DEVELOPMENT OF BRAIN SUBSTRATES FOR PATTERN RECOGNITION IN PRIMATES: PHYSIOLOGICAL AND CONNECTIONAL STUDIES OF INFERIOR TEMPORAL CORTEX IN INFANT MONKEYS

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ABSTRACT. Inferior temporal (IT) cortex is known to be critical for visual pattern perception and recognition in adult monkeys, but not in infant ones. We found that cells in IT cortex of infant monkeys showed adult-like response properties, including form selectivity for complex patterns such as faces, as early as the second month of life. However, the neural responses were weaker and of longer latency, and moreover were virtually absent under anesthesia below about four months of age. Anatomical inputs from visual cortical regions were adult like early in infancy, whereas connectivity patterns with non-visual cortical regions appeared to have a more protracted period of maturation.

1. Introduction

Both humans and nonhuman primates, such as macaque monkeys, are particularly gifted at the cognitive process we refer to as visual pattern recognition. In macaques, some pattern recognition abilities are present in the first weeks of life, whereas others do not attain their adult status until at least three years of age. For example, if a preferential viewing paradigm is used, infant monkeys can distinguish novel stimuli from familiar ones by two weeks, and learn simple brightness and form discriminations within the first month of life (reviewed in Booth and Sackett, 1975; Brickson and Bachevalier, 1984). On the other hand, infant monkeys do not even begin to learn a delayed non-matching-to-sample (DNMS) object recognition task until about four months, and do not achieve adult levels of visual discrimination ability until several years of age (Booth and Sackett, 1975; Bachevalier and Mishkin, 1984). There is a parallel in human development, where, for example, there is some evidence for face recognition in neonates, but adult-like processing strategies for faces take years to develop (Ellis, 1992).

In adult monkeys, a crucial brain substrate for normal pattern recognition capacity is the inferior temporal (IT) cortex, shown in Fig. 1A. The view that IT is critical for visual pattern recognition derives from several lines of evidence (reviewed in Gross, 1973, 1992). First, lesions of this cortex in monkeys or of topologically equivalent cortex in humans produce deficits both in recognizing previously learned patterns and objects and in forming new memories of such visual stimuli. Second, the response properties of cells in IT cortex strongly
suggest that IT participates in coding visual objects. That is, IT cells are frequently selective for some aspect of stimulus shape or for color, and some cells in IT cortex have responses which can be highly specific for behaviorally important stimuli such as primate faces. Moreover, nearly all IT cells respond best to stimuli at the center of gaze, which is consistent with the crucial role of the center of gaze in form perception. Although IT cells respond best at the fovea, their receptive fields are in fact very large and usually extend well into both halves of visual space. Stimulus selectivity is usually similar in different parts of the central portion of the receptive field, just as recognition of familiar objects is largely independent of retinal locus.

![Diagram](Image)

**Figure 1:** A: Location of recording area within inferior temporal cortex is shown as the shaded region on a lateral view of a macaque monkey brain. a, arcuate sulcus; ce, central sulcus; io, inferior temporal sulcus; ip, intraparietal sulcus; la, lateral sulcus; lu, lunate sulcus; pm, posterior medial temporal sulcus; pr, principal sulcus; st, superior temporal sulcus. B: Sequence of major cortical processing stages by which visual information reaches area IT and is passed on to subsequent regions. V1, primary visual or striate cortex; V2, V4 and TEO, extrastriate visual areas of the "ventral visual pathway" (Ungerleider and Mishkin, 1982); ER, entorhinal cortex; H, hippocampus; PH, parahippocampal cortex; PR, perirhinal cortex.

IT cortex (defined here as coextensive with cytoarchitectonic area TE) appears to be the final purely visual processing stage in the ventral occipito-temporal cortical pathway specialized for pattern recognition (Fig. 1B). IT cortex receives visual input from V1 (striate cortex) via a route involving projections from V1 to V2, from V2 to V4, and from V4 to IT both directly and via area TEO. From IT, visual information reaches the hippocampus via synaptic stages in parahippocampal, perirhinal cortex and entorhinal cortex. Direct projections from IT to the striatum and frontal cortex are probably also involved in storage of information about visual objects.

Although we know a good deal about IT cortex in adult monkeys, particularly about its function and physiology, we know much less about the development of this crucial region of cortex. What we do know suggests some interesting paradoxes. For example, although IT lesions produce severe pattern perception and recognition impairments in adult monkeys, they have little or no effect in monkeys in the first year of age or so. This was first shown by Raister and Harlow (1965) and more recently confirmed in detail for a variety of tasks in a series of studies by Bachevalier and colleagues (e.g., Hagger et al., 1985; Bachevalier et al. 1990). Second, as described above, many of the pattern recognition functions that IT supports themselves show a very protracted period of development. Yet, some rudimentary abilities are present close to birth. In order to gain insight into the reasons for the delayed contribution of IT cortex to pattern recognition functions, we began a series of studies on the physiology and afferent connectivity of IT cortex in infant monkeys within approximately the first seven months of life.

2. Physiological Studies

Neural activity in IT cortex in infant monkeys was studied both in animals anesthetized with nitrous oxide and oxygen and in awake animals taught to perform a behavioral eye fixation task. Methods for recording neural activity and behavioral training and general procedures for maintenance and comfort of the infant monkeys are detailed in Rodman (1991).

2.1 Visual Responsiveness

We began by recording from infants between four and seven months of age under nitrous oxide anesthesia and then moved to younger anesthetized infants. We reasoned that use of the anesthetized, immobilized paradigm would allow for more accurate plotting of receptive fields and also allow for comparisons with our laboratory's extensive previous work on adult animals using this paradigm. In addition, we were initially uncertain of the feasibility of recording from awake infant monkeys. Using both three-dimensional objects and projected slides as stimuli, we found that about only about half of the IT cells studied in the anesthetized 4-7 month olds were visually responsive, compared to about 80% in adults (Fig. 2). In monkeys less than four months old, even fewer (about 10%) could be visually driven. Moreover, in the youngest anesthetized infants, action potentials in IT were small and difficult to isolate from background activity, which tended to have a bursty quality. As a control to ascertain that the lack of IT responsiveness was not a general artifact of the recording conditions, we recorded in striate cortex and visual area MT in several of the same sessions in which we failed to find visual responses in IT in infants below four months. Cells in these areas were typically responsive (29 of 34 sites) and stimulus selective, as in the adult. Cells in anesthetized infant MT, for example, had direction tuning curves of comparable bandwidth to that seen in adult MT.

At the time we were recording in anesthetized infant monkeys, the emergence of responses under anesthesia at the rather late age of about four months appeared to fit in quite well with what was known of the development of IT cortex from behavioral data. For example, it is just about at four months that infant monkeys start to be able to do the DNMS task, which is one the commonest measures of object recognition ability in monkeys (Bachevalier and Mishkin, 1984). In addition, Hagger et al. (1988) were finding that the development of metabolic activity levels in IT, using a radiolabeled glucose uptake measure, lagged behind those of earlier visual cortical areas and in fact did not reach adult levels until...
about four months. Still, it seemed possible that cells in IT, which in adults can be affected by a variety of behavioral or "nonretinal" variables (see Gross et al., 1992), might be particularly susceptible to the effects of anesthesia in a very young animal even when cells in other areas were not. Accordingly, we set out to record from IT in awake behaving infant monkeys.

We were able to implant infant monkeys with eye coils for monitoring eye movements (Robinson, 1963) and then train them to fixate so that recording in IT cortex was possible as early as 5 weeks. Using this paradigm, we obtained a very different picture of visual responsiveness in infant IT cortex from that obtained using anesthetized infant monkeys. The incidence of visual responses in these alert animals (see Fig. 2) was not significantly different from that found in either anesthetized adult monkeys or awake behaving ones.

![Graph](image)

**Figure 2**: Incidence of visually responsive isolated neurons encountered in IT in anesthetized and awake behaving infant monkeys and in comparable samples from adults. (a), from Desimone et al., 1984; (b), from Richmond et al., 1983. Modified from Rodman et al. (1991).

Moreover, the recording quality in IT was markedly superior in alert infants to that found in anesthetized ones of the same age, with single units being relatively easier to isolate from background and hold for extended periods of time.

To further compare the visual responsiveness of IT cortex in alert infant and adult monkeys, we made control recordings in an alert adult monkey using identical methods and stimuli. Because of the better recording quality in IT in alert infants as compared to anesthetized ones, we were able to make quantitative measurements of response magnitude to variety of projected images in the infants as well as in the control adult. The average response magnitude (in deviation from baseline firing rate) is shown for each of our standard stimuli for both the infant and adult samples in Fig. 3. Despite the similar incidence of visual responsiveness in the infant and adult samples, IT cells in the infants responded significantly more weakly than did IT cells in the adults. For most stimuli, the average response elicited in the adult IT cells was just about twice that obtained from infant IT cells, showing that the weaker overall response was not due to the ineffectiveness of a few particular stimuli. The overall mean response of the infant IT neurons was approximately 5.2 s/s above (or below in the case of inhibitory responses) the spontaneous rate, compared with an overall mean of 12.6 in adults. Within the infant sample, mean response rate was not, however, correlated with age at the time of recording. Consistent with the smaller magnitude of visual responses in infant IT, infant IT responses had significantly longer latencies with a mean of 196 ms. in the infants vs. 140 ms. in the adult.

![Graph](image)

**Figure 3**: Overall distributions of mean response magnitudes to a set of standard projected stimuli for awake infants and adult macaques. Mean response magnitudes in B are derived from neurons giving statistically significant responses to the stimulus in question and range from 13-26 cells per stimulus in the infant (mean = 18) and from 7-21 cells per stimulus in the adult (mean = 13). See also legend to Fig. 4.

### 2.2 Stimulus selectivity

Although the magnitude of response of neurons in alert infant IT cortex was reduced overall, the incidence and features of stimulus selectivity observed in the alert infant monkeys were strikingly similar to those observed in IT cells of both anesthetized and unanesthetized adult monkeys. As early as the second month of life, individual IT neurons exhibited responses selective for shape (as defined by boundary curvature), for geometrical patterns, and for color. Finally, a few cells showed responses selective for faces. Patterns of stimulus selectivity...
for three IT neurons recorded in awake infant monkeys are shown in Fig. 4. The cell in 4A, recorded in a five and a half week old animal, gave a consistent, long-latency response to an adult monkey face, but not to a scrambled version of the same face, to the face of an infant monkey, or to various control stimuli. 4B illustrates another type of face selective cell also found in adult monkeys, namely one whose responses were selective for profiles. 4C illustrates a cell which responded well not to face stimuli but rather to the black and white images, varying in boundary curvature, which we refer to as “FD stimuli” (Schwartz et al., 1983). As in adult monkeys, either anesthetized or alert, many infant IT cells responded to these stimuli with responses which were graded as a function of the “frequency” (number of lobes) of the FD stimulus.

As a whole, IT neurons in both infant and adult samples were very heterogeneous in their stimulus selectivity. While some, like those in Fig. 4, responded best or only to a particular stimulus or stimulus class, others fired well to most of the stimuli, and still others responded well to a small number of stimuli whose common features were not obvious. To compare the overall selectivity of IT cells in the alert infant and adult samples, we performed a repeated measures analysis of variance of the response magnitude for each cell across the different stimuli, and plotted the ensuing distributions of F-ratios. These distributions did not differ significantly for the infant and adult samples, indicating similar overall levels of selectivity.

Although we encountered far fewer responsive neurons in the anesthetized infant animals, as described above, those which did respond were very similar to cells in the alert infants and adults and in the anesthetized adults we have studied before. Because of the tendency of neurons in anesthetized IT to respond better to three-dimensional objects than to projected images, and because of the difficulties in isolating and holding cells, we were not able to perform the quantitative analysis of responses used for the alert animals on a large number of cells in the anesthetized infant group. However, we did find examples of cells selective for faces, for shape, and for color employing objects in addition to the standard projected slides.

2.3 OTHER PHYSIOLOGICAL PROPERTIES

2.3.1 Receptive fields. Using the anesthetized paradigm, we plotted receptive fields (RFs) of responsive neurons in the 4-7 month group. As in anesthetized adults, RFs of infant IT neurons tended to be large and to extend across the midline into the ipsilateral visual field. Values of median RF size (about 20 deg. by 20 deg.) and incidence of bilateral fields (about two-thirds of the fields plotted) were not significantly different from values obtained from anesthetized adult monkeys. We also attempted to estimate RF size in the alert animals by presenting effective stimuli at various locations in the visual fields for a few neurons. In both infants and the control adult, these limited measurements indicated that IT RFs are more restricted in alert animals, consistent with the findings of Richmond et al. (1983) in adult IT.

Figure 4 (following page): Stimulus selectivity of three IT neurons in alert infant macaques. Rasters of neural activity and post-stimulus time histograms (PSTHs) are shown for individual stimuli. For each stimulus, the arrow under the PSTH and the vertical line in the raster indicate the time at which the monkey achieved fixation of a small central spot. The horizontal line under each PSTH indicates the 500 ms period during which the stimulus was presented. Each line of dots in the rasters indicates an individual trial. The stimuli subtended 3-6 deg. of visual angle and were presented at the center of gaze. Face stimuli, the monkey chow and square were colored slides, and the remainder were white on a dark background.
2.3.2 Spontaneous activity. Somewhat to our surprise, mean rates of spontaneous activity did not differ significantly between anesthetized and alert infant IT samples, being low in both (2.64 and 3.21 spikes/sec for anesthetized and alert respectively). These values, however, differed significantly from the adult values, which in turn did not differ from each other (means of 7.39 and 8.50 spike/sec for anesthetized and alert adult IT cells, respectively). The low spontaneous rates in infant IT in both paradigms suggest that the low response magnitudes in infant IT reflect more general characteristics of cellular function in infant monkeys. For example, the process of integration of inputs, both stimulus-driven and spontaneously active, may be less efficient or faithful as compared to the adult. It is possible that IT cells in very young monkeys simply cannot use their energy stores efficiently enough to permit the rapid repolarization and depolarization of the cell membrane necessary for high rates of action potential generation under either baseline or stimulus-driven conditions.

3. Anatomical Studies

In order to determine whether the pattern of inputs to IT cortex was adult-like during the age window we had studied with physiological techniques, we made injections of the retrograde tracer wheat germ agglutinin-HRP into anterior IT cortex in four infant monkeys (one at 7 weeks, one at 13 weeks, and two at 18 weeks). We then plotted the distribution of labelled neurons throughout the cortex of both hemispheres and compared the patterns of labelling with those seen after similar injections of adult monkeys (Rodman et al., 1990; Rodman and Consuelos, 1992). The findings, described below, are summarized in Table I.

3.1 Input patterns to IT which are similar in infant and adult monkeys

The overall pattern of cortical inputs from occipito-temporal zones in the ipsilateral hemisphere, containing areas known to be predominantly visual in function, was strikingly similar in infant monkeys and in adults. As for adult IT cortex (Fig. 1B), the densest inputs to IT in infant monkeys arise from visual area TEO as well as from portions of IT immediately posterior to the injection site. A moderately dense projection was also found from ipsilateral visual area V4, especially in the portion of this region which represents the central part of the visual field. No "exuberant" connectivity was found with posterior visual areas, such as V2, not known to be connected to IT in the adult animal. In both infant and adult monkeys, inputs to the ipsilateral IT cortex also arise from the superior temporal polysensory area (STP), from parahippocampal areas TF and TH, perirhinal areas 35 and 36, and the temporal pole. These projections are likely to be feedback in nature (Felleman and Van Essen, 1991).

Projections from the contralateral posterior cortex to IT in infant monkeys originated from the same regions which gave rise to IT inputs within the ipsilateral hemisphere. In all cases, the heaviest contralateral labelling was found in a mirror-symmetric region of IT cortex. Projections also arose from contralateral V4 and TEO, as well as from portions of contralateral IT posterior to the injection site. Previous work in our laboratory showed similar inputs after large injections of IT in adult monkeys (Desimone et al., 1980).

In both infant and adult monkeys, sparse to moderate inputs to IT also originate in several portions of ipsilateral frontal cortex. The first of these is a lateral zone lying between the lateral bank of the principal sulcus and the medial bank of the inferior limb of the arcuate sulcus (Fig. 1A), within area 46 of Walker (1940). The second zone is located ventrally, within and around the lateral orbital sulcus.

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Table I: Summary of studies of cortical inputs to area IT in infants and adults. One, two and three pluses indicate sparse, moderate and strong projections, respectively. Parentheses indicate projections which are very weak or uncertain, minus signs indicate projections that have been looked for and found to be absent, and question marks denote pathways whose existence has not yet been sought. Adult comparisons are based both on our own findings (Desimone et al., 1980; Fenstermaker, 1986) and on data from other laboratories (Mesulam and Mufson, 1982; Shiwa, 1987; Morel and Bullier, 1990; Webster et al., 1991).

3.2 Input patterns to IT which appear different in infant monkeys

An exception to the adult-like pattern of occipito-temporal inputs to IT in infants concerned the laminar origins of projections from the contralateral IT cortex. In adult monkeys, cells labelled in the opposite temporal cortex after injections of tracers into IT are found exclusively in the supragranular layers. Likewise, cells labelled in contralateral V4 and TEO of the infants were found exclusively in the upper layers. However, in contralateral IT of the
recognition learning may reflect the weakness of signals deriving from IT cells in at least the first half year of life, as reflected in their low response magnitudes, long response latencies and susceptibility to anesthesia.

The results of the anatomical studies suggest that interactions between IT and non-visual cortical areas may be important in the development of IT's role in visual memory. An immature pattern of connectivity in infant monkeys was seen specifically with portions of cortex known to play a role in learning and visual memory, namely frontal, rhinal and cingulate cortex. Moreover, the more extensive inputs to IT in very young monkeys from contralateral cortical areas (including the projections from the deep layers of the contralateral IT cortex) may be related to the specification of the precise patterns of connectivity which would seem to be required for perceptual equivalence of objects across the midline.

A variety of other factors may also contribute to the extended time course of both the maturation of visual recognition abilities and specifically the contribution of IT cortex to these functions. First, although responses in IT cortex may be relatively developed early in infancy, target structures of IT cortex participating in visual memory may not be. Secondly, although we have documented that basic response properties and the overall degree of form selectivity in IT cortex are adult-like early in life, other parameters which we have not studied, such as temporal pattern of response of individual cells (Richmond et al., 1987), may be different in the infant. In addition, it has been suggested that selectivity patterns of groups or ensembles of neurons may be more relevant for behavior than those of individual cells (Gochin et al., 1992), and such ensemble activity may be different in the young animal. Third, attentional and task-related influences known to affect IT responses in adult monkeys (e.g. Moran and Desimone, 1985; reviewed in Gross et al., 1992) may have functional implications and may not be present (or very pronounced) in the infant monkey. Fourth, there is some evidence that modification of selectivity, rather than the presence of stimulus selectivity per se, is important for visual learning (e.g., Miyashita, 1988) and selectivity patterns of IT neurons may actually be less (or less rapidly) modifiable by experience in the infant. Finally, it will be of interest to obtain recordings in even younger monkeys to determine the characteristics of IT responses closer to birth. The results presented here represent only a first step in understanding the development of the visual cortical mechanisms of pattern recognition abilities in primates.

5. Acknowledgements

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6. References


Walker, A.E. (1940) A cytoarchitectural study of the prefrontal area of the macaque monkey, J. Comp. Neurol. 73, 38-86.