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DURATION OF SPIRAL AFTEREFFECT AS A FUNCTION OF RETINAL SIZE, RETINAL PLACE, AND HEMIRETINAL TRANSFER[1]

SHELDON L. FREUD*

Washington, D. C.

Summary.—This experiment has shown that, although both rods and cones mediate the spiral aftereffect, cone areas give a larger response. Increasing size of the retinal image results in longer durations of SAE but rods are more affected by this increase than are cones. There is a general weakening in aftereffect resulting from "transfer" from one hemiretina to another with cone areas showing greater loss than rod areas. Size of retinal image has been shown to be a potent variable and, in fact, under some small size conditions, normal *S*s fail to observe any effect whatsoever. In view of these findings, it is apparent that size of retinal image is a variable which must be carefully controlled if comparable results are to be obtained. Review of the clinical literature, however, reveals that distance from *S* to spiral and objective spiral size often vary from experiment to experiment. This variation could well account for some of the differences in results of clinical studies. It is proposed that a standard spiral size and testing distance be introduced for clinical use.

In recent years a large number of studies have been done on the diagnostic application of the spiral aftereffect (SAE) as a test for organic brain damage. Little has been done, however, to investigate the underlying physiological mechanisms.

This experiment was designed to study (1) differences in duration of SAE for areas of the retina differing in rod and cone concentrations, (2) the relationship of retinal image-size and strength of effect, and (3) the effect of these two variables on both hemiretinal transfer and non-transfer conditions.

The possibility of a difference between peripheral and foveal sensitivity to the aftereffect was first raised by Aubert (1886). The results of experiments which were designed to study this difference, however, were contradictory. Cords and Brucke (1907) reported that the aftereffect was stronger when viewed peripherally, as did Basler (1909). Wohlgemuth (1911), however, found a stronger effect in foveal vision using duration as a measure of strength. Colored discs gave a marked aftereffect both in dim and bright light, suggesting that both rods and cones were important in the phenomenon. Granit (1928) believed that, since the peripheral retina was more sensitive to movement, it therefore should give a stronger aftereffect.

Other studies have dealt less directly with the question. Kinoshita (1909) reported that the duration of the effect varied inversely with the intensity of

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*Dr. Freud is with the Division of Research and Education, Office of Aviation Medicine, Federal Aviation Agency, Washington, D.C.

illumination, suggesting greater sensitivity for the rods. Holland (1957) stated that the angle of focus was of no importance in producing the aftereffect, thus denying any sensitivity differences between rods and cones.

A review of the literature revealed no systematic study of the effect of size of retinal image upon duration of SAE. Since in clinical application both spiral size and testing distance are often varied, it was felt that data pertaining to image size would be of practical as well as theoretical importance. Two previous studies (Freud, 1962; Von Szily, 1907) yielded significant differences in duration of SAE for hemi-retinal transfer of the effect as opposed to non-transfer. This raised the possibility of an interaction between this "transfer" variable and the variables of "retinal size" and "retinal place."

Method

Subjects

Ten *S*s were chosen from a group of volunteers. The sample of students and clerical employees included 7 males and 3 females with an age range of 17-49, a mean age of 29, and a median age of 28.5. None of the *S*s had a history of recent illness, convulsions, or serious injury.

Apparatus

On a table 30 × 50 × 30 in. was mounted vertically a sheet of pegboard 98 × 30 in. Through the center of the pegboard protruded the drive shaft of the motor used to produce the spiral aftereffect. Attached to the shaft by an acorn nut was a 920° Archimedes spiral, 7½ in. in diameter. To the right of the spiral disc, mounted flush into the pegboard, were four 6-v light bulbs powered by an AC step-down transformer set at 4 v and wired to a pair of switches on the main control panel.

The lights were mounted at 15.42, 30.84, 16.57, and 10.05 in. from the center of the spiral so that when *S* focused on the lights, the angle of focus, i.e., the angles subtended from the center of the fovea to the center of the spiral-image, were 4.5°, 8.5°, 9.5°, and 11.5°, respectively. A DC power supply furnished the power to rotate the disc. By keeping a constant input of 3 v (in accordance with apparatus manufacturer's instructions), a rotation speed of 80 rpm (± 2 rpm) was maintained. Stopping and starting rotation of the spiral was controlled by an X-ray timer built into the main control panel. *S* was seated at a table upon which was mounted a chin rest and an eye-piece with a sliding focal-plane type shutter so constructed that *S* had one eye blocked at all times. By pulling a cord, *S* exposed the previously covered eye and simultaneously covered the previously exposed eye. The table was mounted on roller bearings allowing it to be moved to different distances from the spiral. These distances were such that the eye was 17 ft. 4 in., 8 ft. 4 in., and 4 ft. 4 in. from the spiral, producing a retinal image-size of 2°, 4°, and 8°, respectively.

TABLE 1

THE 14 EXPERIMENTAL CONDITIONS

Condition	Place on Retina	Angle of Focus	Retinal Angle Covered	Size of Retinal Image	Hemiretinal Pairs Used
1	Rod area	8.5°	7.5° - 9.5°	Small (2°)	Same (DD)
2	Rod area	8.5°	7.5° - 9.5°	Small (2°)	Diff. (DB)
3	Mixed area	4.25°	3.25°- 5.25°	Small (2°)	Same (DD)
4	Mixed area	4.25°	3.25°- 5.25°	Small (2°)	Diff. (DB)
5	Cone area	Fovea	—1.0° - 1.0°	Small (2°)	Same (DD)
6	Cone area	Fovea	—1.0° - 1.0°	Small (2°)	Diff. (DB)
7	Rod area	9.5°	7.5° -11.5°	Intermed. (4°)	Same (DD)
8	Rod area	9.5°	7.5° -11.5°	Intermed. (4°)	Diff. (DB)
9	Cone area	Fovea	—2.0° - 2.0°	Intermed. (4°)	Same (DD)
10	Cone area	Fovea	—2.0° - 2.0°	Intermed. (4°)	Diff. (DB)
11	Rod area	11.5°	7.5° -15.5°	Large (8°)	Same (DD)
12	Rod area	11.5°	7.5° -15.5°	Large (8°)	Diff. (DB)
13	Cone area	Fovea	—4.0° - 4.0°	Large (8°)	Same (DD)
14	Cone area	Fovea	—4.0° - 4.0°	Large (8°)	Diff. (DB)

Procedure

The spiral apparatus, lights, eye-piece, and timer button were demonstrated to *S* who was then told that he would be focusing at times on the center of the spiral and at other times directly at one of the 4 lights. He was instructed to avoid looking directly at the spiral disc unless told to do so, and was given specific instructions for each test condition.

The angle of focus and size of retinal image were varied independently by changing the point of focus and the distance between *S* and the spiral. Calculating the image size and angle of focus was done in the standard manner (Graham, 1951).

Each *S* was administered a series of 14 trials consisting of variation of conditions along the following three dimensions: (a) *place*: rod vs cone areas of the retina; (b) *size*: small, intermediate, and large areas of the retina; and (c) *transfer*: same hemiretina vs different (homonymous) hemiretinae. Hemiretinae were labeled for convenience according to the following code: Left temporal "A," left nasal "B," right nasal "C," and right temporal "D." The 14 conditions (described in Table 1) were randomly assigned.

RESULTS AND DISCUSSION

The results for the group are given in Table 2 and graphically in Fig. 1. These results show that (1) cone areas give larger effects than rod areas. (2) increasing the size of the image is associated with an increase in duration of SAE, and (3) larger effects are obtained under the non-transfer condition than under the transfer condition.

TABLE 2

MEANS AND STANDARD DEVIATIONS OF DURATIONS OF SAE FOR SIZE, PLACE, AND TRANSFER

	Rods		Cones		Rods		Cones	
	Same	Diff.	Same	Diff.	Same	Diff.	Same	Diff.
	Small				Intermediate			
M	1.11	0	6.13	3.49	4.62	1.75	7.57	3.18
SD	.57	0	1.62	1.00	1.04	1.30	1.28	1.19
	Large							
M	6.53	5.95	9.19	5.36				
SD	2.29	1.45	1.74	1.43				

The results of an analysis of variance performed on the estimates of duration are shown in Table 3. The main effects of size, place, and transfer are all significant. First order interactions are also significant but not the second-order interactions.

TABLE 3

SUMMARY OF ANALYSIS OF VARIANCE FOR DURATIONS OF SAE

Source	*SS*	*df*	*MS*	*F*	*p*
A (Size)	338.27	2	169.13	105.70	.01
B (Place)	186.47	1	186.47	147.99	.01
C (Transfer)	197.96	1	197.96	44.58	.01
D (*Ss*)	61.14	9	6.79		
A × B	52.16	2	26.08	130.40	.01
A × C	16.13	2	8.07	6.06	.01
A × D	28.77	18	1.60		
B × C	33.22	1	33.22	15.37	.01
B × D	11.31	9	1.26		
C × D	34.00	9	4.44		
A × B × C	6.20	2	3.10	3.13	
A × B × D	3.62	18	.20	.20	
A × C × D	23.85	18	1.33	1.34	
B × C × D	19.49	9	2.16	2.18	
A × B × C × D	17.85	18	.99		
Total	1030.44	119			

Note.—Error terms are A × D for A, B × D for B, C × D for C; A × B × D for A × B, A × C × D for A × C, B × C × D for B × C, A × B × C × D for second-order interactions.

Four possibilities concerning the relationship of rods and cones to the duration of SAE were considered in the introduction. Two of these, (1) that rods and cones are equally effective in producing the aftereffect and (2) that the aftereffect is a pure rod phenomenon, can be rejected on the basis of finding that, in general, longer durations of SAE are found for projections onto cone areas than for projections onto primarily rod areas. This finding *could* be accounted for by assuming that the effect is mediated by cones. If this explanation were correct, decreasing the cone concentration should result in a corresponding reduction in duration of effect. As can be seen in Fig. 1, however, the cone concentration (Bartley, 1951) drops off much more rapidly than does the strength of the effect. Thus, the latter data do not, then, support mediation by cones only. Further evidence against this view is the lack of difference between foveal and peripheral areas for the "large-transfer" condition (Table 2). It appears then that the SAE is associated with stimulation of either rods or cones but that cones are more effective.

Other findings of this experiment are consistent with a general knowledge of rod-cone functioning. The results in Table 2 indicate that rods are more affected by increasing size of the image than are cones. This would be expected on the basis of a "ceiling effect" for the cones. The concentration of cones falls off very rapidly beyond the fovea whereas the concentration of

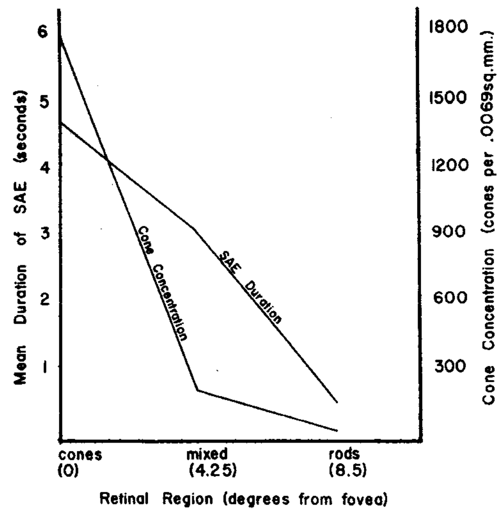

FIG. 1. Comparison of durations of SAE and cone concentrations for 3 retinal regions

rods remains high for large areas of the periphery. A major concentration of cones is to be found in the 2° foveal area used in the "small-cone" condition. Increasing size beyond "small" (2°), however, adds relatively fewer cones compared to the increase in rods for a similar change in size of image.

In general, "transfer" weakens the effect but the cones are more affected than the rods. It is known (see Polyak, 1941, pp. 319-348) that the cone-cortical connections approximate a one-to-one system whereas this is not the case for rods. Thus, for the cones, very precise connections between retinal points and cortical points exist while for the rods, retinal *areas* are connected to cortical points. As has been previously pointed out, homonymous hemiretinae do not project to precisely the same points on the cortex (Teuber, *et al.*, 1960, pp. 113-116). For the cones, then, when the effect is transferred between hemiretinae, the precise relationship is distorted and a considerable reduction in effect could be expected. In the case of the rods, since less precise retinal-cortical correspondence exists, the difference between the retino-cortical projections for "same" (non-transfer) and "different" (transfer) conditions is relatively small. For this reason, the loss in duration of aftereffect under the transfer condition should be less for predominantly rod areas.

The effects of size were clearly significant. An increase in size of image yields an increase in duration of effect. It should be noted that under certain size conditions the effect is lost for normal *Ss*. This obviously is of great importance in the diagnostic use of the SAE where failure to observe the aftereffect is considered evidence of organic brain damage.

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