64-17

Founded in 1887 by STANLEY HALL

OFFPRINTED FROM

THE AMERICAN JOURNAL OF PSYCHOLOGY

EDITED BY

KARL M. DALLENBACH
UNIVERSITY OF TEXAS

AND

M. E. BITTERMAN
BRYN MAWR COLLEGE

E. B. NEWMAN
HARVARD UNIVERSITY

WITH THE COÖPERATION OF

E. G. BORING, Harvard University; W. K. ESTES, Stanford University; J. P. GUILFORD, University of Southern California; HARRY HELSON, Kansas State University; E. R. HILGARD, Stanford University; FRANCIS W. IRWIN, University of Pennsylvania; F. NOWELL JONES, University of California, Los Angeles; G. L. KREEZER, Washington University; D. G. MARQUIS, Massachusetts Institute of Technology; ARTHUR W. MELTON, University of Michigan; W. C. H. PRENTICE, Wheaton College; T. A. RYAN, Cornell University

THE PHYSIOLOGICAL LOCUS OF THE SPIRAL AFTER-EFFECT

By SHELDON L. FREUD, Office of Aviation Medicine,
Federal Aviation Agency, Washington, D.C.

September, 1964, Vol. LXXVII
pp. 422-428

Published by The American Journal of Psychology, Department of Psychology, University of Texas, Austin, Tex.

THE PHYSIOLOGICAL LOCUS OF THE SPIRAL AFTER-EFFECT

By SHELDON L. FREUD, Office of Aviation Medicine,
Federal Aviation Agency, Washington, D.C.

It has long been known that if an Archimedes spiral is rotated, an illusory motion of swelling or shrinking, depending on the direction of rotation, will be perceived. If, after the spiral is rotated, it is stopped and *S* looks at a stationary spiral, an after-effect of motion opposite to that produced by the moving spiral will be seen. This after-effect is called the Spiral After-Effect (*SAE*).

Although numerous studies on the use of the *SAE* as a diagnostic test for organic brain-damage have been published, these studies have largely ignored the theory underlying the effect and have not investigated the crucial question of the physiological locus of the *SAE*. Theories that have been proposed to explain the appearance of the effect fall into two general categories: (1) peripheral theories, which attribute it entirely to processes within the retina itself; and (2) central theories, which take the position that the effect is a result of processes within cortical or sub-cortical structures.

A demonstrated transfer of the effect from a stimulated to an unstimulated eye has been generally accepted as strong evidence of centrality. Results of a number of studies on interocular transfer, however, have been far from consistent and the question of this transfer has remained an unresolved subject of debate in the literature since 1871, when Dvorak published a report of observed transfer.[1] Among the early studies, Exner, Von Szily, and Ehrenstein also reported transfer while Budde, Hunter, and Durop failed to find it.[2] More recently, Holland reported 70% transfer,[3] and Day cites Seagrim as having obtained transfer.[4]

* Received for publication July 11, 1962. This paper is based upon a portion of a Doctoral dissertation completed at the University of Connecticut. The writer is indebted to Dr. A. Robert Rollin for his assistance in this study.

[1] V. Dvorak, Versuche über Nachbilder von Reizveränderugen, *Sitz. Akad. Wiss. Wien,* 61, 1871, 257-262.

[2] S. Exner, Ueber das Sehen von Bewegungen und die Theorie des zusammengesetzten Auges, *Sitz. Akad. Wiss. Wien,* 72, 1875, 156-189; A. von Szily, Zum Studium des Bewegungsnachbildes, *Z. Psychol. Physiol. Sinnesorg.,* 42, 1907, 109-114; Walter Ehrenstein, Versuche über die Beziehungen zwischen Bewegungs- und Gestaltwahrnehmungen, *Z. Psychol.,* 96, 1925, 305-352; E. Budde, Ueber metakinetische Scheinbewegungen und über die Wahrnehmung von Bewegungen, *Arch. Anat. Physiol.,* 1884, 127-152; W. S. Hunter, The after-effect of visual motion,

It is difficult to evaluate these studies, since many variables now known to be important in determining the intensity of the *SAE* were often not reported (*e.g.* speed of rotation, lighting, size of spiral, testing distance, and duration of fixation). It is likely that the conflicting results stem from incomplete control of these variables.

A carefully controlled study of interocular transfer might have resolved the question. By applying the technique of hemiretinal transfer, however, it was possible to obtain the same information as in simple interocular transfer and, in addition, to relate the effect more precisely to the known neural pathways of the visual system. In the hemiretinal technique, one hemiretina is stimulated by a rotating spiral and a stationary spiral is then projected upon a different hemiretina. If cortical processes are crucial, transfer of the after-effect should occur between homonymous hemiretinas (*i.e.* those which project to the same cortical hemisphere) and transfer should *not* occur between non-homonymous hemiretinas (*i.e.* those which project to different cortical hemispheres). On the other hand, if the crucial processes take place at the retinal level, transfer would be expected between hemiretinas of the same eye rather than between hemiretinas in different eyes. This latter explanation is based upon the well-known fact that there are multiple and complex interconnections within a single retina but no known direct interconnections between the two retinas.[5]

Two experiments were carried out. In the first, transfer of the *SAE* was determined by having *S* report 'yes' or 'no' if the effect appeared in the unstimulated hemiretina after stimulating a homonymous hemiretina. In the second experiment, *S* reported presence of effect by pressing a button connected to an interval-timer. In this way, a measure of the duration of the effect was obtained.

Experiment I

Subjects. Ten *S*s were selected from among undergraduate students, graduate students, and clerical employees at the University of Connecticut. Included in the sample were 7 men and 3 women with an age-range of 17 to 49 yr., a mean age of 29.0 yr. and a median age of 28.5 yr. None of the *S*s had a history of recent illness, convulsions, or serious injury.

Apparatus. The apparatus consisted of a table, 50 in. long and 30 in. wide, and 30 in. high, which had mounted vertically upon it a sheet of peg-board enclosed in

Psychol. Rev., 21, 1914, 245-277; G. Durop, Le problème des impressions de movement consecutives d'ordre visuel, *Année Psychol.,* 29, 1928, 1-56.

[3] H. C. Holland and H. R. Beech, The spiral aftereffect as a test of brain damage, *J. Ment. Sci.,* 104, 1958, 466-471.

[4] R. H. Day, On interocular transfer and the central origin of visual after-effects, this JOURNAL, 71, 1958, 789.

[5] S. L. Polyak, *The Retina,* 1941, 319-348.

a frame 17 × 13 in. Through the center of the peg-board protruded the drive-shaft of the Spiral After-Effect Apparatus. Attached to the shaft was a standard (920°) Archimedes spiral, 7¼ in. in diameter. A DC power-supply provided the power to rotate the disk. Speed of rotation was fixed at 80 r.p.m. by means of a Strobotac, and recalibration was done by adjustment of the readings of voltage and amperage on the power-supply prior to testing each *S*. Starting and stopping of the spiral-rotation was controlled by an X-ray timer built into the main control-panel. On either side of the spiral, at a distance 6½ in. from the center of the spiral, was a 6-volt bulb mounted flush into the peg-board. These bulbs were wired to an on-off-on switch mounted on the control-panel, thus allowing *E* to switch lights rapidly. An AC step-down transformer set at 4 v. served as an independent constant source of power for the lights. Built into the frame surrounding the apparatus was a sliding door which, when closed by *E* after each trial, blocked the entire apparatus from *S*'s view. All of the exposed portions of the apparatus, with the exception of the spiral-disk itself, were painted a flat light gray. *S* was seated behind a table 8 ft. from the spiral. Attached to the table on an adjustable shaft was an eye-piece with a sliding shutter of the focal-plane type, 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.

Procedure. The general procedure was to have *S* focus upon one of the lights with one eye, thus causing the image of the rotating spiral to fall upon a predetermined hemiretina. Then, at the end of the period of rotation, *S* was switched to a particular eye and a particular focusing light so that the image of the stationary spiral fell upon either the same or a different hemiretina, as required by the experimental design.

S was given a demonstration of the after-effect and shown how the eye-piece of the apparatus was operated. He was instructed to maintain his focus on the selected light and to avoid looking directly at the spiral itself. General instructions were given on the procedure for switching eyes and lights, and detailed instructions were given for all eye-light combinations. *S* reported presence or absence of after-effect by responding with 'yes' or 'no.'

For purposes of identification, the four hemiretinas were labeled in the following manner: left temporal, A; left nasal, B; right nasal, C; and right temporal, D. Hemiretinas A and C correspond to the homonymous pair projecting upon the left cortical hemisphere, and hemiretinas B and D correspond to the homonymous pair projecting upon the right cortical hemisphere.

The following procedure was employed for stimulating and testing the hemiretinas:

Hemiretina	Eye	Light
A	left	left
B	left	right
C	right	left
D	right	right

The 16 conditions (8 homonymous and 8 non-homonymous) were given in random order to each *S*, with a 15-sec. rest-period between trials. A rest-period of 1 min. was given at the end of the eighth trial.

Results. Transfer occurred in all 80 of the homonymous hemiretinal conditions and in only 4 of the non-hemiretinal conditions. The Chi-square for these data is 144.76; $p < 0.01$.

Discussion. The results of Experiment I clearly demonstrate that homonymous hemiretinas transfer the *SAE,* while non-homonymous hemiretinas fail to do so. The report of transfer in four of the non-homonymous trials can be accounted for by *S*'s inability to maintain perfect focus upon the light. If *S* should glance momentarily at the spiral instead of maintaining his focus upon the light, the after-effect could appear. Another possibility is the general tendency on the part of the *S*s, while engaged in a difficult discriminative task, to report the presence of an effect when it is actually absent (false positives). It is to be noted that these four reports of after-effect in the non-homonymous conditions were spontaneously described by the *S*s as "weak" or "different" compared to the effect seen in the demonstration prior to beginning the experiment.

The almost perfect correspondence between these results and the predictions one would make by assuming that the effect takes place at the visual cortex can be considered as extremely strong evidence for at least a major central component of the *SAE.* They do not, however, conclusively rule out the possibility of a retinal contribution.

In our conditions of transfer, one hemiretina was stimulated with a moving spiral; when the spiral was stopped, another hemiretina was exposed to the stationary spiral. Transfer was defined as a report of the *SAE* under these conditions.

Two physiological explanations for this transfer will be considered. Presumably, the *SAE* results from the interaction of neural firings produced by the present stimulation of the stationary disk with some 'trace' in the nervous system of the previous stimulation produced by the moving disk. One possibility is that the 'trace' represents a neural change or process at the cortical level and interaction takes place there. An alternative possibility is that the trace is at the retinal level and these neural changes or processes result in a particular pattern of firing to the cortex. The *SAE* would then occur upon a meeting at the cortex of these firings of the trace from one hemiretina. It is clear that either explanation requires a cortical or central process. With the latter explanation the possibility of a major retinal contribution remains.

One alternative experiment suggests itself, which, while not a conclusive test of the absence of a retinal contribution as discussed above, could

rule out the possibility of any interaction at the retinal level (*i.e.* firings of the trace and firings due to present stimulations interacting in the retina). If the intensity of the after-effect resulting from the stimulation and testing of a pair of homonymous hemiretinas (*e.g. A–C*) could be shown to be equal to the intensity of effect obtained when the *same* hemiretina (*e.g. A–A*) was both stimulated and tested, it would follow that no part of the effect was due to stimulated hemiretina *A*'s interacting with tested hemi-

TABLE I

MEAN DURATION OF SAE

	Homonymous hemiretinas							
	AA	*BB*	*CC*	*DD*	*AC*	*CA*	*BD*	*DB*
M	7.50	7.65	7.93	8.08	3.92	3.93	3.67	4.08
SD	2.06	2.73	1.95	2.29	1.95	1.71	1.27	1.58
	Non-homonymous hemiretinas							
	AB	*BA*	*CD*	*DC*	*AD*	*DA*	*BC*	*CB*
M	.05	.02	.05	.03	0	0	0	0
SD	.14	0	0	0	0	0	0	0

retina *A*. What is required, then, is a comparison between the strength of effect for 'same' and 'different' hemiretinas. This comparison was included in Experiment II.

EXPERIMENT II

In an attempt to rule out any retinal contribution to the *SAE* as discussed in Experiment I, a test of the *SAE* for the 'same–different' conditions was conducted. In addition, a measure of the *SAE* made it possible to evaluate more precisely the non-homonymous retinal responses.

Method. The *S*s were the same as in Experiment I. The same apparatus was used, except for the addition of an interval-timer attached to a button which *S* used to report duration of the *SAE*. The procedure was basically the same as in Experiment I, except that *S* reported presence and duration of *SAE* by means of button and timer described above.

Results. The results of Experiment II are shown in Table I. The mean duration of the *SAE* for the 'same' (non-transfer) hemiretinal condition was 7.79, as opposed to a mean value of 3.90 for the 'different' (transfer) condition.

A comparison of these means resulted in a t of 3.89 ($p < 0.01$). This finding demonstrates that the *SAE* is significantly greater for the 'same' (non-transfer) condition.

The difference between homonymous and non-homonymous hemiretinas found in Experiment I was confirmed. The after-effect occurred between the homonymous hemiretinal pairs in all 80 of the trials, but between non-homonymous pairs in only 5 of the 80 trials. The range for the mean duration of the *SAE* for non-homonymous responses (0.02–0.05) was clearly of a different order of magnitude than the range for the mean duration of the *SAE* of homonymous hemiretinal responses (3.67–8.08).

Discussion. With respect to the attempt to rule out retinal interaction by comparing 'same' (non-transfer) and 'different' (transfer) hemiretinal conditions, it is apparent that it is not supported by the results since 'same' conditions yield significantly greater durations of the *SAE* than 'different' conditions. In the process of transferring the *SAE* from one hemiretina to a different (homonymous) hemiretina, some of the effect is lost.

Two possibilities will be considered to explain the reduced after-effect under the condition of transfer. The first, previously considered, is that retinal interaction contributes to the *SAE* in the 'same' (non-transfer) conditions, but obviously cannot do so in the 'different' (transfer) condition. An alternative explanation may be made on the basis of very recently published anatomical evidence regarding projections from the retina to the visual cortex. According to Teuber, homonymous hemiretinas do not project to precisely the same points on the visual cortex.[6] Thus, if hemiretina *A* (left-temporal) projects to Point 1 on the cortex and its homonymous hemiretina *C* (right-nasal) projects to Point 2 (rather than to the same point), differences such as those obtained might well be expected.

The findings regarding homonymous hemiretinal transfer obtained in Experiment I are confirmed. The amounts of transfer are almost identical. In every case of the 80 homonymous hemiretinal pairs, transfer occurred, and in only 5 of the 80 non-homonymous trials was transfer reported. This was of very brief duration (0.20 to 0.48 sec.) and of a completely different order of magnitude from the homonymous scores (1.22 to 14.80 sec.). Thus again, we have evidence of a major central contribution to the *SAE*.

SUMMARY

It was the purpose of this study to investigate the physiological locus of the Spiral After-Effect (*SAE*). Experiment I demonstrated 100% transfer

[6] H.-L. Teuber, W. S. Battersby, and M. B. Bener, *Visual Field Defects after Penetrating Missile Wounds of the Brain,* 1960, 113-116.

between homonymous hemiretinas and almost total absence of transfer between non-homonymous hemiretinas. In Experiment II, duration of the *SAE* was found to be longer for the conditions of non-transfer than for the conditions of transfer; hence, the possibility of a retinal contribution to the after-effect could not be conclusively ruled out. In this experiment, a quantitative study of hemiretinal transfer confirmed the results obtained in Experiment I. It was concluded from these experiments that a major central component exists for the Spiral After-Effect.