

# Stimulus selectivity and state dependence of activity in inferior temporal cortex of infant monkeys

(visual cortex/visual receptive fields/cortical development/pattern recognition)

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**ABSTRACT** Inferior temporal cortex is necessary for visual object recognition in adult primates but is less critical in infants. Nonetheless, in macaques as young as 6 weeks old, inferior temporal neurons showed adult-like visual response properties, including form selectivity and bilateral receptive fields, indicating that extended maturation and visual experience may not be necessary for adult-like encoding of complex objects. However, before the animals were 4 months old, visual responsiveness was found in inferior temporal cortex only in awake monkeys performing a behavioral task and not in anesthetized ones, suggesting that extraretinal factors profoundly influence function in “association” cortex in developing as well as mature animals.

A persistent question in the fields of psychology and biology has been that of the relative roles of experience and innate organization in the development of perception. While extensive studies on primary visual (striate) cortex have clearly shown a role for both types of influence on simple properties such as orientation selectivity and binocularity (1), much less attention has been paid to the development of physiological mechanisms of complex recognition ability. Primates in particular show an impressive ability to recognize complex objects by sight, including, but not limited to, subtly differing faces, food objects, and arbitrary experimental stimuli. One brain region implicated in both perception and retention of complex stimuli is the inferior temporal (IT) cortex, a portion of visual “association” cortex that receives visual information indirectly from striate cortex (2, 3). In adult monkeys, IT cortex damage produces severe and permanent deficits in visual recognition, and lesions of corresponding cortex in humans produce similar impairments (2–4). The physiological properties of IT neurons in adult animals include selectivity for stimulus form and color, consistent with a role in object recognition, and their large bilateral receptive fields (RFs) suggest a role in stimulus generalization across retinal translation (3, 5).

Several types of evidence indicate, however, that IT cortex may not contribute fully to visual recognition ability in the monkey until after the age of 6 months or older. For example, IT lesions made in infancy have relatively minor effects on recognition ability whether tested immediately or later in life (6–10). Moreover, visual recognition ability itself develops to an adult level only slowly over the first year or more (11–13). Finally, studies of metabolic activity (14) confirm that IT cortex may be functionally immature until at least 4–6 months of age. Are the unique properties of IT neurons available to encode visual objects in very young monkeys, or are extended periods of visual experience necessary to produce adult-like properties? To address this question, we recorded in IT cortex in infant monkeys (age range, 5.5 weeks

to 7 months). The care and use of the animals in this study were performed in accordance with federal and institutional guidelines.

We found the receptive field properties and stimulus selectivity of visually responsive IT cortex cells in the infant monkeys to be strikingly similar to those reported in previous studies of adult IT cortex (3, 5, 15, 16). In addition, there was a profound effect of behavioral state. Visually responsive cells were virtually absent in anesthetized animals <4 months old and were found less frequently in 4- to 7-month olds than in the adult under anesthesia.

## MATERIALS AND METHODS

We recorded from IT cortex [cytoarchitectonic area TE (17)] (Fig. 1A) in infant macaques (16 *Macaca fascicularis* and 1 *Macaca mulatta*) in repeated sessions. Animals were studied both under anesthesia and in an alert recording paradigm. Recording methods for anesthetized animals were modified from those used for adult animals (15) and are described in detail in a separate report (18). Briefly, a week before the first recording session, a recording chamber and headbolt were implanted under anesthesia and aseptic conditions. For recording, the animal was anesthetized with a 7:3 mixture of N<sub>2</sub>O/O<sub>2</sub> to which 2% halothane was added, maintained under N<sub>2</sub>O/O<sub>2</sub>, immobilized with pancuronium bromide, and artificially respired. The pupils were dilated and the eyes were refracted and covered with contact lenses. Recording sessions lasted 10–12 hr, were separated by a minimum of 1 week, and ranged from 1 to 10 sessions per animal. For alert recording, a scleral search coil was also implanted under anesthesia (18, 19). A week later, these animals were trained to fixate a 0.3° spot for 700–1000 ms within a 2°–3° window for a juice reward. The monkey sat in a miniature primate chair padded with soft towels for tactile comfort within a magnetic coil apparatus for monitoring eye position (18, 20). All recordings were made with tungsten electrodes (Frederick Haer), and neuronal spikes were amplified, displayed, isolated, and recorded as described before (21).

Visual stimuli consisted both of three-dimensional objects and of images flashed on a tangent screen under computer control. The stimuli were similar to those used previously for adult monkeys—namely, (i) a standard set of complex objects including head models, monkey dolls, brushes, and plastic food objects, and (ii) slides of monkey faces, scrambled faces, lines, control objects, and “FD” stimuli presented under computer control. [FD stimuli are derived from a formalism for describing boundary curvature (16, 22). The FD stimuli used in this study varied in frequency (cycles per perimeter), which corresponds to the number of lobes (Fig.

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Abbreviations: IT, inferior temporal; RF, receptive field.

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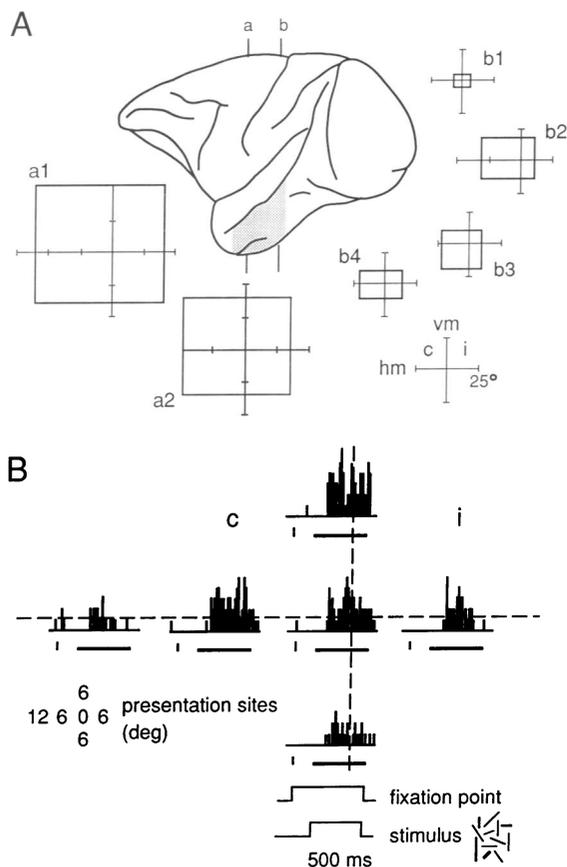


FIG. 1. (A) Location of recording area (shaded in lateral view of macaque brain) and bilateral RFs of IT cortex cells in anesthetized infant monkeys, taken from levels a and b. hm, Horizontal meridian; vm, vertical meridian; c, contralateral visual field; i, ipsilateral visual field. (B) Responses (poststimulus time histograms) obtained at different sites in visual field to the stimulus (a set of lines) in an alert infant monkey performing the behavioral task shown (*Inset*); 200 ms after the monkey fixated a small spot of light, the stimulus came on for 500 ms.

2). In adult monkeys, many IT neurons are selective for the frequency of FD stimuli (16).]

**RESULTS**

The results are based on a total of 384 neurons isolated within IT cortex. RFs in IT cortex of infant monkeys are shown in Fig. 1. As in the adult, two-thirds of the RFs in the anesthetized animals extended at least 3° across the midline into the ipsilateral field (Fig. 1A), and response strength was invariably best at the fovea and stronger contralaterally than ipsilaterally. RF size was harder to assess in the alert infants, but clear evidence of ipsilateral responsiveness was found (Fig. 1B), even in very young animals.

The types of stimulus selectivity shown by individual IT neurons in the alert infants <4 months old were similar to those exhibited by adult IT cortex cells under either anesthetized or alert conditions (Fig. 2). Many infant IT cortex cells were selective for form, as exemplified by tuning for boundary curvature (Fig. 2A). Selectivity within a set of standard face and nonface stimuli is shown in Fig. 2B. Some cells responded only to a single image (cells 1 and 3), whereas others (e.g., cell 2) showed responses to many but not all images in the set. A few (e.g., cell 4) responded only to specific profiles. Many of the visually responsive neurons studied in the anesthetized animals 4–7 months old also

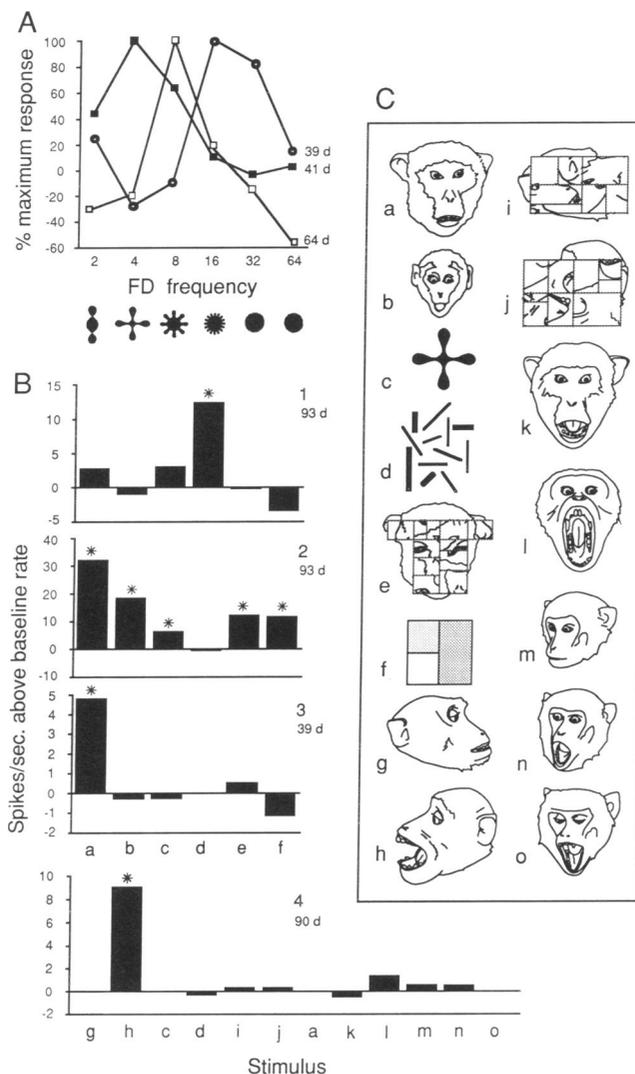


FIG. 2. Stimulus selectivity of IT neurons in alert infant macaques. Stimuli were white on a dark background (FDs, stimuli c and d in C) or colored (remaining stimuli), subtended 3°–6° of visual angle and were presented for 10 trials at the center of gaze. (A) Tuning curves for FD frequency. Stimuli are shown below. (B) Responses from individual IT cortex cells to the set of stimuli shown in C. Asterisks indicate statistically significant responses. (C) Stimuli: a, adult front view, passive; b, baby front view, threat; c, FD; d, lines; e, scramble of a; f, multicolored square; g, adult profile 1; h, adult profile 2; i, scramble of g; j, scramble of h; k, adult front view, threat; l, adult front view, yawn; m, adult 3/4 view, passive; n, adult 3/4 view, threat; o, adult 3/4 view, yawn.

showed stimulus selectivity, particularly for the three-dimensional objects.

To characterize the selectivity of the alert infant IT sample as a whole, we calculated for each cell the percentage of projected stimuli that elicited statistically significant responses and plotted the distribution of this measure (Fig. 3). Responses were considered significant if mean firing rate during stimulus presentation differed from mean baseline firing rate on the same trials (*t* test; *P* < 0.05). This distribution mirrors the selectivity characteristic of adult IT cortex: while some cells are very specific in their stimulus requirements, many respond to a subset of complex stimuli whose critical features are often unclear (3).

The incidence of visually responsive cells in each of the experimental groups and in several comparable studies of adult IT cortex is summarized in Fig. 4. Anesthetized monkeys <4 months old had very few responsive IT cortex cells,

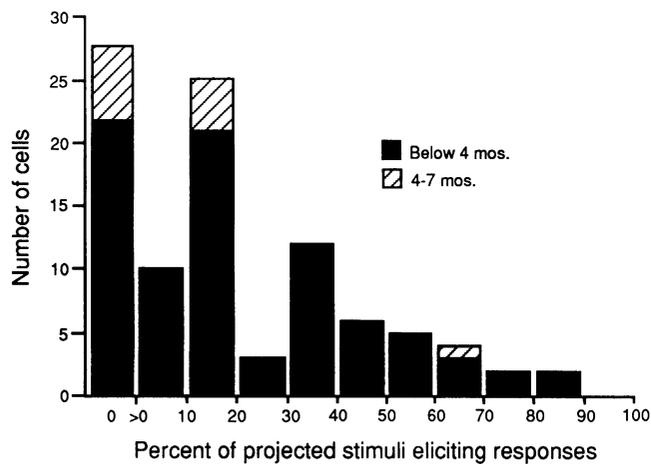


FIG. 3. Distribution of selectivity in the population of IT neurons studied in alert infant macaques. Bar corresponding to 0 indicates cells unresponsive to projected stimuli.

and those 4–7 months old had only about half of the adult complement. However, the incidence of visual responsiveness in alert animals <4 months old was not significantly different (by  $\chi^2$  test) from that found in either anesthetized adult monkeys or awake behaving ones. To ensure that the very low incidence of responsiveness in anesthetized animals <4 months old was not due to an impairment of the animal's condition, control recordings were made in striate cortex and extrastriate visual area MT (middle temporal area) in the same sessions in which we failed to find responses in IT cortex. Cells in these areas were typically responsive (29 of 34 sites) and stimulus selective, as in the adult (24–26), suggesting that the effect of anesthesia was relatively specific to IT cortex. In addition, three of the alert recording subjects were restudied under anesthesia when they were 3–3.5 months old. In these sessions, only 1 of 30 IT cortex cells was responsive under anesthesia, although we subsequently found more responsive units when the monkeys were again studied while awake. This control suggested that the effects of anesthesia on IT cortex were not irreversible ones produced in the earliest recording sessions. A similar lack of responsiveness in IT cortex was found in macaques between 4 and 11 weeks old when heavily sedated with diazepam (27).

### DISCUSSION

These results show that basic response properties of IT neurons are present in macaques as young as 5.5 weeks old,

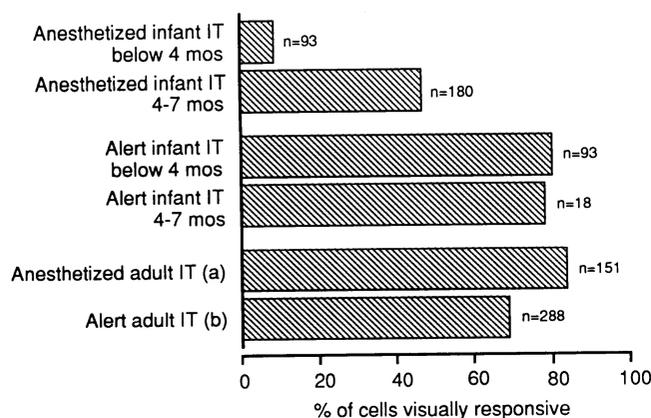


FIG. 4. (A) Incidence of visually responsive neurons as percentage of total cells studied for anesthetized and alert infant monkeys and for comparable samples obtained from adult monkeys. (a), From ref. 5; (b), from ref. 23.

indicating that protracted periods of maturation and visual experience may not be necessary for adult-like encoding of complex visual objects. Why, then, does visual object recognition achieve adult levels only slowly? Although the response properties and also the pattern of cortical inputs to IT cortex may be relatively mature at these ages, or even at birth (28, 29), there is evidence that patterns of connectivity with other structures participating in recognition memory are still developing (29). In addition, while the present results show adult-like properties in IT cortex of infant monkeys, further work is needed to determine whether subtle quantitative differences in response magnitude or tuning might be present. Furthermore, in adult monkeys both IT cortex activity and visual recognition performance are profoundly influenced by extraretinal variables such as attention, effort, and stimulus significance (23, 30, 31), and these influences may not be fully operative in the very young monkey. Indeed, the paucity of visual responsiveness under anesthesia in IT cortex in infant monkeys attests to the importance of behavioral state on the function of this area, an influence apparently absent in "lower-order" areas such as striate and MT. Accordingly, the development of IT cortex in monkeys appears to be an excellent model for the convergence of genetic, sensory, and cognitive factors in the genesis of complex abilities such as visual recognition.

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