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TEMPORAL CHANGES IN VISUAL SENSITIVITY (CFF)-DURING AND AFTER PROLONGED MONOCULAR DEPRIVATION ¹

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ABSTRACT. A series of experiments has demonstrated that a prolonged period of monocular deprivation (up to 14 days) produces no change in the CFF of the occluded eye. However, the performance of the non-occluded eye is characterized, first, by an initial depression or impairment of the CFF and, second, by a subsequent enhancement effect of a progressively increasing magnitude. Furthermore, this interocular effect in the non-isolated eye was still present 14 days *after* the termination of deprivation. These findings are related to Sharpless's (1964) concept of "disuse of neural pathways." In addition, some general implications of these results for research in the area of sensory deprivation are discussed.

RESUMEN. Una serie de experimentos ha demostrado que un periodo prolongado de privación monocular (14 días) no produce cambios en la fusión crítica de frecuencia (FCF) del ojo cerrado. Sin embargo, las respuestas del ojo no-cerrado se caracteriza, primero, por una depresión o desorden de la FCF y, en segundo lugar, por un efecto de exageración de magnitud progresivamente creciente. Aún más, este efecto interocular en el ojo no-aislado estaba aún presente 14 días *después* de la terminación del período de privación. Estos hallazgos se relacionan con el concepto de Sharpless (1964) del "desuso de las vías neurales." Además, se comentan en este trabajo algunas implicaciones generales de estos resultados para la investigación en el área de la privación sensorial.

During the past seven years, a series of studies conducted at this laboratory have demonstrated that a one-week period of visual deprivation (binocular) can produce a significant improvement on various measures of cutaneous, auditory, olfactory, and gustatory sensitivity, effects which are long-lasting in nature (see Zubek, 1969, pp. 236-240, for review). Furthermore, we have recently shown that on such tasks as tactual fusion frequency and auditory flutter fusion frequency, both involving intermittent stimulation, the developmental curve is characterized by a progressive improvement in performance as a function of duration of visual deprivation (Milstein & Zubek, 1971; Pangman & Zubek, 1972). Although such intersensory facilitatory effects have been reported, no serious attention has been paid to the functional status of the visual modality itself. Will this sense modality, deprived of stimulation for a prolonged period of time, also show an increase in sensitivity? This is an important question, particularly since

several investigators have shown that a prolonged period of tactual deprivation of a small circumscribed area of the skin can result in a significant increase in tactual acuity and absolute pressure sensitivity (Aftanas & Zubek, 1963a, b; 1964; Heron & Morrison, unpublished study; Weinstein et al., 1967).

In the only directly relevant study, Duda (1965) reported that seven days of binocular deprivation (constant darkness) produced no effect on the visual critical fusion frequency (CFF). Further supporting evidence for this negative finding has been provided by numerous sensory and perceptual isolation studies in which both visual *and* auditory deprivation was employed. These studies, using durations ranging from 2 hours to 14 days, have all yielded negative results on the CFF and on several measures of brightness discrimination (see Zubek, 1969 for review, pp. 212-214). The only contrary finding has been reported by Nagatsuka (1965) who observed a significant decrease in the CFF after two days of perceptual deprivation.

One possible explanation for the failure of these studies to show an improvement in visual sensitivity is that they all have employed binocular deprivation (either darkness or unpatterned light), a procedure which does not require any compensatory adjustment of the visual system since both eyes are exposed to constant conditions. It is possible, therefore, that a compensatory improvement might be demonstrated if the visual deprivation was to be restricted to only one eye, and more specifically, if the visual measures were to be taken from the non-occluded eye. This use of the non-isolated eye is somewhat analogous to the employment of auditory and cutaneous measures in a prolonged visual deprivation experiment where neither of these measures involves a receptor field that has undergone sensory restriction. This procedure, as our earlier research has indicated, can produce pronounced sensory facilitatory effects.

A further suggestion that an improvement in the non-occluded eye may occur is provided by the literature on therapeutic ophthalmology which indicates that the application of a patch over the "good" eye of young children, for at least a week, frequently produces a beneficial or corrective effect in the other eye, particularly in the treatment of such occulo-motor disorders as strabismus (squint) and amblyopia (Adler, 1962; Costenbader, 1966; Lyle & Wybar, 1967). Although this body of clinical literature has not demonstrated the production of an actual improvement in visual sensitivity, nevertheless, the possibility exists that such a phenomenon might occur, even in the adult, especially if the occlusion of the eye should be for a prolonged period of time.

The purpose of this series of experiments was two-fold. First, can a significant improvement in the resolving power of the eye, as determined by the CFF (a measure of temporal visual acuity), be demonstrated following one week of monocular deprivation? Second, if such a phenomenon can be demonstrated, what is its temporal course of development during an extended period of time?

METHOD AND RESULTS

Experiment I

The main objective of the first experiment was to determine the changes in the CFF of the non-occluded eye after 7 days of monocular deprivation of the dominant eye.

Twenty-eight male university students, all with normal vision, were subdivided into an experimental and control group, each containing 14 subjects. The experimental subjects were required to live, in groups of two, for a period of one week in a large windowless room (3.66 m x 14.02 m) which was furnished with sofas, comfortable chairs, study desks, and contained such facilities as a radio, television set, playing cards, and reading material. A washroom, a kitchenette, and sleeping quarters were located adjacent to this furnished room. During the entire period, the experimental subjects wore a black patch over the dominant eye. Periodic checks were made to ensure that there were no light leaks.

A 15-minute period of binocular dark adaptation was imposed upon both groups of subjects prior to the pre-experimental CFF determinations. Similarly, on the post-test, a week later, the controls were initially dark adapted, binocularly, for 15 minutes and the experimentals monocularly (the nonoccluded eye; the other eye had already been covered for one week) to ensure that both eyes would be adequately dark adapted. Fifteen minutes of adaptation was felt to be sufficient for a small, centrally fixed test target. Although the use of a longer adaptation period, e.g., 30 minutes or even greater, had been considered, this was felt to be inadvisable since the obtained results, if negative, could be attributed to the production of a binocular rather than a monocular deprivation condition which the bulk of the literature indicates does not affect the CFF (e.g.. Doane et al., 1959; Duda, 1965; Leiderman, 1962; Zubek, 1964).

The stimulus consisted of a white light, at an initial flicker frequency well above fusion, which was presented monocularly by means of a cold cathode

modulating lamp mounted at the rear of a standard viewing chamber (Lafayette, Model 1202c). The angular subtense of the centrally fixated stimulus was 2°10', assuring full foveal stimulation. The flicker generating apparatus (Grason-Stadler, Model E622) was set at a light-dark ratio of 0.50 and a lamp current reading of 22.6 mA. The descending method of limits was used, with eight trials being presented to each eye. Since the main objective of the experiment was to determine the CFF in the non-occluded eye (non-dominant), this eye was tested *first* at both the pre- and post-test sessions.

The control subjects were also tested monocularly (the non-dominant eye first) after a meal and at the same time interval and at the same time of the day (between 8:45 and 9:30 a.m.) as the experimentals. However, they were not confined to the laboratory during the one-week period. Both groups of subjects were run concurrently.

The results revealed no significant pre-post differences in the mean CFF of either eye of the control group or of the occluded eye of the experimentals. However, the non-occluded eye showed a significant improvement of 2.47 cps ($p \leq .001$). All subjects showed the effect with the individual gains ranging from 0.87 to 5.62 cps. Since both eyes of the same subject were tested, it is possible that the negative finding on the occluded eye may have resulted from the prior CFF determinations in the other eye, especially since Sherrington (1906) and others have reported an interocular CFF effect. In order to test this hypothesis, the dominant eye of eight additional subjects was occluded for one week and this eye only was tested. No significant pre-post difference was obtained, thus indicating that the negative results in the occluded eye cannot be accounted for by prior visual stimulation of the other eye. (For further details of this experiment as well as the next two, see Bross and Zubek, 1972).

Experiment II

The purpose of the second experiment was to determine whether the same phenomenon would also occur if the non-dominant or weaker eye was visually deprived for one week. In this study, 10 experimental and 10 control subjects were used. Again, the results indicated no change in either eye of the controls or in the occluded eye of the experimental group. A mean improvement, however, of 1.84 cps ($p \le .01$) was observed in the non-occluded eye. All subjects, but one, showed the effect with the gains ranging from 0.87 to 4.50 cps.

Experiment III

The purpose of the third experiment was to determine the temporal

course of development of this facilitatory phenomenon during one week of monocular deprivation of the dominant eye. Sixteen experimental and 16 control subjects were tested at intervals of 0, 1/3, 1, 2, 3, 5, and 7 days, each session being preceded by 15 minutes of dark adaptation. Since the repeated measurement of the CFF in the occluded eye at various temporal periods would disrupt the constancy of the monocular deprivation condition, the CFF determinations in the experimental group were restricted to the nonoccluded eye (non-dominant). These results were then compared with those derived from the non-dominant eye of the controls.

Figure 1 shows that the experimental subjects, relative to the controls, exhibit a progressive increase in CFF, of a negatively accelerated nature, as a function of duration of monocular deprivation. An analysis of variance performed on this data revealed a significant difference between the two groups ($F^{=}$ 56.99, p < .001), a significant change over days (F = 54.66, p < .001), and a significant interaction effect (F = 44.14, p < .001). Subsequent t-tests indicated a significant difference at all durations (p's < .001) except at 0 and 8 hours. All 16 experimental subjects showed an improvement in the CFF at the end of the one-week period (mean = 2.34 cps).

In an attempt to determine the approximate duration of the aftereffects, three of the experimental subjects were tested at follow-up intervals of 3 and 7 days *after* the removal of the eye patch. Their mean CFF values at 0 and 7 days of monocular deprivation, and on post-occlusion days 3 and 7, were 38.21, 42.75, 41.12, and 38.92, respectively. Furthermore, all three subjects showed the same temporal pattern thus indicating that a sizeable aftereffect in the non-occluded eye is still present one week after the removal of the patch from the other eye.

Experiment IV

In view of the negatively accelerating functional relationship that was obtained, a further study, using eight experimental and eight control subjects, was conducted to determine the nature of the developmental pattern over a 14- rather than a 7-day period. The CFF of the non-occluded eye was tested at intervals of 0, 1, 3, 5, 7, 9, 11, and 14 days of monocular deprivation and subsquently for another 14 days after the removal of the eye patch. A negatively accelerating improvement was again observed during the first 7 days; this was followed by a level performance from day 7 to day 9, and finally, there occurred a sudden increment of approximately 1 cps on day 11, an increment that was maintained at this higher plateau on day 14. The presence of these two distinct 'limbs' in the developmental curve



Fig. 1. Temporal changes in the CFF of the non-occluded eye (non-dominant) of the experimental subjects, exposed to one week of monocular deprivation, relative to the temporal changes in the non-dominant eye of the controls.

is puzzling. They may indicate the involvement of either two different neural centers or of two types of fibers in the visual system. Another possibility is that the second limb represents the involvement of the reticular activating system. Only future electrophysiological research can provide a satisfactory answer to this unusual finding.

The results of the follow-up tests revealed that after the termination of monocular deprivation, the magnitude of the interocular effect in the nonisolated eye gradually decreased with time. However, it was still present to some degree, 14 days later, the last follow-up day. Thus, this experiment as well as the preceding one clearly indicates that this facilitatory phenomenon is of a long-lasting nature, persisting for many days.²

Subsequent to this study, the CFF of the occluded eye, in eight additional subjects, was determined over a 14-day period, particularly to ascertain whether a compensatory depression of the CFF might occur between day 11 and day 14, the interval which is characterized by the second limb. No systematic changes of any type occurred during the entire two-week deprivation period or in the subsequent follow-up period.

Experiment V

This conclusive demonstration of an improvement in the CFF is puzzling in the light of two 50-year old studies conducted by Allen (1923) and Hollenberg (1924). Both of these investigators reported that 3 hours of monocular deprivation (darkness) produced a *decrease* in the CFF of the non-occluded eye, an effect which was observed on 15 different wavelengths ranging from 410 mu to 750 mu. These results, in conjunction with our own, seem to suggest that prolonged monocular deprivation may *initally* produce a depression of the CFF in the non-occluded eye followed *subsequently* by an enhancement effect. This hypothesis was tested in Experiment V and was confirmed.

A black patch was placed over the dominant eye of 15 experimental subjects for a period of 24 hours. The CFF of the non-occluded eye was then determined at intervals of 0, 3, 6, 9, 15, and 24 hours, each test period being preceded by 15 minutes of dark adaptation and a meal accompanied by a chocolate bar (to control for possiblle effects of changes in blood sugar level). These results were then compared with those obtained from the comparable eye (non-dominant) of 15 controls who were confined for 24 hours in the same "apartment-like" quarters as were the experimentals, thus ensuring the same environmental and dietary conditions for both groups of subjects. The 30 subjects were run concurrently, in groups of three, i.e., 2 experimentals -1 control, 2 controls +1 experimental, etc.

Subsequently, another group of 9 subjects was added for the purpose of studying the changes in the occluded eye which previously had not been tested.

Figure 2 summarizes the results. It can be seen that there is no change in the CFF of the occluded eye at any temporal period. However, the CFF of the non-occluded eye exhibits an initial depression, thus confirming the 50-year-old results of Allen and Hollenberg, a reversal towards the baseline level at 9 hours, and finally an enhancement effect at 24 hours, a finding consistent with our previous results. An analysis of variance revealed a significant change over hours (F = 21.82, p < .001) and a significant interaction effect (F = 20.29, p < .001). A series of two-tailed t-tests, comparing the relative performance of the two groups of subjects at the various temporal periods, indicated that the decrease in the CFF at 3 and 6 hours, the reversal from 6 to 9 hours, and the increase at 24 hours were all statistically significant (p's < .01).

An examination of the individual performance of the 15 experimentals suggested the presence of two main types of "reactors" (see Fig. 3). The first type, representing a third of the sample, showed a prolonged period of depression with an enhancement effect occurring only at 24 hours, while the second type was characterized by a relatively brief period of depression at 3 and 6 hours, followed subsequently by an enhancement effect of progressively increasing magnitude. It is possible that these two general response patterns may be a reflection of possible differences in the degree of stress experienced by the experimental group after being exposed to the novelty of wearing an eye patch. Although no measures of stress or affect were administered, we had the distinct impression that the first type of subject was somewhat more apprehensive and complained more often during the experimental period than did the second type.

From some further research at this laboratory, it is evident that this depression-enhancement phenomenon is also present in the dominant nonoccluded eye, it's pattern is not affected by the use of 30 rather than 15 minutes of dark adaptation at the six test periods, and finally, it can be obtained even when the subject is awake during the entire 24-hour period. This last condition was introduced because in Experiment V an eight-hour period of sleep had been interpolated in the interval after the completion of the 15-hour test and one hour prior to the start of the 24-hour test. Further confirmation of the fact that sleep *per se* was not a confounding variable, particularly in producing the sizeable enhancement effect at 24 hours, is provided by the observation that most of the subjects in Experiment V



Fig. 3. (top). Individual performance of subject A who shows an enhancement of the CFF, in the non-occluded eye, relatively early in the experimental period. (Bottom). Individual performance of subject B who shows an enhancement effect only at the end of 24 hours of monocular deprivation.

showed an increased CFF some hours *before* going to bed, an effect which then increased in magnitude with time (see Fig. 3). *Experiment* VI

The question now arose as to whether this depression-enhancement phenomenon resulted from an absence of patterned vision or whether it was due to an absence of visual stimulation per se. A study was, therefore, conducted in which 14 experimental subjects were required to wear a white translucent patch for 3 days, the CFF being taken from the non-isolated eve at intervals of 0, 3, 6, 9, 15, 24, 48, and 72 hours. Each test period was preceded by 15 minutes of binocular dark adaptation since the occluded eve was exposed to homogeneous illumination rather than darkness. These results were then compared with those obtained from the comparable eve of 14 controls who also were required to spend 3 days in the "apartmentlike" quarters. No significant differences were obtained at any temporal period nor was any trend toward an improvement in the non-occluded eye observed. Negative results were also obtained in an additional 7 subjects in whom the occluded eye was tested over the 3-day period. Thus, it is clear that this depression-enhancement phenomenon has been produced by an absence of visual stimulation per se.

Experiment VII

The next question which arose was whether the enhancement effect in the non-occluded eye, before it returns to normal in the period *after* removal of the patch from the other eye, may not be *preceded* by a depression of the CFF i.e., is there a possibility that the post-deprivation after-effects may be characterized by a "rebound" type of process? This hypothesis is now being tested in an on-going experiment. So far, data have been obtained from 8 experimental and 8 control subjects.

In this study, the CFF of the non-occluded eye is being measured before and after 1 day of monocular deprivation (darkness) and *subsequently* during a 2-day follow-up period, the post-measures being taken at intervals of 3, 6, 9, 12, 24, 36, and 48 hours after the removal of the eye patch. All 8 subjects have shown a sizeable enhancement effect at the end of the oneday period of deprivation, thus again confirming our earlier results. In the follow-up period, however, the performance of these subjects fell into two distinct categories. Four subjects showed a pronounced depression effect (or an initial overshooting of the baseline) at the first post-test period (3 hours) and then a gradual return to the baseline or pre-experimental CFF level. On the other hand, the remaining 4 subjects showed no evidence of an initial overshooting of the baseline but rather a gradual decrease in the magnitude of the phenomenon with time.



Fig. 2. (top). Temporal changes in the CFF of the non-occluded eye (non-dominant) of the experimental subjects, exposed to 24 hours of monocular deprivation, relative to the temporal changes in the non-dominant eye of the "live-in" controls. (Bottom). Temporal changes in the CFF of the occluded eye exposed to 24 hours of darkness.

In view of these results, what is the relationship of these two types of subjects to the two types described in Experiment V who differed in their performance *during* the experimental period? Since in the present study we had deliberately avoided the use of interpolated tests *during* the one-day occlusion period, in order to minimize any possible confounding effects on subsequent performance, we decided to conduct a pilot study on 3 subjects but employing interpolated tests. Although the sample was small, the results were clear-cut. The one subject who overshot the baseline at the 3-hour follow-up period showed a prolonged period of depression in the preceding experimental period whereas the two subjects who did not show it, exhibited, previously, only a brief period of depression. This study will shortly be completed using a much larger sample.

In conclusion, the results of this on-going experiment raise one important question. Why was no indication of an initial overshooting of the baseline observed in any of the two-week subjects of Experiment IV whose post-deprivation performance was followed up for two weeks? The probable answer is that it might have been seen had the test period been extended by another week or so.

DISCUSSION

Although numerous experimental variables are known to affect the CFF, it is difficult to understand how any of them can account for our results on the non-occluded eve. Their unusual *temporal* nature, together with the persistence of the phenomenon for many days, suggests the disturbance or reorganization of function of some neural mechanism(s) in the higher levels of the visual system. It is our belief that prolonged monocular deprivation may be producing changes in certain areas of the primary sensory system, changes similar in nature to the denervation supersensitivity which is known to occur in the higher neural centers following partial surgical deafferentation at lower levels of the central nervous system (Cannon & Rosenblueth, 1949; Stavraky, 1961). For example, Spiegel and Szekely (1955) observed that lesions in the posteroventral nucleus of the thalmus (relay nucleus for touch) are subsequently followed, after an initial period of depression, by a hyperexcitability of the somesthetic cortex. A similar effect has also been observed in the visual system. Burke and Hayhow (1960) reported a dramatic increase in the lateral geniculate response to repetitive optic nerve stimulation after the visual receptor cells were selectively destroyed. (It is interesting to note that over a century ago, Marshall Hall (1841) observed that "the first effect of injury done to the nervous system is a diminution of its functions, whilst the second or ulterior effect is the augmentation of these functions.")

In view of such reports, it is possible that the monocular occlusion procedure may be producing a state of temporary partial deafferentation of the visual system, a condition which is reflected behaviorally in the production of our depression-enhancement phenomenon. (Further evidence for this hypothesis is provided by the fact that this phenomenon resulted from an absence of visual stimulation per se rather than from an absence of patterned vision.) However, this deafferentation is of a functional rather than of a surgically-induced nature i.e., it is produced by depriving the normal biologically intact organism of some of its accustomed visual stimulation. This hypothesis is consistent with Sharpless's (1964) recent revision of the "Law of Denervation" (Cannon & Rosenblueth, 1949) whose main thesis is that the reported supersensitivity phenomena result from prolonged disuse of neural pathways. "Disuse may be the result of drugs, privation of sensory experience, or, most commonly, injury produced by severance of nervous pathways." Furthermore, he states that supersensitivity is a compensatory process which occurs as a consequence of "a radical and sustained change in the level of input to an excitable structure."

This explanation which we are proposing possesses the merit of bringing together our findings, the data on increased cutaneous sensitivity which is known to occur in human subjects following partial occlusion of the skin, as well as the various surgically or drug-induced supersensitivity phenomena, all under the same general concept of "disuse of neural pathways." It does not, however, adequately account for the presence of the phenomenon in only one eye nor does it indicate the specific neural locus of the interocular effect. Only future behavioral and electrophysiological research can provide a satisfactory answer to these two important problems.³

One of the important questions which these experiments raise is whether the temporal pattern of changes in visual sensitivity observed in the nonoccluded eye is specific to the CFF, a measure of temporal visual acuity, or whether it can be obtained using other types of visual tasks. A partial answer to this question has recently been provided by Dusansky (1968). In this unpublished doctoral dissertation, six different visual tasks were presented tachistoscopically at intervals of 0, 6, 12, 24, and 48 hours of monocular deprivation (darkness). The results indicated a significant improvement in spatial visual acuity (broken circles) and perception of curvature in both the non-occluded and occluded eye, an effect which was present at all durations from 6 hours and on. No significant changes in either eye, however, were observed on measures of brightness sensitivity, color saturation, number recognition, and recognition of geometric patterns. These results were interpreted as being consistent with a denervation supersensitivity explanation.

Since an improvement on two measures was observed in both eves, and since no indication of an initial depression of performance was evident, it would appear that our phenomenon may be specific to the use of a visual task involving intermittent stimulation. This, however, may not be the case. First, Dusansky employed a lengthy battery of tests thus providing a considerable degree of visual stimulation. Second, the measures were presented separately to the right and left fields of the test eve. It is conceivable. therefore, that if our procedure and that of Allen (1923) and Hollenberg (1924) had been used i.e., a centrally fixated target and only one measure (e.g., visual acuity), the obtained results may have agreed more closely with those which we have reported. There is also a possibility that an initial depression or impairment of performance might have been detected in the Dusansky study if measurements had been taken at several temporal periods prior to 6 hours e.g., at 1, 2, and 3 hours. It may be that on certain types of visual tasks this depression effect is only evident shortly after the initiation of monocular deprivation.

In conclusion, there are four general implications of our results for research in the area of sensory deprivation. First, they indicate that the monocular deprivation technique may provide a new method of attacking the complex problem of the physiological mechanism's underlying sensory deprivation effects (see Zubek, 1969), an approach which can be used both in human studies and in electrophysiological investigations employing animals. Second, it is difficult to see how any theory of expectancy, set, or of demand characteristics (see Suedfeld, 1969) can adequately account for this depression-enhancement phenomenon which is of a long lasting nature. Third, since we obtained different results depending on whether darkness or unpatterned illumination was employed, further evidence has been provided for the non-equivalence of the sensory deprivation and perceptual deprivation techniques in the production of isolation effects. Finally, our data suggest that some of the apparently contradictory results which have been reported in the earlier isolation chamber studies, particularly those involving durations of one day or less and employing various sensory and perceptual-motor measures, may be accounted for by differences in the duration of their experimental conditions. (It is interesting to note that

the most commonly used periods have been 3, 9, 12, and 24 hours.) As we have demonstrated, performance on the *same* measure may be either impaired, improved, or not affected, the specific effect being dependent upon the duration of deprivation that was employed. It has been assumed by many previous investigators that this experimental variable is probably not too important and therefore can be ignored. This assumption is no longer valid.

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FOOTNOTES

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z It is interesting to note that no instances of any changes in eye-dominance were found in any of the 14-day experimental subjects nor in those who were employed in our subsequent studies.

3 It might be fruitful to take electrophysiological records from various levels of the visual system of the cat or monkey during prolonged *non-surgical* occlusion of one eye and the presentation of visual stimuli to this as well as the other eye, but in separate experiments. Only this type of parallel study may be able to provide us with a more satisfactory or specific explanation of our interocular phenomenon.