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Contrast Sensitivity in One-eyed Subjects

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The effects of early monocular form deprivation on the developing mammalian visual system, and the anatomical and physiological consequences of early monocular enucleation, suggest that the remaining eye of human subjects who had the other eye removed early during development might be capable of supernormal performance. To test this inference, the achromatic contrast sensitivity of the remaining eye of subjects who had the other eye removed at different ages after birth was compared with that of normal subjects tested under monocular and binocular conditions. The results show that all subjects who had an eye removed during early development had a higher contrast sensitivity than the better eye of control subjects. Furthermore, the earlier in development that the eye was removed, the lower the spatial frequency at which contrast sensitivity is enhanced compared with measurements made in the better eye of control subjects, and the larger the range of spatial frequencies over which contrast sensitivity is supernormal.

Contrast sensitivity Enucleation Development Hypersensitivity

INTRODUCTION

The central visual pathways in many mammals, including man, continue to mature after birth. The outcome of these maturational events can be substantially altered by abnormal visual experience during a so-called sensitive period of development. The duration of this sensitive period in man is not fully known, although it is believed to persist well into childhood (Vaegan & Taylor, 1980). Thus, monocular pattern deprivation during infancy and childhood can lead to amblyopia, a condition in which visual acuity and sensitivity to luminous contrast are depressed, often associated with other disturbances of visual perception in the visually deprived eye (for review see Hess, Field & Watt, 1990).

As shown in many experiments, the physiological and anatomical effects of early monocular pattern deprivation on the developing visual system of the cat and the monkey are that a substantially larger proportion of the primary visual cortex is devoted to the undeprived eye at the expense of the deprived eye (for reviews see Hubel, Wiesel & LeVay, 1977; Sherman, Guillery, Kaas & Sanderson, 1974; Mitchell & Timney, 1984; Blakemore & Vital-Durand, 1986). This change in the normal ocular dominance pattern suggests that monocular enucleation during childhood should result in the remaining eye being capable of mediating better performance than either eye of a person, or animal, with normal binocular vision (Barlow, 1975; Freeman & Bradley, 1980). Curiously this has rarely been tested, and never in human subjects by measuring contrast sensitivity, although Bisti and Trimarchi (1993) found that the contrast sensitivity of two cats that had one eye removed prenatally was slightly higher at medium spatial frequencies than that of normal cats tested monocularly, although it was lower than normal at spatial frequencies less than 0.5 c/deg.

There is other evidence, of a different nature, which also suggests that the remaining eye of a subject who has had the other eye removed early during development might be supernormal. The development of the visual system proceeds, in part, through an initial overproduction of neurons and excessive arborization of axons, followed by the selective elimination of axons and aberrant connections to establish the mature pattern. For instance, in the foetal monkey each optic nerve contains about 2.85×10^6 axons, compared with 10^6 in the adult, and the optic axons from both eyes initially overlap in the dorsal lateral geniculate nucleus (dLGN) (Rakic, 1981, 1986). Several studies have shown that monocular enucleation can substantially reduce the normal death of ganglion cells in the remaining eye and preserve, and perhaps expand, their central connections (for reviews see Rakic, 1986; Guillery, 1989). For example, the removal of an eye during the first half of gestation (i.e. before the ocular segregation of the dLGN) results in the optic nerve of the remaining eye containing about 40% more fibres than in a normal monkey and in the dLGN being uniformly innervated by the remaining eye (Rakic, 1981). In infant rats, the expansion of the projection of the remaining eye in the ipsilateral dLGN following enucleation is also present at the cortex (Lund, Cunningham & Lund, 1973; Yee, Murphy & Van Sluyters, 1987). Moreover,

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Heywood, Silveira and Cowey (1988), using averaged visually-evoked potentials, showed that the remaining eye of adult rats who had the other eye enucleated shortly after birth had substantially higher contrast sensitivity than that of normal rats tested monocularly. This has not been examined in other mammals but the receptive fields in striate cortex in cats deprived of one eye prenatally are smaller than those of normal cats (Shook, Maffei & Chalupa, 1985; Shook & Chalupa, 1986) even though the functional properties of cells in the dLGN that project to the striate cortex are not similarly altered (White, Chalupa, Maffei, Kirby & Lia, 1989).

In the monkey much of the elimination of optic axons occurs during the third trimester and is thought to continue at a lower level postnatally (Rakic & Riley, 1983). If a similar phenomenon occurs in man, monocular enucleation or retinal destruction during the neonatal period should result in the remaining eye being capable of higher sensitivity, not just on the basis of a change in the normal ocular dominance pattern in the striate cortex, but also because there are more retinal ganglion cells in the remaining eye.

There are few psychophysical investigations of the performance of the undeprived eye and these have yielded mixed results. Freeman and Bradley (1980) demonstrated that subjects who had monocular deprivation (from a variety of causes) during childhood had higher vernier acuities when tested through their undeprived eye than control subjects tested monocularly. However this finding has not been replicated by others (González, Steinbach, Ono & Rush-Smith, 1992). Moreover, Johnson, Post, Chalupa and Lee (1982) examined vernier acuity thresholds in two identical twins, one of whom had a congenital posterior subcapsular cataract. The monocular vernier acuity threshold in the nondeprived eye of the affected twin was not significantly different from that of the normal twin.

There is evidence that different aspects of visual performance (e.g. optokinetic nystagmus and detection of disparity) develop at different rates and during different periods. However, contrast sensitivity is perhaps the most basic of all visual abilities and one that almost certainly reflects the number of retinal ganglion cells and their central representation (Robson, 1980). Furthermore, at low to medium spatial frequencies it is not limited only by the modulation transfer function of the eye, unlike grating acuity. We therefore compared the contrast sensitivity function of the remaining eye of subjects who had an eye removed at different ages after birth with that of control subjects tested monocularly and binocularly.

MATERIALS AND METHODS

Subjects

Nine subjects who had an eye removed between 2 months and 13yr of age were allocated to three groups on the basis of their age when the eye was removed (see Table 1). All subjects in the "very early" and the "early" groups had an eye removed for retinoblastoma during infancy. The eye must have been abnormal for weeks and perhaps many months before its removal. Subjects in the "late" group had an eye removed following trauma to that eye. The remaining eye of all the monocular subjects was ophthalmologically normal in appearance and in Snellen acuity. Three subjects with normal binocular vision and Snellen acuity were tested.

Contrast sensitivity

Contrast sensitivity was measured with a Prisma VR100 Grating Generator (Millipede Electronic Graphics Ltd). Sinusoidally modulated gratings were presented on a 15 in. monitor, with a P4 phosphor, a screen resolution of 744 displayed lines and 100 Hz frame rate. Gamma correction, to adjust for non-linearity in the voltage–luminance relationship was carried out in software. Sensitivity to stationary gratings of 0.58, 1, 2, 4, 8, 16 and 32 c/deg was measured in random order. For each spatial frequency, contrast thresholds were measured as follows. The seated subject faced the monitor, subtending approx. 4 × 3 deg, at a distance of 5 m in a dimly lit room. Each estimate of contrast threshold for a grating of a particular spatial frequency was made over 50 trials. For a single trial, a vertical grating at a contrast of 75% was initially presented on either the left or the right half of a split screen where the remaining half of the screen contained a blank field of the same mean luminance (86 $cd \cdot m^{-2}$). A brief tone indicated stimulus onset. The subject was required to press one of two buttons, one in each hand, to indicate the position of the grating. The response terminated the trial and was accompanied by a further tone. For a further 49 trials the spatial position of the grating was varied randomly between the left and right side of the display monitor, with the constraint that the position was never the same for

TABLE 1. Details of ages and Snellen visual acuity of patients and normal subjects

Subject	Age at enucleation	Years of monocular vision	Snellen visual acuity
Very early group			
NR	< 2 months	15	6/6
LC	13 months	22	6/4.5
AK	6 months	23	6/4.5
Early group			
PD	1 yr 4 months	24	6/6*
SS	3 yr 8 months	18	6/6
YH	1 yr 11 months	21	6/6
Late group			
JD	11 yr	35	6/3
RI	13 yr	26	6/3
LM	13 yr	28	6/4.5
Binocular controls			
KW	n.a.	22†	6/3
AF	n.a.	25†	6/3
OD	n.a.	20†	6/6*

*Spectacle-corrected vision.
†Subject age in yr.
n.a., not applicable.

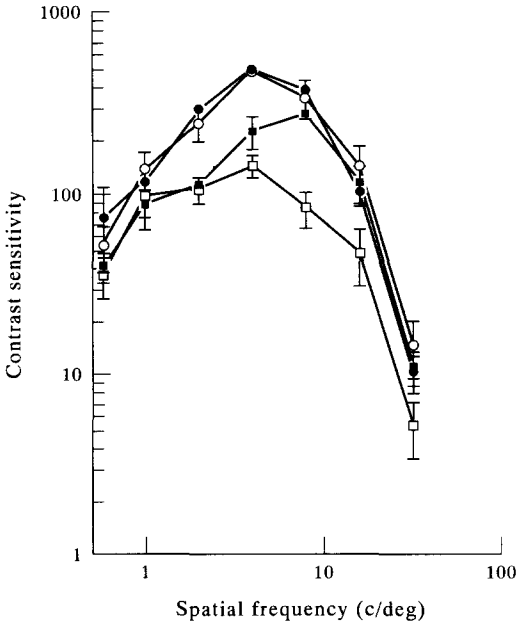

FIGURE 1. The contrast sensitivity of monocular subjects in the very early (●), early (○) and late (■) groups, and of binocular subjects using their better eye (□). Vertical bars indicate SEM.

more than three consecutive trials. If three consecutive correct responses were made, the contrast of the grating was halved. A single error resulted in a similar proportionate increase in contrast. This titration procedure stabilizes performance at 79% correct (Weatherill & Levitt, 1965). Contrast threshold was defined as the mean contrast of the last three inflections on a graph of trial number plotted against contrast. Each measurement was repeated at least twice but usually three times. The contrast sensitivity at each spatial frequency was calculated from the median contrast threshold of these measurements.

The better eye of control subjects was defined as the eye with the highest contrast sensitivity, at any spatial frequency. Thus, in some subjects the "better" eye had higher contrast sensitivities at some spatial frequencies, and lower contrast sensitivities at other spatial frequencies.

RESULTS

Contrast sensitivity of one-eyed subjects and normal subjects tested through their better eye

The contrast sensitivity of the three groups of subjects who had enucleations at different ages after birth and that of control subjects tested through their better eye is shown in Fig. 1. Analyses of variance, using groups and spatial frequency as factors, revealed a difference amongst groups ($F = 38.82$, d.f. 3, 6, $P<0.001$), which depends on the spatial frequency ($F = 6.76$, d.f. 18, 56, $P<0.001$). Separate group comparisons were made on the basis of Tukey's *a posteriori* test. There was no difference among groups at low and high spatial frequencies ($P > 0.05$ at 0.58, 1, 16 and 32 c/deg). In the mid-spatial frequency range the contrast sensitivity of subjects in the very early group was no different from that of subjects in the early group ($P > 0.05$ at 2, 4 and 8 c/deg). Both groups had a significantly higher contrast sensitivity than subjects who had an eye removed much later in life and normal control subjects tested through their better eye at 2 and 4 c/deg ($P < 0.05$ at 2 c/deg and $P<0.01$ at 4 c/deg). Thus, at 4 c/deg the contrast sensitivity of the very early group was 504 (SE = 33) compared with 492 (SE = 34) for the early group, 227 for the late group (SE = 46) and 144 for the control group (SEM = 20).

The contrast sensitivity of the late enucleation group appears to differ from that of normal subjects at 4 c/deg (mean contrast sensitivity of the late enculeation group was 227 compared with 144 of the control group). However, there was no statistical difference between them ($P > 0.05$), although at 8 c/deg the contrast sensitivity of all enucleated groups was not significantly different ($P > 0.05$) but is higher than that of the normal group of subjects tested through their better eye ($P < 0.05$).

Contrast sensitivity in one-eyed subjects and in normal subjects tested binocularly.

The contrast sensitivity of the enucleated groups and that of normal subjects tested binocularly is plotted in Fig. 2. There was a difference amongst the groups ($F = 18.37$, d.f. 3, 6, $P<0.001$), which again depended on spatial frequency ($F = 4.11$, d.f. 18, 56, $P<0.001$). The peak contrast sensitivity of normal subjects tested binocularly was 264 (SE = 41) and this is significantly lower than that of the groups of subjects who had an eye removed early during development ($P < 0.05$ at 4 c/deg). At all other spatial frequencies there were no statistical differences between the enucleated groups and the normal binocular group ($P > 0.05$ at 0.58, 1, 2, 8, 16 and 32 c/deg).

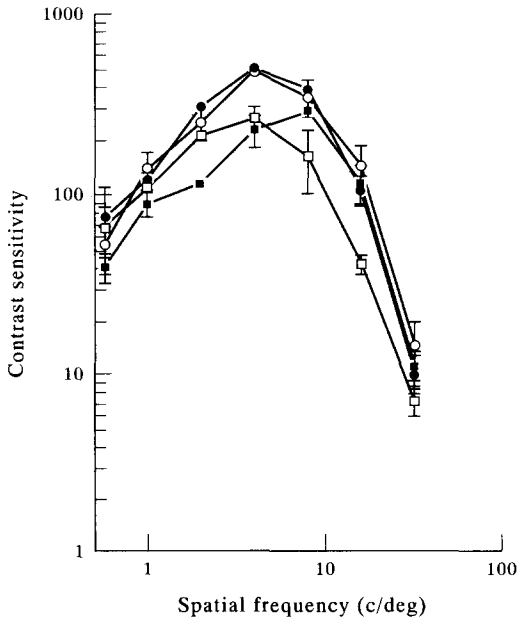

FIGURE 2. The contrast sensitivity of monocular subjects in the very early (●), early (○) and late (■) groups, and of binocular subjects using both their eyes (□). Vertical bars indicate SEM.

DISCUSSION

All three groups of one-eyed subjects had a higher contrast sensitivity than that of normal subjects tested with their better eye. The higher contrast sensitivity of the one-eyed groups was restricted to certain spatial frequencies and the earlier the eye was removed, the lower the spatial frequency and the larger the range of spatial frequencies at which contrast sensitivity was elevated. The two groups who had an eye removed early during development, because of retinoblastoma, had a higher contrast sensitivity than the normal group of subjects tested using their better eye throughout the mid-spatial frequency range. This difference is substantial, so much so that the peak contrast sensitivity (at 4 c/deg) of subjects with early enucleation exceeds that of normal subjects tested *binocularly*. Subjects who had an eye removed later during development had a higher contrast sensitivity than normal subjects tested through their better eye at 8 c/deg.

During development, contrast sensitivity improves at different rates for different spatial frequencies, reaching adult levels sooner with lower spatial frequencies than higher frequencies. In macaque monkeys, contrast sensitivity at 1–5 c/deg reaches adult levels by about 20 weeks, whereas sensitivity to gratings higher than 15 c/deg is still improving at 40 weeks (Boothe, Williams, Kiopres & Teller, 1980; Boothe, 1984). The peak contrast sensitivity increases from about 1 c/deg at 10 weeks to an (adult) level of about 4–5 c/deg by 20 weeks. The development of human contrast sensitivity in man has not been as intensively studied as that of monkeys. At 1 month babies show no low frequency fall-off, and their overall sensitivity is low. At 2–3 months the contrast sensitivity function resembles that of the adult's in shape, but is lower and its peak is shifted towards the lower spatial frequencies (Atkinson, Braddick & Braddick, 1974; Atkinson, Braddick & Moar, 1977; Banks & Salapatek, 1978, 1981). The overall sensitivity becomes adult-like between 3 and 4 yr of age (Atkinson, French & Braddick, 1981). Our findings suggest that there is a period during development when removal of one eye is followed by a substantial improvement in the contrast sensitivity of the remaining eye at some spatial frequencies which have not yet reached their optimum contrast sensitivity. Interestingly, the contrast sensitivity at 16 and 32 c/deg was similar in all groups.

There is evidence that the P-pathway (arising from P—or beta—retinal ganglion cells and innervating the parvocellular dLGN) is largely responsible for contrast sensitivity at spatial frequencies above 4 c/deg and that both the P-and the M-pathway (magnocellular pathway) subserve contrast sensitivity at lower spatial frequencies (Schiller, Logothesis & Charles, 1990). Very early enucleation should improve the contrast sensitivity, although not necessarily equally, at all spatial frequencies because both pathways have not yet fully developed. However, a later enucleation would be expected to improve contrast sensitivity at high but not at low spatial frequencies if the M-pathway has fully developed and the P-pathway has not. However, there is anatomical evidence that the P-pathway is ontogenically older and develops earlier than the M-pathway. For example, in the monkey, there is no significant growth in the parvocellular laminae of the dLGN 8 days after birth; the magnocellular layers in contrast continue to grow until adulthood (Headon, Sloper, Hiorns & Powell, 1981). Correspondingly, the number of spines on cortical cells that receive a parvocellular geniculate input decreases to adult levels sooner than does the number of spines on cells in layers receiving primarily a magnocellular input (Boothe, Greenough, Lund & Wrege, 1979).

There is also evidence in some mammalian species that the fibre order in the optic tract mimics the chronological order in which axons arrive during development, with the fibres in the deeper (dorsal) part of the optic tract arriving earlier than the fibres in the superficial part of the optic tract (Walsh & Guillery, 1985; Guillery & Walsh, 1987; Walsh & Polley, 1985). Reese and Cowey (1990) have shown that the Pß axons and Pα axons are largely segregated within the optic tract in macaque monkeys, with the Pß axons lying predominantly in the deep (dorsal) part of the optic tract and the Pα axons lying more superficially, in the ventral portion of the optic tract. If this chronologically-based segregation within the optic tract also occurs in the human brain, it implies that the P-pathway is ontogenetically older than the M-pathway, and suggests that an enucleation much later in life should improve the contrast sensitivity of subjects tested through their remaining eye at low spatial frequencies. This is contrary to the findings. Subjects who had an eye enucleated later in life (11–13 yr) had similar contrast sensitivities to normal subjects at low spatial frequencies and a significantly higher contrast sensitivity at 8 c/deg. In conclusion, it is not clear that the spatial-frequency dependent increase in contrast sensitivity with age at enucleation can be adequately explained on the basis of a differential effect on either the P- or the M-channel. Their contribution could be examined by comparing the performance of one-eyed and normal observers on psychophysical tests appropriate for each channel, e.g. luminance contrast at low spatial and high temporal frequencies of the M-channel and pure chromatic contrast at low temporal frequencies for the P-channel.

In the rat, neonatal monocular enucleation reduces the normal death of ganglion cells in the remaining eye and also preserves, and even expands, their connections with the brain (Lund *et al.*, 1973; Yee *et al.*, 1987). Prenatal enucleation in monkeys is known to produce larger than normal numbers of optic axons in the remaining eye (Rakic & Riley, 1983). There is also evidence that the elimination of the excessive number of optic axons which begins during the latter half of gestation in the monkey continues into the post-natal period (Rakic & Riley, 1983). If this occurs in man, then enucleation during the post-natal period could result in an expanded retinal ganglion cell population in the remaining eye and might explain the higher contrast sensitivity of enucleated subjects (at the spatial frequencies tested).

In human subjects, however, it is still not known whether there is any substantial increase in the number of

ganglion cells in the remaining eye following removal of a pathological eye post-natally. Provis, van Driel, Billson and Russell (1985) estimated the number of axons in the optic nerves of human fetuses at different gestational ages, and concluded that the period of apoptosis is almost complete by 29 weeks of gestation. Although they excluded "doubtful" axons and growth cones from their estimates of axon numbers they comprised only a small percentage of the total population and therefore it is unlikely that the total population of axons in the optic nerve was greatly underestimated. However, if an enucleated eye has been diseased since before birth its retinal projections, and therefore those of the normal eye, could well be abnormal.

The pattern of ocular dominance columns in the primary visual cortex of the adult brain is not present at birth and can be changed by environmental influences (for review see Mitchell & Timney, 1984). Early monocular lid closure in the monkey results in the deprived eye occupying only 20% of the area in the striate cortex, with the undeprived eye representing the remainder (Le Vay, Wiesel & Hubel, 1980; Swindale, Vital-Durand & Blakemore, 1981). Single cell recordings from the striate cortex of such animals have shown a similar physiological dominance by the undeprived eye. There are few binocularly driven cells and most of the monocular neurons can be driven only by stimuli delivered to the non-deprived eye (Hubel *et al.*, 1977; Blakemore, Garey & Vital-Durand, 1978). Of the few cells that do respond through the deprived eye, all have poor spatial resolution and contrast sensitivity (C. Blakemore & F. Vital-Durand, unpublished observations, cited in Blakemore, 1991). However, even if the remaining eye captured all the cortical cells that would have been influenced by the other eye, the improvement should still be no greater than a factor of 1.414 (i.e. $\sqrt{2}$), a number that satisfactorily accounts for the improvement in sensitivity that occurs from monocular to binocular viewing. It is noteworthy that the peak contrast sensitivity of subjects who had the other eye removed early during development is far better than that of normal subjects tested *binocularly*. This suggests that years of practice with monocular viewing also contributes to the hypernormal performance, as the psychophysical results of McKee and Westheimer (1978) on normal subjects also suggest. Whether this is true of the similar improvement reported briefly by Freeman, Abramson and Nordmann (1989) is unclear. Furthermore, extended practice cannot be the sole explanation because the "late" operated subjects also had years of practice but their performance only exceeded that of the normal subjects monocularly and at 8 c/deg.

One of the most striking properties of neurons in both primary and secondary cortical visual areas of cats and monkeys is not just their binocularity, but their binocular inhibitory interactions, e.g. the inhibition underlying tuning to retinal disparity (Poggio, Gonzalez & Krause, 1988) and binocular rivalry (Lehky, 1988; Mueller, 1990). Much of this inhibition is intracortical. If removing an eye leads eventually to the complete disappearance of this binocularly based intracortical inhibitory system, individual cortical neurons, now all activated by the remaining eye and permanently released from much of their inhibition, might be more sensitive to monocular contrast than the normal population of neurons activated by both eyes simultaneously or by either normal eye alone. We are now testing this electrophysiologically in rats.

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