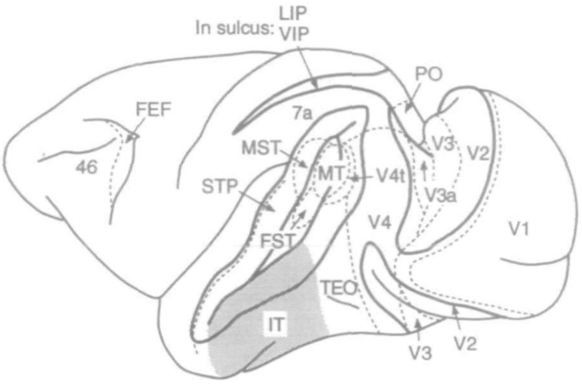


Figure 1. Location of visual areas, including IT cortex (*shaded area*), shown on a lateral view of the macaque brain in which posterior sulci have been "opened up." *FEF*, frontal eye field; *FST*, fundus of the superior temporal sulcus visual area; *LIP*, lateral intraparietal area; *MST*, medial superior temporal area; *MT*, middle temporal area; *PO*, parieto-occipital area; *STP*, superior temporal polysensory area; *VIP*, ventral intraparietal area; *V1, V2, V3, V3a, V4, V4t*, visual areas 1, 2, 3, 3a, 4, and transitional 4, respectively; *46*, cytoarchitectonic area 46.

Effects of Early Lesions of IT Cortex

To what extent do any of the abilities described above actually draw on IT cortex in the infant monkey? Early studies by Raisler and Harlow (1965), involving large lesions including area TEO and more posterior visual cortex as well as cytoarchitectonic area TE, indicated significant sparing of pattern recognition ability when such lesions were made as late as a year of age. Investigations of effects of dorsolateral frontal lesions in infancy (Goldman, 1971) confirmed that some portions of "association" cortex might remain uncommitted until well into the first year of life. A series of studies by Bachevalier and Mishkin and their colleagues, begun in the 1980s, has provided additional evidence that the contribution of IT to some aspects of visual behavior, like that of portions of frontal cortex, is a delayed one. They found, for example, that bilateral lesions of IT made in the first month of life spare visual recognition as assessed by DNMS tested at 10 months of age (reviewed in Bachevalier, 1990). Moreover, unlike lesions of dorsolateral frontal cortex, where the animal "grows into" a deficit (Goldman, 1971), DNMS ability remains intact several years subsequent to neonatal IT damage (Bachevalier and Mishkin, 1988). The lack of impairment on DNMS after early lesions of IT cortex may be at least partly explicable by the consideration that other structures contribute to performance on this task, even in adult animals (Bachevalier and Mishkin, 1986; Zola-Morgan and Squire, 1993). However, visual recognition capacity as as-

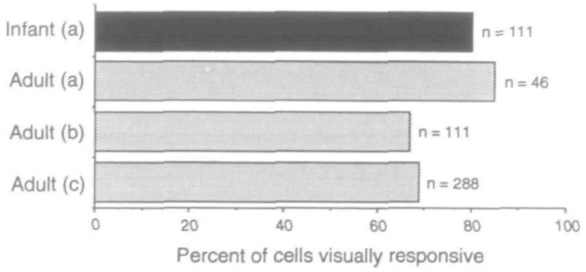


Figure 2. Incidence of visually responsive single neurons in IT cortex in awake infant and adult macaques performing a fixation task. Data are from, in *a*, Rodman et al. (1993b); *b*, Gross et al. (1979); and *c*, Richmond et al (1983). Infant sample was drawn from 93 IT neurons in four animals below 4 months of age and 18 neurons in one animal between 6 and 7 months at the time of recording.

sessed by the preferential viewing paradigm is also spared by early lesions of IT (Bachevalier, 1990). More critically, performance on the object-pairs visual discrimination task is also preserved after neonatal IT damage (Bachevalier et al., 1990), except for a transient deficit in female infants (see below), whether tested in infancy or later in life (Bachevalier and Mishkin, 1988). Thus, the sparing induced by early IT lesions appears to be a lasting one, suggesting that other structures are capable of compensating for at least some of the effects of early damage to this region.

Physiological Development of IT Cortex

In adult monkeys, the majority of IT cells are visually responsive. They are often selective for some aspect of stimulus shape, pattern, or color, although a minority of IT cells respond indiscriminately to nearly all stimuli tested. Most frequently, IT cells respond to a subset of a stimuli tested, whose unifying features are not always clear (see Gross et al., 1993, for discussion of coding properties of IT cells). Typically, IT neurons have large bilateral receptive fields with similar stimulus selectivity throughout, suggesting that they play a role in coding the identity of objects despite changes in their retinal position ("stimulus equivalence across retinal translation"; Gross and Mishkin, 1977). As mentioned above, a few IT cells are highly selective for specific stimuli, most notably faces. Are monkeys born with IT cells having these properties, or is an extended period of specific visual experience or neural maturation required for them to develop?

Response Properties in Infant IT

Receptive Fields and Incidence of Responsiveness

Our laboratory has compared the response properties of cells in IT cortex of infant monkeys 5 weeks to 7 months of age with those of IT cells in adults under both awake behaving and anesthetized conditions. Methods for recording in infant monkeys were adapted (Rodman, 1991) from standard procedures for recording in adult IT cortex. In awake behaving animals, the proportion of IT neurons that can be visually driven is not significantly different in infant and adult animals (Fig. 2), with no trend toward increasing numbers of responsive neurons present with increasing age within the age window studied (Rodman et al., 1993b). Receptive fields carefully plotted under anesthesia tend to be large and bilateral in IT cortex of adult monkeys (reviewed in Gross et al., 1993); this is also true in anesthetized infants (Fig. 3). Median IT field size is similar in infant and adult monkeys (about 20° on a side for both) and proportions of bilateral fields are likewise similar (~65%) (Rodman et al., 1991, 1993b). There is some evidence that receptive fields are notably smaller under awake, fixating conditions for infant monkeys (Rodman et al., 1993b), as others have found experimentally for adult monkeys (Richmond et al., 1983) or predicted on the basis of modeling studies (Gochin, in press).

Types of Stimulus Selectivity

Cells in infant IT show varying levels of selectivity for stimulus form (Figs. 4, 5). As in adult IT, a small proportion of cells in infant IT are selective for faces as a class of stimuli (Rodman et al., 1993b); a few, also as in adults, are selective for particular face images or particular face *views* (Fig. 4*A*). Selectivity for shape as defined by boundary curvature is similar in infant and adult IT cortex; a similar proportion of cells show tuning for the frequency of Fourier descriptor (FD) stimuli in both samples (Fig. 4*B*; see Schwartz et al., 1983, for details of the stimuli). We also found cells selective for color, for arbitrary geometrical patterns, and for particular 3D objects.

Degree of Stimulus Selectivity

The distribution of the overall *degree* of selectivity in the infant and adult IT samples was similar as well. As in adult IT cortex, while a few cells in infant IT respond only to a single image (e.g., top and bottom bar graphs in Fig. 5*A*), others respond to many but not all images in a tested set (e.g., middle bar graph in Fig. 5*A*), or to a smaller subset of stimuli that lack obvious common features. To compare the overall degree of selectivity of IT cells in infant and adult macaques, a repeated-measures ANOVA was performed on the response magnitude values for each cell across the different projected stimuli in our standard sets; the resultant distribution of *F* ratios (Fig. 5*B*) did not differ significantly between infant and adult samples. Moreover, for both infant and adult IT samples, the vast majority of *F* ratio values for individual cells were themselves highly significant, confirming that most cells in both groups had differential patterns of responsiveness useful for providing information about the identity of the stimulus (Rodman et al., 1993b, see also Gross et al., 1993, for discussion).

Strength of Signals

Unit Activity and Response Latency

Despite the adult-like stimulus selectivity of IT cells in infant macaques, they respond consistently more weakly than do IT cells in adult monkeys to a variety of stimuli (Fig. 6*A*). However, mean response magnitude for individual cells was not correlated with age

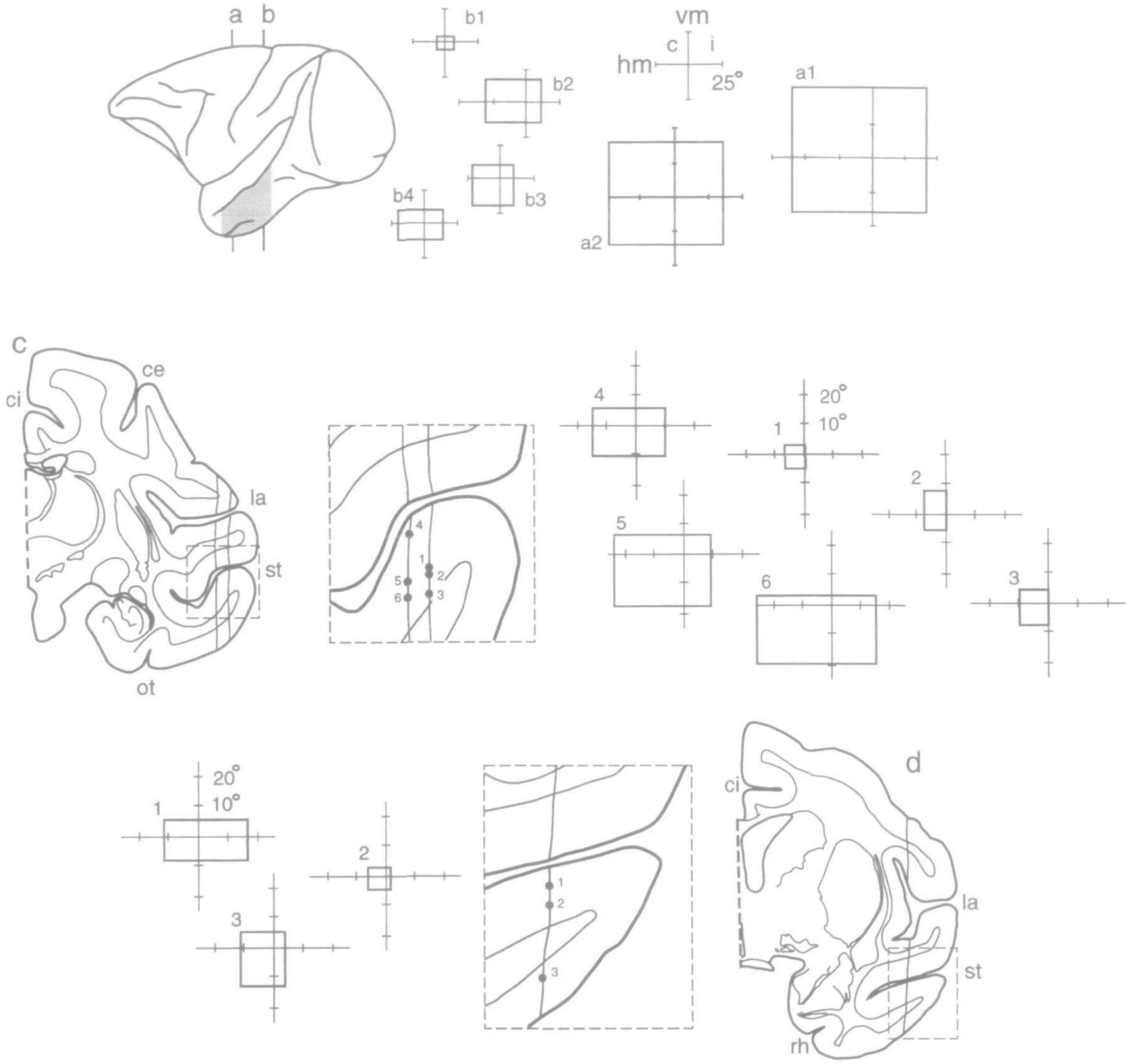


Figure 3. Receptive fields of IT cortex cells plotted in four electrode penetrations in anesthetized infant monkeys. *c*, contralateral visual field; *ce*, central sulcus; *ci*, cingulate sulcus; *hm*, horizontal meridian; *i*, ipsilateral visual field; *la*, lateral sulcus, *ot*, occipitotemporal sulcus; *rh*, rhinal sulcus; *st*, superior temporal sulcus; *vm*, vertical meridian. Adapted from Rodman et al. (1991).

at time of recording within our infant sample (Rodman et al., 1993b); this may be due in part to the fact that most of our data in alert infant monkeys were obtained in a relatively narrow window between 1.5 and 3.5 months. In addition, latencies to visual response are longer and more variable (Rodman et al., 1993b) than in adult monkeys. Moreover, visually driven activity in IT is almost entirely suppressed by anesthesia until about 4 months (Fig. 6*B*), despite the presence of responses in other visual cortical areas, and is less commonly elicited in animals 4-7 months than in adults (Rodman et al., 1991, 1993b). Interestingly, *spontaneous* activity levels are also depressed in infant IT cortex relative to adult IT in both anesthetized and awake behaving subjects (Fig. 6*C*). Thus, low levels of visually driven activity may reflect more general membrane properties of IT neurons, or cortical cells in general, in infant monkeys.

Metabolic Activity Levels

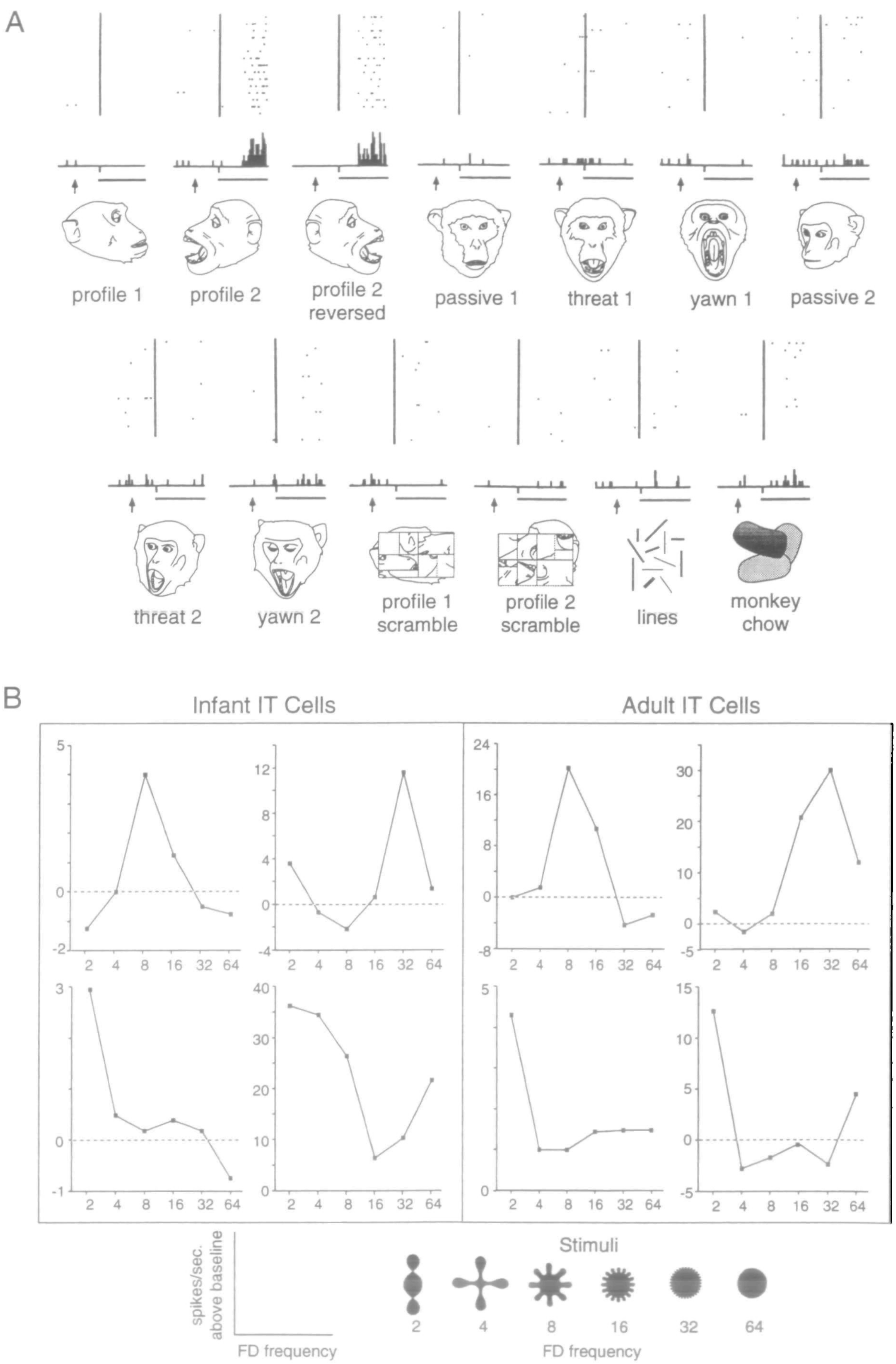
The absence of responses in IT cortex under anesthesia until the age of about 4 months and the weakness of driven and spontaneous activity in alert IT in the first few months are consistent with experiments on development of overall metabolic activity levels in temporal cortex. Using a 2-deoxyglucose technique to measure energy utilization, Bachevalier et al. (1991) showed that development of metabolic activity levels in IT during visual stimulation lagged behind that of more posterior visual areas and did not reach adult levels until about 4-6 months.

Anatomical Development of IT Cortex

Development of Connectivity

Cortical Connections

In adult monkeys, IT (area TE) receives visual information originating in striate cortex only indirectly, via


A
profile 1
profile 2
profile 2 reversed
passive 1
threat 1
yawn 1
passive 2
threat 2
yawn 2
profile 1 scramble
profile 2 scramble
lines
monkey chow
B
Infant IT Cells
Adult IT Cells
5
0
-2
12
8
4
0
-4
24
16
8
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-8
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10
0
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0
-5
2
4
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16
32
64
spikes/sec. above baseline
FD frequency
Stimuli
2
4
8
16
32
64
FD frequency

several stages in extrastriate cortex, such that direct visual inputs arise predominantly from areas TEO, parahippocampal cortex, and to a lesser extent V4. Significant inputs also arise from perirhinal cortex, area STP, and other regions of the anterior superior temporal sulcus, and ipsilateral frontal cortex (reviewed in Desimone and Ungerleider, 1989; Felleman and Van Essen, 1991; Gross et al., 1993). We have compared the cortical connectivity of IT in infant and adult monkeys by making injections of retrograde tracers (WGA-HRP or cholera toxin B-subunit) into IT in eight infant monkeys ranging from 2 to 18 weeks and in three adult animals. These studies reveal that the overall pattern of occipitotemporal inputs, that is, from areas that are mainly visual in function, are similar in adult monkeys and in infants (Figs. 7, 8) (Rodman et al., 1990, 1993a; Rodman and Consuelos, 1994). However, infant IT cortex appears to receive transient inputs from a set of areas not primarily visual in function, although these may have some role in visual behavior. These include (1) the insula (Fig. 8), (2) anterior cingulate cortex just above the corpus callosum (Figs. 8, 9*A*), and (3) the same portions of contralateral frontal cortex that are labeled within the ipsilateral hemisphere of both infants and adults (Figs. 7, 8). In addition, IT in monkeys 7 weeks of age or less receives proportionally more inputs from cells in the deep layers of the contralateral IT cortex than does IT in adult monkeys (Rodman et al., 1993a; Rodman and Consuelos, 1994; H. Rodman, K. Nace, and C. Gross, unpublished observations). In addition to these transient inputs to IT in infant monkeys, IT also provides more widespread *outputs* to perirhinal and parahippocampal cortices than are found in adult monkeys (Webster et al., 1991a; Rodman and Consuelos, 1994; Fig. 9*B*). Finally, visual area TEO (also called PIT; see Felleman and Van Essen, 1991) also provides transient projections to parahippocampal cortex in newborn monkeys (Webster et al., 1991a). Thus, both the cortical inputs and outputs of inferior temporal visual areas undergo considerable refinement in a postnatal period extending to at least 7 weeks after birth and possibly longer.

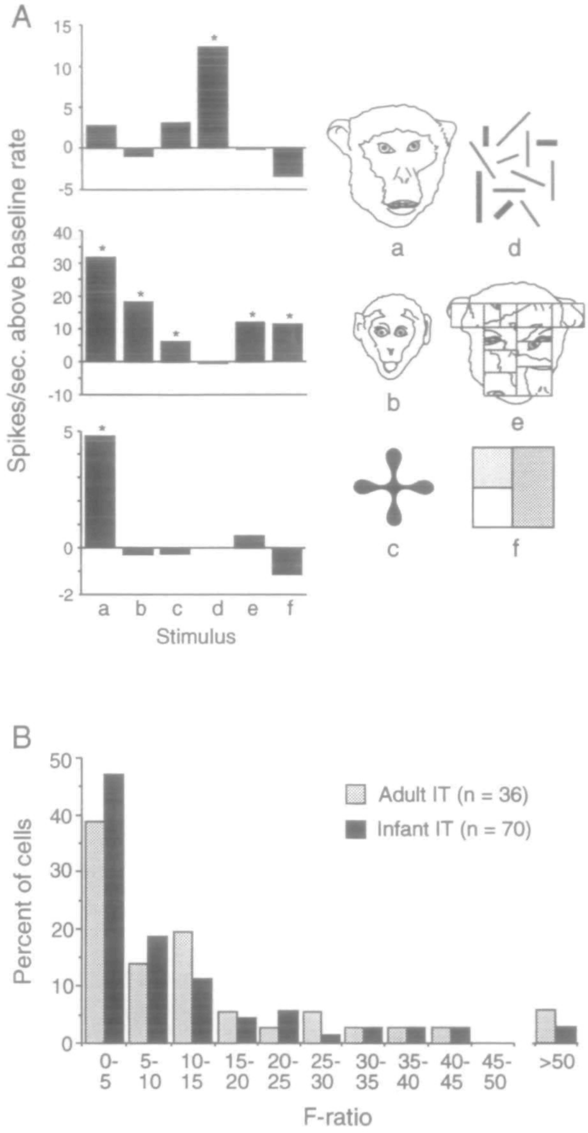

Figure 5. Patterns of selectivity of cells in IT cortex. *A*, Bar graphs illustrating responses to set of standard images (shown to the *right*) for three cells in infant IT cortex. *Asterisks* indicate statistically significant responses. Adapted from Rodman et al. (1991). *B*, Comparison of distributions of *F* ratios from repeated-measures ANOVA for each responsive IT cell in awake infant and adult monkeys. Adapted from Rodman et al. (1993b).

Subcortical Connections

In both infant and adult macaques, IT cortex (area TE) is reciprocally connected with the pulvinar, the amygdala, and the claustrum, and in addition receives inputs from a variety of nonvisual structures such as the locus coeruleus, raphe, basal forebrain, reticular formation, and several thalamic nuclei. The major nonreciprocal subcortical outputs of both TE and TEO target the striatum (Webster et al., 1993a; Rodman, Nace, and Gross, unpublished observations). However, in infant monkeys there also appears to be a widespread projection from TE to the superior colliculus as well as an increased projection to the nucleus medialis dorsalis of the thalamus and tail of the caudate (Webster et al., 1993b). In addition, inferior temporal area TEO provides an expanded projection to the amygdala in infancy, and receives an augmented projection from the dorsal lateral geniculate nucleus (Webster et al., 1991a, 1993b). Interestingly, the nor-

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Figure 4. Responses of neurons in IT cortex. Stimuli were black and white (FDs, lines) or colored (all other stimuli) images projected onto a screen and subtended 3–6° at the fovea. *A*, Cell in IT cortex of a 3-month-old alert infant monkey that was selective for a particular profile view. For each stimulus, the *arrow* under the poststimulus time histogram (PSTH) indicates the time at which the monkey fixated the central fixation spot, the *horizontal line* under the PSTH indicates the 500 msec period during which the stimulus was presented, and the *vertical line in the raster diagram* above each PSTH indicates the time of stimulus onset. *B*, Examples of responses tuned to boundary curvature (FD frequency) in IT cortex of awake infant and adult macaques. Adapted from Rodman et al. (1993b).

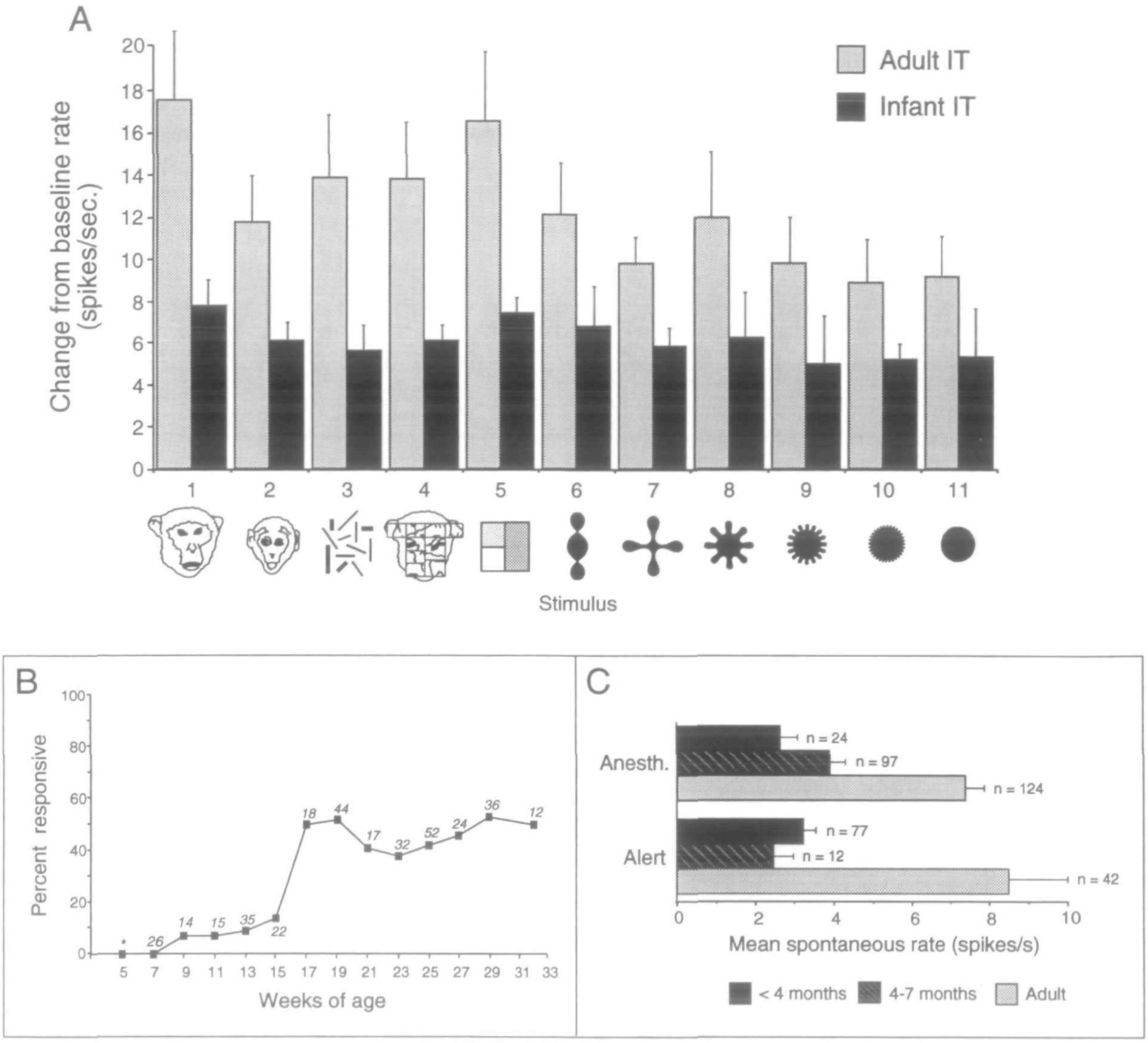

Figure 6. Signaling properties of IT cortex in infant monkeys. *A*, Overall mean response magnitudes of samples of IT cells in awake infant and adult macaques to individual members of standard set of projected stimuli. *B*, Emergence of IT responses as a function of age under anesthesia. *C*, Mean spontaneous activity values of IT neurons in infant and adult macaques. *A* and *B* are adapted from Rodman et al. (1993b).

mally transient expanded projection from TEO to the amygdala is maintained after early lesions of area TE (Webster et al., 1991b).

Development of Intrinsic and Commissural Fiber Systems

Primate IT cortex, like other "association" areas, is not fully myelinated until much later than other cortical regions, in fact not until well after the first year of life in monkeys (Flechsig, 1876; Yakovlev and Lecours, 1967). For example, at the age of 7 months, when both striate cortex and visual area MT are clearly recognizable in a myelin stain, the dense adult pattern of myelination is just beginning to emerge in IT (H. R. Rodman, unpublished observations). This gradual increase in myelination in the postnatal period is likely to be related to the longer latencies to visual response seen in infant IT cortex.

In adult monkeys, IT cortex receives interhemispheric information almost exclusively through the anterior commissure, with a small contribution from the corpus callosum to posterior parts of TE (Pandya et al., 1971; Zeki, 1973; Van Essen et al., 1982). Both the corpus callosum and anterior commissure go through

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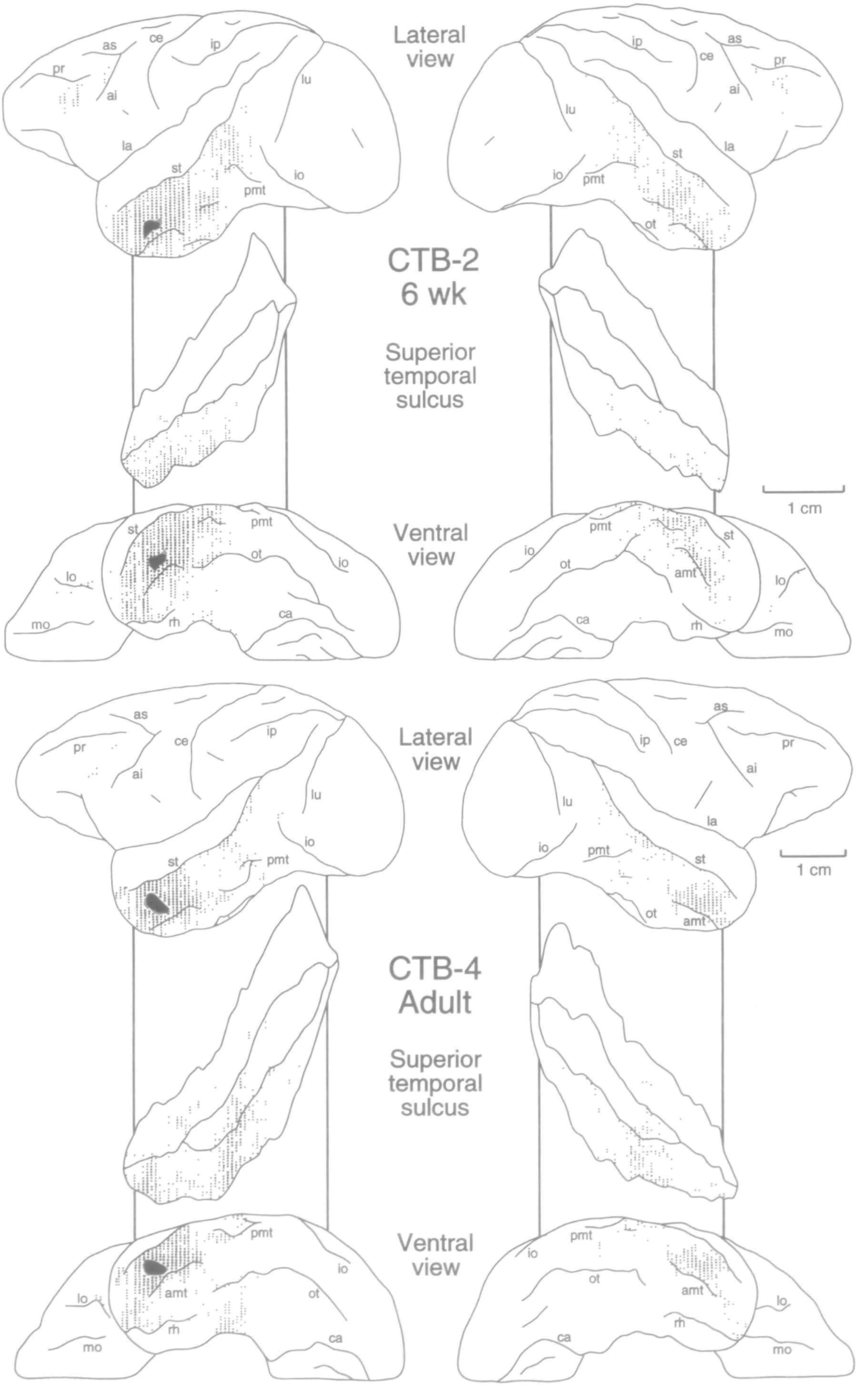
Figure 7. Overall pattern of retrograde labeling following injection of anterior IT cortex in an infant monkey and an adult monkey, shown on lateral and ventral reconstructions of each hemisphere and on flattenings of the superior temporal sulcus. *Small, medium,* and *large dots* represent sparse, moderate, and dense labeling, respectively. *ai*, inferior arcuate sulcus (s.); *amt*, anterior medial temporal s.; *as*, superior arcuate s.; *ca*, calcarine s., *ce*, central s.; *io*, inferior occipital s., *ip*, intraparietal s.; *la*, lateral s.; *lo*, lateral orbital s.; *lu*, lunate s.; *mo*, medial orbital s.; *ot*, occipitotemporal s.; *pmt*, posterior medial temporal s.; *pr*, principal s.; *rh*, rhinal s; *st*, superior temporal s.


Lateral view
CTB-2
6 wk
Superior temporal sulcus
Ventral view
1 cm
pr
as
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Lateral view
CTB-4
Adult
Superior temporal sulcus
Ventral view
1 cm

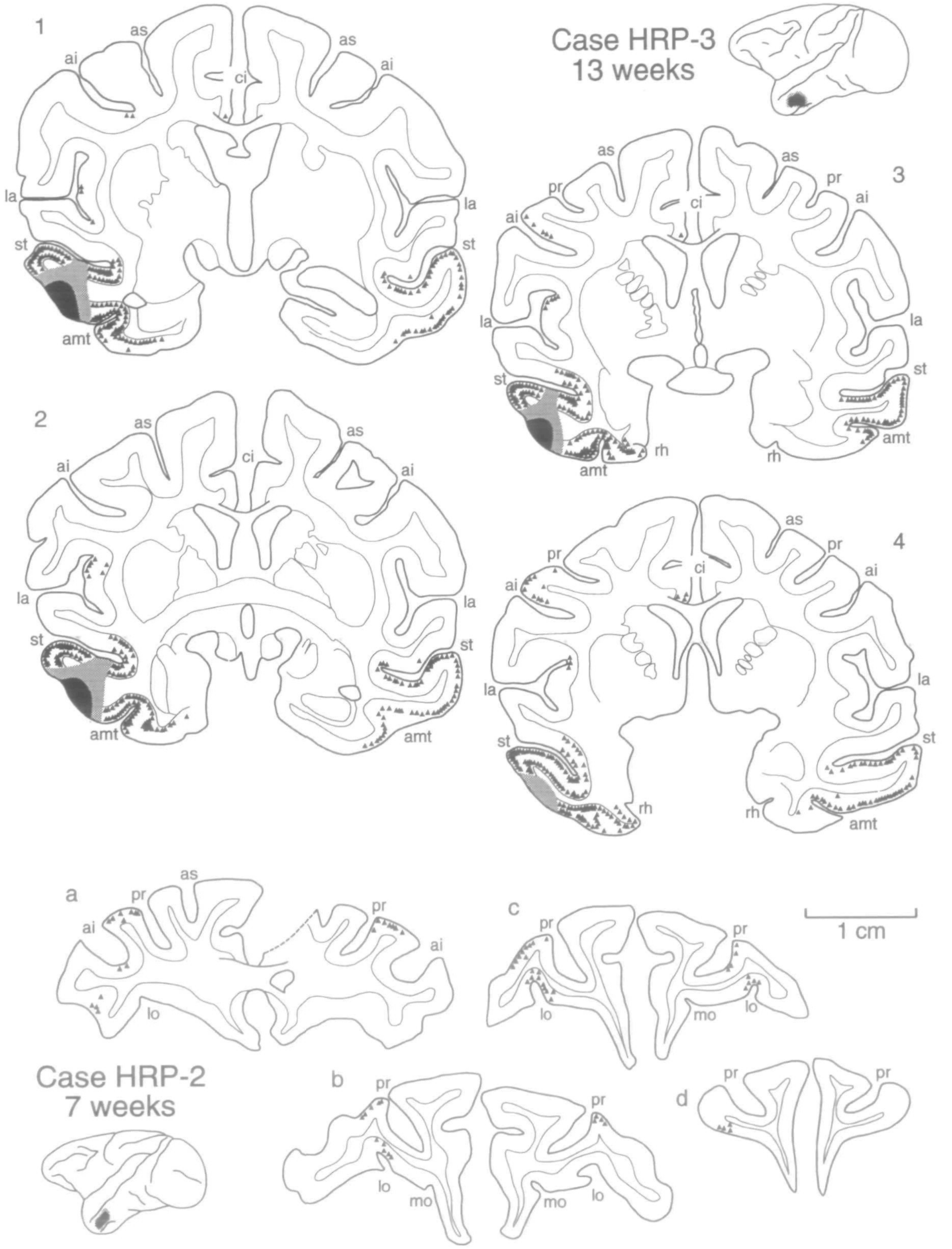

Figure 8. Cross sections illustrating locations of retrogradely labeled cells (*triangles*) in anterior temporal lobe (*A*) and frontal lobe (*B*) of infant monkeys. *Density of triangles* represents density of labeling. *A* is adapted from Rodman and Consuelos (1994). *ci*, cingulate sulcus; for other abbreviations, see Figure 7.

a postnatal period of massive retraction or loss of supernumerary axons that extends for 3-4 months after birth, although much of the loss takes place in the first postnatal month (LaMantia and Rakic, 1990, in press). Retraction of "exuberant" commissural connections has long been known as a feature of visual cortical development in many species (e.g., Innocenti et al., 1977; Berman and Payne, 1982; Cusick and Lund,

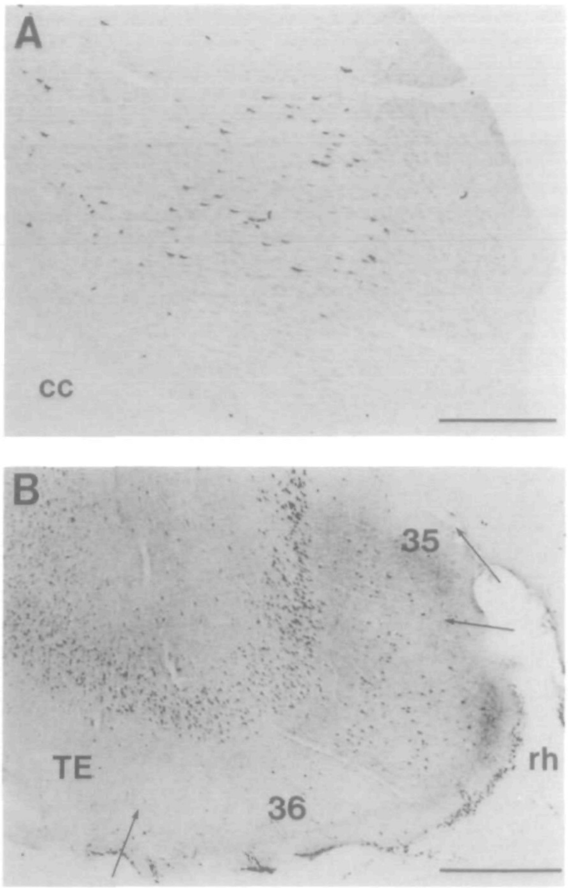

Figure 9. Bright-field photomicrographs of WGA-HRP labeling in 7-week-old infant monkey. Neutral red counterstain. *A*, Cingulate cortex. *cc*, corpus callosum. *B*, Rhinal cortex. Note anterograde label in layers I and IV. *35, 36*, cytoarchitectonic areas of the rhinal cortex; *rh*, rhinal sulcus. Adapted from Rodman and Consuelos (1994). Scale bars: *A*, 200 μm; *B*, 500 μm.

1982), but has appeared less critical in monkey (e.g., Dehay et al., 1986). Presumably, the transient projections we have found from contralateral frontal cortex and deep layers of contralateral IT are among those eliminated in the postnatal period of reshaping of commissural connections. The period of postnatal axon elimination in these commissures largely coincides with the postnatal period of cortical synaptogenesis prior to eventual reduction of synapse number back to adult levels beginning in the second half of the first year (e.g., Rakic et al., 1986), and LaMantia and Rakic (1990) suggest that this axon elimination may help refine local synaptic circuitry. In the case of IT cortex, loss of commissural connections from contralateral temporal cortex may contribute to the establishment of large bilateral receptive fields with qualitatively similar response properties throughout (reviewed in Gross et al., 1993).

Development of Specific Circuitry within IT Cortex

A remarkable synchrony of overproduction of both synaptic contacts (Rakic et al., 1986) and neurotransmitter receptors (Lidow et al., 1991) takes place within the first 2-4 months after birth in a variety of cortical areas, including frontal association cortex as well as primary visual and motor cortices. Very little is known about development of synaptic contacts or chemically specific circuitry within IT cortex itself, although there is no good reason to suspect that IT deviates from the pattern described by Rakic et al. and Lidow et al. for other cortical areas. Concentrations and rates of synthesis of neurotransmitter molecules themselves, however, are known to have more regionally diverse developmental schedules (Goldman-Rakic and Brown, 1982), although no data are presently available for IT.

In adult monkeys, the basal forebrain cholinergic system projects to IT, as well as to other cortical areas, and has been suggested to play a role in the formation of visual object memories (e.g., Aigner et al., 1991), possibly by influencing attentional processes (Voytko et al., 1992; Zola-Morgan and Squire, 1993). Receptor binding studies indicate that at birth muscarinic cholinergic ligand binding is relatively low and undifferentiated in all visual areas, including IT, outside of the primary visual cortex, where the adult laminar pattern is just beginning to emerge (Bachevalier et al., 1991). Further ontogenetic analysis of this system may well provide insights into the development of IT function.

Sex Differences in the Development of IT Cortex

Bachevalier and colleagues found that male infant rhesus monkeys take, on average, several weeks longer to be able to perform on the object-pair discrimination task described above (reviewed in Bachevalier and Hagger, 1991). The absolute level of performance shown by male infants was tightly and inversely correlated with plasma testosterone levels (both male performance and testosterone levels varied widely overall), and the overall performance of infant males on the task could be elevated to that of females as a result of neonatal gonadectomy. These findings led Bachevalier and colleagues to hypothesize that high levels of circulating testosterone around birth in male monkeys retard the maturation of either IT itself or its projection targets, resulting in poorer discrimination performance relative to female infants. Consistent with this view, neonatal IT lesions lead to a transient impairment on the object discrimination task only in infant females, suggesting that the cortex begins to be functionally committed earlier in female monkeys (Bachevalier and Hagger, 1991).

In our own physiological studies, we did not find consistent differences in response properties in alert infant monkeys as a function of gender, possibly because of the use of a limited number of animals and the small size of the overall data sample. In anesthetized infants, however, we found a pattern of responsiveness suggestive of that reported by Bachevalier and Hagger (1991). Whereas all infant female monkeys tested had similar levels of visual responsiveness under anesthesia at 4-7 months of age, in male infants the incidence of responsiveness varied more widely and was largely suppressed in two of three cases, possibly indicative of an extended period of immature functioning in these infants (Fig. 10). Clearly, more

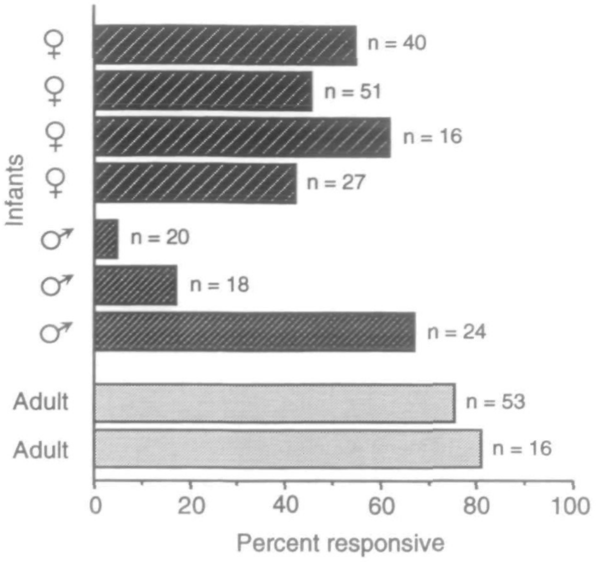

Figure 10. Visual responsiveness of isolated single neurons in anesthetized IT cortex as a function of gender in infant monkeys, and in male adults.

work is needed to determine if circulating androgens have an organizational effect on IT cortex that is expressed at the level of unit properties, as well as behavior, in the first year in life in the macaque.

Discussion

The delayed contribution of IT cortex to visual recognition, and the slow development of adult capacity are evidently not due to a *nonspecificity* of IT neuronal responses early in life. Nor do these phenomena appear to be due to an immaturity of afferent cortical projections providing visual signals. Instead, the limited role of IT early in life and the protracted maturation of visual recognition learning may reflect the weakness of neuronal signals deriving from IT in at least the first half year, as reflected in the low response magnitudes of infant IT cells, their long latencies, and susceptibility to anesthesia. Interactions between IT and nonvisual cortical areas may be important in the emergence of IT's role in visual memory. In fact, an immature pattern of connectivity in infant monkeys was seen specifically with portions of cortex known to play a role in visual memory and attention, namely, frontal, rhinal, and cingulate cortex, and from the insula, a polymodal association area.

On one hand, the immaturity of IT cortex within the first few postnatal months appears to reflect phenomena specific to IT cortex, or at least to "high-order" cortical regions. For example, we found that suppression of evoked and spontaneous activity under anesthesia early in life was relatively specific to IT, and its myelination and callosal connectivity lag behind that of other visual cortical areas such as striate cortex. On the other hand, it is intriguing that ontogenetic changes in pattern recognition behavior, physiology, and cortical connectivity of IT cortex all take place within a developmental window characterized by rapid accretion of synapses and receptor sites throughout neocortex. Thus, the postnatal development of IT is also likely to reflect developmental mechanisms common to diverse cortical regions (see also Bourgeois et al., 1994).

Four classes of questions appear particularly important in future analysis of the development of IT cortex, as follows.

What Developmental Changes Take Place in the Ability of IT Neurons to Code (Represent) Visual Objects, and What Do These Tell Us about the Extent to Which Circuitry in IT Cortex Is Prewired or Emergent?

In our initial studies, we found cells in alert infant monkeys capable of coding faces as a class of stimuli (those that responded to faces in general), cells that were selectively responsive to specific face views (i.e, profiles), cells sensitive to boundary curvature in much the same way as cells in adults, and even cells selective for color. Moreover, degree of stimulus selectivity is similarly distributed in adult and infant monkeys. However, these results are, in many ways, only a beginning.

Selectivity Patterns and the Coding of Objects

Little is known at present of the critical features underlying response patterns of IT cells in either infant or adult monkeys. In adults, the work of Tanaka et al. (1991) suggests that the selectivity patterns of some IT neurons can be broken down into relatively simple configurations of stimuli, but does not suggest a "basis set" or alphabet of any sort (see also Albright and Gross, 1990, for discussion of the inadequacy of Fourier descriptors as an "alphabet" for shape used by IT cells). There is evidence that some face-selective neurons in adult monkeys are driven by specific facial features, but others are clearly driven by some aspect of the "gestalt" of a face (reviewed in Desimone, 1991; Gross and Sergent, 1992). In addition, selectivity patterns of *groups* or ensembles of neurons may convey more information about the identity of objects than those of individual neurons (Rolls, 1992; Gochin et al., 1994). Further studies are needed to determine whether "critical features" for IT cells are relatively restricted early in development, and whether ensemble formation (i.e., information content inherent in groups of neurons) has a developmental time course that can be related to other behavioral or physiological changes.

Perceptual Constancies and Frames of Reference

Both lesion studies and physiology suggest that IT is involved in recognizing the identity of stimuli despite changes in their location in the visual field, changes in perspective, and changes in lighting and size. Physiologically, IT cells in adult monkeys tend to retain their selectivity for a given stimulus across changes in these parameters (e.g., Schwartz et al., 1983), and this property has been believed to play an important role in perceptual constancy of objects (Gross and Mishkin, 1977). However, we do not yet know when IT cells begin to show selectivity invariant over changes in retinal position, over changes in stimulus size, or over changes in perspective of view of a given object. There are several reasons why these questions are important theoretically. First, maintained selectivity for shape at different locations in the visual field or with stimuli of different sizes would confirm that infant IT cells, like adult ones, generate responses on the basis of something other than local features. Second, although both adult humans and monkeys can identify visual forms under varied or degraded conditions, children are markedly poorer at it (Carey and Diamond, 1977; Foreman and Hemmings, 1987; Diamond and Carey, 1990), and the gradual emergence of perceptual constancies may be related to the emergence of invariance of response in IT. Third, invariance of selectivity relates to the distinction popularized by Marr (1982) between object encoding in viewer-centered (i.e., perspective-dependent) and object-centered (perspective-independent) frames of reference, a distinction that has been applied to IT cells (Perrett et al., 1992; Rolls, 1992). In adult monkeys, especially with regard to face-selective cells, there appear to be separate populations of cells that code objects relative to these different coordinate systems, and the two frames of reference (relative to oneself/relative to object) may independently provide biologically useful information (see Perrett and Mistlin, 1990). A general feature of the development of pattern recognition may be the generation of object-centered frames of reference as the animal gains experience with a given object under different viewing conditions.

What Developmental Changes Take Place in the Ability of IT Cells to Contribute to Memory Functions and to Provide Signals about Stimulus Novelty and Familiarity?

As mentioned in the introductory remarks, IT cortex appears to play a role not only in representing objects but also in providing signals about their novelty, familiarity, and/or recency of appearance, signals that may help redirect visual attention as well as playing a role in memory (reviewed in Desimone, 1992; Gross et al., 1993; Desimone et al., in press). The types of signals that IT cells provide that are candidates for memory traces or more generally indicators of stimulus familiarity or novelty include (1) passive "habituation" and response suppression to repeated stimulation with a given object; (2) differences in responses to match and nonmatch stimuli in delayed match-to-sample (DMS) tasks, including enhanced responses when a specific object is anticipated; (3) delay-period activity in DMS tasks, a possible correlate of working memory or visual rehearsal when an object is not physically present; and (4) changes in stimulus selectivity with learning. Because of the behavioral limitations of very young infant monkeys, changes in responsiveness and in delay-period activity in DMS tasks (e.g., Gross et al., 1979; Fuster, 1990; Colombo and Gross, 1994; Desimone et al., in press) are unlikely to be possible to study in a developmental context. However, some of the types of putative memory signals identified above should be amenable to study in infant monkeys. Habituation to repeated stimulus presentation is, in fact, found under passive conditions (anesthesia) in both adult monkeys (Miller et al., 1991a) and infant ones (Rodman et al., 1993b). In adult monkeys, suppression of responses to stimuli that have become familiar has now been reported by several groups (Baylis and Rolls, 1987; Miller et al., 1991b), and can be long-lasting (Riches et al., 1991); systematic decline of response magnitude with familiarity has not yet been investigated developmentally. Likewise, enhancement of response as a function of attention, task relevance, or expectation of a specific object (Richmond and Sato, 1987; Fuster, 1990; Spitzer and Richmond, 1991; Desimone et al., in press) has not been addressed in infant monkeys. Finally, changes in patterns of selectivity in IT in adult monkeys have been reported to take place both rapidly (Rolls et al., 1989) and over periods of time (Miyashita, 1988; Kobatake et al., 1993); these can even include generation of selectivity for novel objects not normally explicitly represented by IT (Logothetis et al., 1993). It will be of great interest to determine if these and other plastic changes in IT cortex arise in concert with behavioral milestones such as the emergence of capacity on pattern recognition tasks within the first 6 months, or of adult-like levels of ability somewhat later in ontogeny.

How Does the Development of Interactions Between IT Cortex and Other Brain Regions Contribute to IT's Role in Visual Behavior?

The results of our anatomical studies suggest that interactions between IT and areas that are not primarily visual in nature may be important in the development of IT's role in visual recognition functions. In fact, an immature pattern of connectivity is present in infant monkeys specifically with areas known to play a role in visual attention and memory, that is, frontal, rhinal, and cingulate cortex (see Rodman et al., 1993b, for references). These areas may themselves be immature, precluding the completion of circuits between IT and other areas that underlie visual memory. Changes in patterns of connectivity between IT cortex and frontal cortex are especially interesting in this regard. In adult monkeys, lesions of the portions of frontal cortex connected with IT produce impairments in visual recognition (Bachevalier and Mishkin, 1986), and these regions show stimulus-selective visual responses and maintained activity in the delay period of visual match-to-sample tasks (Wilson et al., 1993; Desimone et al., in press). Moreover, Fuster et al. (1985) used a cooling paradigm to show mutual influences between IT cortex and frontal cortex during the performance of a visual discrimination task. These phenomena and other observations led Desimone et al. (in press) to propose that frontal cortex exerts a "top-down" influence on IT neurons that "primes" them to respond strongly to a stimulus the monkey is anticipating. In support of this notion, it has been recently reported that certain pharmacological manipulations that bolster or impair visual recognition performance lead to increased or decreased coupling, respectively, of neuronal responses in frontal cortex and in IT (Dudkin et al., 1993a,b). Thus, a mature pattern of connectivity between IT cortex and frontal cortex may be a precondition to the full participation of IT in visual recognition memory.

What Types of Mechanisms Are Used to Translate Maturation of Circuitry and/or Environmental Stimulation into Changes in Coding and Mnemonic Abilities, and Are These Mechanisms Similar in the Developing and Adult Animal?

Temporal Contiguity Alone

Mere temporal contiguity may be an important mechanism of association formation in the nervous system, both during development and in mature animals (Hebb, 1949; Stryker, 1991). With regard to IT cortex, Miyashita (1988) has shown that temporal contiguity of objects without any explicit functional association is sufficient to cause them to be conjointly represented in IT cortex, although explicit association is also effective (Sakai and Miyashita, 1991). Since different views of objects tend to be presented in close temporal succession (e.g., when one looks at an object while either the object or the viewer is in motion), mere temporal succession with a specific range of delays between successive views may be a critical factor in the generation both of object-centered frames of reference and of other perceptual constancies. Experiments measuring efficacy of changes in selectivity patterns of IT neurons as a function of passive temporal association should indicate whether this mechanism is particularly important during development.

Experience with Stimuli of an Affective Nature or in Affective Contexts

Experience with stimuli of an affective nature or in affective contexts may also be a crucial mechanism by which circuitry emerges in IT, both in an early "critical period" and later in life. For example, faces may be special for primates—and come to be disproportionally represented in IT cortex—merely because they are highly salient stimuli that appear in highly emotionally significant contexts. In particular, when viewed early in life, faces have two critical characteristics: they signify enormously important resources related to sustenance, warmth, and survival, and second, they differ only in relatively subtle ways that command attentional resources. It should be possible to test the hypothesis that these are the aspects of face stimuli that cause them to acquire specialized processing substrates in temporal cortex by asking if animals exposed in infancy to arbitrary but subtly differing geometrical stimuli in important contexts grow up to have disproportionate numbers of IT cells devoted to their analysis. Investigation of responses to face stimuli in neonatal monkeys and in monkeys brought up with restricted exposure to faces would also bear on this question.

Two "Sensitive Periods" for the Development of "Association" Cortices?

The majority of the experiments described in this article have been predicated on the assumption that the most important ontogenetic changes in IT cortex take place during a sensitive period early in life, that is, within the first half year or so. There are a number of good reasons for this; after all, critical windows for development of circuitry in striate cortex consist of the first several months of postnatal life, important behavioral capacities emerge during this period, and there are important changes in the connectivity of IT cortex within the first half year. Finally, basic properties of IT neurons are adult-like early in life, at least by 4 months. All of this suggests that important developmental changes do take place within the first half year, changes that may build on or reflect an innate predisposition of IT cells to respond selectively to certain types of stimuli.

However, there may be a second and much more protracted developmental process in what might loosely be called "association" areas such as IT to permit the development of mature function, as reflected in the long period of maturation of pattern recognition functions, the weakness of signals deriving from IT cortex in at least the first 7 months of life, and the very protracted time course of myelination. As described in the previous section, there is accumulating evidence that a characteristic property of adult IT cells seems to be an ability to change patterns of selectivity and also levels of responsiveness as the animal encounters new and significant stimuli that must be represented within the pattern recognition system. The important property that develops within IT and other so-called "high-order" cortices may not be response patterns per se but rather the efficient reorganization of circuitry as the animal becomes more practiced at learning new visual objects and patterns. Accordingly, the development of so-called "high-order" or association areas such as IT may include a second sensitive period characterized by gradual acquisition of types of plasticity not present in infancy and that may encompass the greater part of adult life. If this is true, one might predict that response patterns of individual neurons in temporal cortex are actually *less* able to be influenced by environmental manipulations in infancy than later in life (Rodman et al., 1993b).

Notes

1. In this article, "area IT" or "IT cortex" is considered to be synonymous with cytoarchitectonic area TE; in a few sections, where indicated, data related to cortex immediately posterior to TE (cytoarchitectonic area TEO or "PIT") are also described, as this region is included in the designation "inferior temporal cortex" by some workers.

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