Cytochrome oxidase activity in the striate cortex and lateral geniculate nucleus of the newborn and adult macaque monkey

H. Kennedy, J. Bullier, and C. Dehay

Laboratoire de Neuropsychologie Expérimentale, INSERM-Unité 94, 16, Avenue du Doyen Lépine, F-69500 Bron, France

Summary. The laminar location of cytochrome oxidase staining has been compared in the lateral geniculate nucleus and area 17 in newborn and adult macaque monkeys. In area 17 of the adult, the distribution of cytochrome oxidase activity confirmed published findings. In the newborn animals, the tissue reacted as strongly for cytochrome oxidase as in the adult but the pattern of labelling was different in two respects. Firstly in layer 1 activity was stronger and occupied a wider portion of this layer. Secondly, cytochrome oxidase staining in layer 4C occupied two separate bands, a small narrow band at the bottom of 4Cβ and a wider one occupying the full width of 4Cα and spilling over into 4B. The pattern of cytochrome oxidase activity did not appear to be influenced by eccentricity in the newborn whereas, in the adult, label in 4C was more intense in cortex subserving central vision. In the lateral geniculate nucleus of the adult, the magnocellular layers and the most dorsal parvocellular layer reacted most strongly for cytochrome oxidase. In the newborn, parvocellular layers were more uniformly labelled and the difference between parvo- and magnocellular layers more pronounced. These results are discussed in relationship to the development of thalamo-cortical projections in the monkey.

Key words: Monkey -- Striate cortex -- LGN -- Cytochrome oxidase -- Development

Introduction

Cytochrome oxidase (Cyt. Ox.) is a mitochondrial enzyme used in the cell for the production of energy. The spatial distribution of Cyt. Ox. activity in histological sections reflects local differences in metabolic activity and has proved especially useful for exploring afferent connections as well as regional functional specialization (Wong Riley 1979; Livingstone and Hubel 1984). Within area 17 of the macaque zones of high Cyt. Ox. activity have been found to correspond to regions of thalamic terminals (Horton and Hubel 1981; Livingstone and Hubel 1982). In the past few years, there has been considerable interest in the termination of the lateral geniculate nucleus (LGN) in area 17 of the developing monkey. During the first two months of life the extent of the cortical territory occupied by the afferents from each eye can be influenced by visual experience (Hubel et al. 1977) and it has been shown that the phenomena of plastic rearrangement of the inputs from the two eyes and the normal process of development are synchronised (LeVay et al. 1980). We have therefore examined the distribution of Cyt. Ox. activity to see if this would suggest differences in thalamo-cortical projections between newborn and adult monkeys.

Methods

Three newborn cynomolgus monkeys (Macaca irus) aged 30 to 48 h were used in these experiments. Three adult monkeys served as controls. Two of the newborns were part of a series investigating callosal connectivity in the neocortex using horseradish peroxidase. The third animal received an injection of wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP) in the white matter underlying area 17, 20 h prior to sacrifice. The concentration of WGA-HRP was 2% in saline and the injections were made using micropipettes with a broken tip of 50–100 μm diam.

Animals were perfused under deep anaesthesia with isotonic saline followed by one liter of 1% pafaroaldehyde and 1.25% glutaraldehyde in phosphate buffer. This aldehyde mixture was passed for 45 min and followed with a 10% sacrose solution for a similar length of time. The brains were blocked and stored for at least 12 h in sucrose. The brain was then sectioned (60 μm) on a
Fig. 1A–D. Laminar location of Cyt. Ox. activity in newborn and adult monkeys. Nissl stain of newborn (A) and adult (C) monkey. Cyt. Ox. activity in newborn (B) and adult (D) monkey. Photomicrographs of Nissl stain taken at same scale (scale bar = 308 μm). Enlargement of photomicrographs of Cyt. Ox. have been made so as to compensate for differential shrinkage.
4Cα and the lower part of 4B. These results suggest that the bands of Cyt. Ox. activity in layer 4C might correspond to regions of dense LGN input separated by a region of sparse LGN input.

It has been reported that there is a denser band of Cyt. Ox. activity along the base of layer 4C in the adult (Wong-Riley and Carroll 1984). This is not readily apparent upon visual inspection of our material (Fig. 2). By looking at optical density thresholds, we found that there is an increase in activity which, however, only occurs in cortex subserving central vision (Fig. 4). These results might reflect the richer input from the parvocellular layers of the LGN to cortex subserving the fovea (Connolly and Van Essen 1984) and are consistent with other differences in Cyt. Ox. staining in layers 2 and 3 between cortex subserving different regions of the visual field (Livingstone and Hubel 1984). Optical density measurements therefore show that the pattern of Cyt. Ox. staining observed in layers 4C of the newborn has a more pronounced similarity with that found in the adult cortex subserving central vision.

Cyt. Ox. activity in the LGN is not uniformly distributed in the different laminae (Fig. 5). In the adult, the two magnocellular layers and layer 6 showed marginally higher levels of Cyt. Ox. activity, confirming previous findings (Wong-Riley and Carroll 1984). In the newborn, the magnocellular layers were much more densely stained and the parvocellular layers more weakly stained than in the adult, so that the overall difference between the two sets of layers was greater in the younger animals (Fig. 5). On some sections, layer 6 did appear in the newborn to be slightly more deeply stained than the other parvocellular layers.

Discussion

The present results show that the pattern of Cyt. Ox. activity in the LGN and striate cortex changes during development. In the adult animal, the magnocellular laminae of the LGN project to layer 4Cα while the parvocellular layers project mainly to 4Cβ (Hubel and Wiesel 1972). Our results show that in the newborn, the magnocellular pathway exhibits a higher Cyt. Ox. staining than the parvocellular pathway. This suggests that, during early stage of development, there is a difference in the activity of neurons in these two parallel pathways.

In the cortex, the outstanding differences in Cyt. Ox. activity are in layers 1 and 4C. The stronger label in layer 1 could mean that inputs to this layer (e.g. from the pulvinar) are relatively more active in the newborn. Within layer 4, major developmental changes concerning afferents from the LGN take place during the first six weeks of life. During this period, there is a sorting out of afferents from the LGN laminae innervated by each eye (Hubel et al. 1977; LeVay et al. 1980). Our results show that the pattern of Cyt. Ox. activity and thalamic input into layer 4 in the newborn (Fig. 3) is different from the adult pattern. It is possible to interpret this difference in terms of the developmental processes taking place in this layer.
The difference between newborn and adult observed in layer 4Cβ suggests that the input to this layer is more immature at birth than is the input to layer 4Cα. There is evidence that the magnocellular layers of the LGN are established earlier (Rakic 1976) and might mature quicker than do the parvocellular layers (Garey and Saini 1981; Gottlieb et al. 1985) so that input to 4Cα could preceed that to layer 4Cβ. Studies on axons terminating in layer 4C also support a late development of 4Cβ (Blasdel and Lunde 1983). There is also evidence from experiments on the plasticity of ocular dominance columns to suggest major developmental differences between the two subdivisions of layer 4C. LeVay and co-authors (1980) concluded from reverse suture experiments that anatomical plasticity is terminated earlier in layer 4Cα than is in 4Cβ. They interpreted these results as indicating either that the differential effect is the consequence of a relatively greater loss of territory by the deprived eye in 4Cα (i.e. a greater susceptibility of magnocellular terminals to deprivation) or that plasticity is terminated earlier in the magnocellular afferents. Our results indicating a later development of the parvocellular input to 4Cβ reconcile both these interpretations: the precocious magnocellular input to layer 4Cα would make it more susceptible to early deprivation and the late development of input to 4Cβ would prolong plasticity in this layer.

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