A study of the Sherrington effect¹

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In his studies of binocular fusion of flicker, Sherrington found a very small difference between CFFs when the eyes were synchronously stimulated and when they were alternately stimulated by two binocularly fused test patches. He concluded that the phenomena of alliance and antagonism which he had demonstrated in the motor system did not obtain in the sensory (visual) system. Later investigators found that this "Sherrington effect" was slightly larger than Sherrington reported, and it has been held as evidence of a definite, though perplexingly small, degree of binocular interaction. In the experiment reported here, the Sherrington effect was found to be about five times greater than it has previously been reported to be.

Sherrington (1904) conducted some notable investigations of the integrative action of the nervous system in its motor aspects. One of his major discoveries was that of "correlation of reflexes about a final common path." He showed that some reflexes termed "allied" reflexes reinforce one another as they emerge along the final common path. Other reflexes, termed "antagonistic" reflexes, inhibit one another from use of the path.

Could such alliance and antagonism be demonstrated in the sensory functions of the nervous system? Sherrington attempted an answer through investigation of the sensory phenomenon of binocular flicker fusion by testing "to what degree the visual singleness of the observed surface [two test fields binocularly superimposed] sensed through right eye and left eye together, is due to direct confluence of the sensory paths excited by the right-eye and left-eye images respectively."

In his first of three series of experiments, involving what he termed "symmetrical flicker," Sherrington determined the binocular critical fusion frequency (CFF) for two experimental conditions, viz, synchronous (Sherrington's term) stimulation of the two eyes vs alternate stimulation of the two eyes.

Fig. 1. Top half shows two sector disks arranged to give binocular synchronous stimulation. Bottom half shows the arrangement for alternate stimulation. In both cases the disks counterrotate.

Sherrington's apparatus was a rather complicated rotating lantern. A simpler apparatus, which has typically been used by later investigators, is schematized in Fig. 1. Two test fields are separated by a septum so that one is viewed by each eye. One field has a fine vertical diameter line and the other a horizontal line. When the two fields are binocularly superimposed by a prism in front of each eye, the resultant single field is seen to have a delicate black cross. By arranging the vanes of two sector disks, geared together as shown in the top half of Fig. 1, it can be seen that the two test fields will be synchronously occluded and exposed as schematized in Fig. 2. By simply rotating one disk through 60 deg on its shaft, as shown in the bottom half of Fig. 1, the alternating condition, Fig. 3, is achieved. (Note that this simple apparatus permits one to employ any desired intermediate condition between synchronous and alternate.)

Sherrington reasoned that if alliance and antagonism characterized the binocular visual system then the CFF in the alternate condition, in which the visual system is

continuously stimulated by one test field or the other, would have a much lower CFF than the synchronous condition. But not so: Mean CFF for the alternate condition was found to be just 1.2 cps below that for the synchronous condition, and Sherrington described this difference as being "very small." He concluded that:

"The experimental evidence indicates absence (practically entire) of any interference between the flicker processes so initiated. The right and left 'corresponding retino-cerebral points' do not when tested by flicker reactions behave as though combined or conjugate to a single system."

In a second series of experiments, involving "asymmetrical flicker" (unequal frequencies of stimulation of the two eyes), Sherrington did find some evidence of interference. For this condition, the binocular combination was nearly 5 cps below that found in the symmetrical condition. Differences almost as great were found when one test field was only a

Table 1
Mean Binocular CFFs for Synchronous Stimulation and the Drop in CFF
for Alternate Stimulation Reported by Four Investigators

Investigator		Mean CFF for Synchronous Condition (cps)	Mean Drop in CFF from Synchronous to Alternate Condition (cps)	Mean Percentage Drop in CFF from Synchronous to Alternate Condition
Sherrington	Experiment 1	48.3	1.2	2.5
Ireland	Experiment 2	31.5	3.0	9.5
	(2 Sessions)	32.8	3.4	10.3
Baker	Experiment 1	47.9	2.2	4.6
		34.4	1.6	4.6
	Experiment 2	32.5	2.0	6.1
		29.8	1.8	6.0
		31.8	1.9	5.9
	Experiment 3	29.6	1.6	5.4
		27.7	1.5	5.4
		29.6	2.3	7.7
	Experiment 4	27.2	1.4	5.1
		24.4	1.7	7.0
		30.2	2.0	6.6
	Experiment 5	27.9	1.6	5.7
		25.7	1.8	7.0
		30.6	2.0	6.5
	Experiment 6	27.9	1.4	5.0
		25.7	1.8	7.0
		30.6	2.0	6.5
	Experiment 7	27.9	1.4	5.0
		25.7	1.8	7.0
		30.7	2.3	7.5
	Experiment 8	28.5	1.8	6.3
		25.9	1.9	7.3
		30.9	2.5	8.1
		29.5	2.6	8.8
		27.2	2.7	9.9
		30.1	2.4	7.9
	Experiment 9	28.8	2.4	8.3
		26.5	2.7	10.2
		26.3	1.9	7.2
	Experiment 10	24.8	1.4	5.6
		23.4	1.7	7.2
		31.2	1.1	3.5
		29.4	1.4	4.7
		27.0	1.4	5.2
		31.1	1.0	3.2
	Experiment 11	29.1	1.1	3.4
		26.7	1.2	4.5
Perrin	Experiment 1	44.1	3.0	6.8
Mean			1.8	6.4

have not previously been reported in this form.

It can be seen that experimental conditions were such as to generate mean CFFs ranging from about 48 to about 24 cps. The mean size of the effect is 1.8 cps, or a mean drop of 6.4% between synchronous and alternate stimulation. The mean size of the effect for the Ireland and Baker experiments is statistically significant in every case. (Sherrington had no statistical tests available and Perrin did not report statistical tests of significance.) Baker's Experiments 2, 3, and 4 involved

a test field subtending 2 deg, 53 min, and 38 min, respectively. The respective mean sizes of the effect are 1.8, 1.66, and 1.8 cps, indicating that within this range of visual angles subtended the size of the effect is virtually constant rather than positively correlated. These data contradict Perrin's second finding.

A final point with respect to Table 1 concerns the relation between the size of the effect and mean CFF consequent to field luminance. In each of Baker's Experiments 2 through 11, field luminance was varied over three values, viz, 8, 5.5,

and 3 fL, and each of the three mean values tabled for each experiment is for these three luminances, respectively (in Experiments 9 and 11 there were additional experimental conditions so each mean value is for each luminance in each condition). Inspection of the central column, showing mean size of the effect in cps, reveals no relation between the size of the effect and mean CFF. The brightest field resulted in the largest effect in 7 of 12 cases and the smallest in 3 cases. But the dimmest field resulted in the largest effect in 4 of the 12 cases and the second largest effect in 7 cases; in fact, the dimmest field resulted in the smallest effect in just 1 of the 12 cases. These data contradict Perrin's third finding.

We suggest that Perrin's results may reflect an artifact of his method. It was noted above that Perrin achieved synchronous and alternate stimulating by changing the radial distance from shaft center to test fields. Such a change results in a change of the rate of stimulus (field) occlusion by a rotating sector and it was recently shown (Baker & Monty, 1969) that rate of stimulus occlusion is a major factor in determining the CFF.

NEW FINDINGS

Background

Experiment 11 reported by Baker (1952d, and Table 1) was concerned with activation of both occipital lobes through intermittent stimulation of the lateral halves of a single retina. A test field was arranged with a heavy vertical diameter line, Fig. 5. A septum could not be used but a pinpoint of light in the center of the line served as a fixation point.

Sector disks could not be employed; instead, "instantaneous" neon sources behind the two halves of the test field (sealed from each other) were illuminated in phase, giving synchronous stimulation, or 180 deg out of phase, giving alternate stimulation.

Fig. 5. The test field employed by Baker (1952d).

Fig. 2. A representation of light and dark phases (exposures and occlusions) for the condition of binocular synchronous stimulation.

fraction as bright as, or brighter than, the other.

Nevertheless, Sherrington's general conclusion was that:

"The above experiments on binocular flicker and brightness show that during binocular regard of an objective image each uniocular mechanism develops independently—at least as to steadiness of brightness and intensity of brightness—a sensual image of considerable completeness. The singleness of the binocular perception arises from the combining of these elaborated uniocular sensations: it is the product therefore of a psychical synthesis that works with already elaborated sensations contemporaneously proceeding. Such synthesis lies obviously more within the province of study of the psychologist than of the physiologist."

This finding was interpreted by many to imply that CFF was peripherally determined. Ireland (1950) reexamined the problem. Ireland found a mean difference of 3.2 cps, with CFFs for the synchronous and alternate conditions being significantly different statistically from the mean intermediate CFF obtained for monocular fusion. Ireland considered his results as "offering definite evidence for the importance of central factors in the phenomena of flicker and fusion."

In the series of 11 experiments reported by Baker and Bott (1951) and by Baker (1952a, b, c, d), Ireland's results were confirmed, the mean difference found being 2.2 cps. The difference was found, too, when the right lateral halves of the two foveas (and hence the right occipital lobe only) were synchronously and alternately stimulated, and also when the two lateral halves of a single fovea (and hence both occipital lobes) were so stimulated.

Fig. 4. Perrin's method of obtaining binocular synchronous (left) and alternate (right) stimulation.

The differences between synchronous and alternate forms of stimulation found by these later workers, while significantly different statistically in every case, were not large. The question arises as to how large is large enough to permit an unequivocal inference of interaction.

Perrin (1954) reported a study of binocular flicker, based upon Sherrington's work, which he (Perrin) began 20 years earlier. In discussing the problem of largeness with respect to the difference between CFF in the simultaneous and alternate condition, he hypothesized, for the alternate case, that:

"It would therefore appear that the combined nervous impulses that become translated into consciousness would be perfectly constant since those from one retina would exactly interlace with those from the other. The alternate critical frequency, in other words, might be expected to approach zero."

In reviewing the same problem, Pirenne (1962) stated that, "When the intermittent stimuli are out of phase [alternate] the total flux of light reaching the visual system is constant. Any simple hypothesis of summation between the eyes, according to which flicker should never be seen with out-of-phase binocular stimulation, is thus ruled out."

Perrin (1954) coined the term "Sherrington effect" for the slight difference between fusion frequencies for

Fig. 3. A representation of light and dark phases for the condition of binocular alternate stimulation.

the synchronous and alternate conditions, and set about studying factors which influenced the effect. To obtain synchronous and alternate stimuli, Perrin employed the ingeniously simple arrangement of apparatus shown in Fig. 4: The two conditions were obtained by raising or lowering the shaft of a sector disk. Notice that this raising and lowering resulted in a difference in radial distance from shaft center to test fields.

Perrin's three main findings were as follows. He found that the Sherrington effect "is certainly present, since it can be reproduced, so the significant feature would seem to be that it exists at all." He noted that the size of the effect reported by Sherrington was "about 3 percent," whereas his own data indicated a drop of 6.8% in CFF from synchronous to alternate stimulation.

His second finding was that as the test field was decreased in visual subtense from 2 deg to $\frac{1}{2}$ deg, the Sherrington effect was decreased. He noted, however, that Baker's data did not indicate such a relation.

Perrin's third finding was that "the Sherrington effect is directly proportional to the mean critical frequency," critical frequency being varied by variations in field luminance.

THE SIZE OF THE SHERRINGTON EFFECT

Table 1 shows the size of the Sherrington effect found by the four investigators for foveal test fields subtending 2 deg or less. The Baker data, from numerous experimental conditions,

Because a septum could not be used, there was probably some spreading of illumination, in the alternate condition, to the contralateral portion of the retina. Nevertheless, the Sherrington effect was demonstrated for each eye and at each of the three levels of luminance (the data are those reported in Table 1, Experiment 11). The effect was relatively small, ranging from 1.0 to 1.4 cps, or from about 3% to 5%, but was statistically significant at the .01 level or better in each case.

Evidence was gained, therefore, that the Sherrington effect is demonstrable not just by binocular stimulation, but also when the twin neural systems proceeding from a single retina are appropriately stimulated, i.e., by "firing" geniculate/occipital areas in synchrony or alternately.

The effect, however, is small. It's as though the "separate" geniculate/occipital areas were separate in name only, being interconnected in parallel to a common seat of sensation (or, to use Sherrington's terminology, "as though combined or conjugate to a single system"). When one geniculate/occipital area is quiescent (during a dark phase in an alternate mode of intermittent stimulation) and the common seat is activated by the other area it has nearly the same ability (within 1 to 2 cps) to temporally resolve intermittent visual stimuli as it has when stimulation is synchronous.

Hypothesis

If a common seat of sensation exists, then surely, like the final common path, it must be differentially responsive to "allied" and "antagonistic" forms of stimulation to a much greater degree than has been demonstrated to date. Consequently, the issue is raised concerning the *appropriateness* of the form of stimulation which has been employed. In the experiment reported below, a novel form of stimulation was employed.

Method

The apparatus was arranged as shown in

Fig. 1, without the septum, but with some additions. Figure 6 shows the additions in plan view. A is a half-silvered mirror through which the right test field with its fine vertical line could be seen, though at considerably reduced luminance. B is a full mirror, which reflected the left test field onto A. By a simple adjustment of B, the two test fields could be monocularly observed side by side. A rheostat in the circuit to B allowed the E to make a visual brightness match. When matched, B was moved again so that the two fields were superimposed and seen as a single field with the fine black cross. Seen in combination, the image of A was slightly larger than that of B, but this slight difference was easily ignored in making the observations which followed.

Fig. 6. The arrangement of the apparatus, in plan view, to give monocular synchronous and alternate stimulation.

By this arrangement, both halves of a single fovea were treated identically in both synchronous and alternate conditions (unlike Experiment 11, discussed above), but during the alternate condition of stimulation one geniculate/occipital area would not be "quiescent." Assuming a "common seat," the consequences should be a greatly lowered CFF in the alternate condition of stimulation.

Results

The results for 24 trained Os are shown in Table 2. Each tabled value is the mean of 10 successive readings.

Discussion and Conclusion

This experiment has demonstrated that the alliance and antagonism which Sherrington demonstrated in the motor system also characterizes the visual system to a marked degree.

The definite existence of the Sherrington effect has been a puzzle for over half a century because of its small magnitude, but it is not small: When the visual system is appropriately stimulated, the effect is found to be larger by a factor of five than the mean of the values previously reported. When the visual system is explored binocularly with intermittent stimulation in and out of

Table 2
Mean Monocular CFFs for Synchronous Stimulation and the Drop in CFF for Alternate Stimulation for 24 Os.

Subject	Mean CFF for Synchronous Condition (cps)	Mean Drop in CFF from Synchronous to Alternate Condition	Mean Percentage Drop in CFF from Synchronous to Alternate Condition
1	31.5	9.7	30.8
2	31.1	10.4	31.1
3	37.2	13.9	37.3
4	30.5	10.3	33.7
5	34.0	10.4	30.6
6	31.9	11.4	35.7
7	29.4	8.0	27.2
8	33.6	12.7	37.7
9	36.7	9.0	24.5
10	36.2	9.7	26.8
11	27.8	9.2	34.9
12	32.8	12.0	36.6
13	37.0	11.9	32.1
14	34.7	10.6	30.5
15	33.3	9.1	27.3
16	32.0	10.5	32.8
17	39.6	11.6	29.3
18	39.8	12.5	31.4
19	31.1	10.1	32.4
20	30.8	8.4	27.2
21	30.5	7.2	23.6
22	38.3	12.7	33.1
23	33.7	7.3	21.6
24	36.2	8.0	22.1
Mean		10.3	30.4

phase, or when the lateral halves of a single fovea are similarly stimulated, the effect is almost completely masked by neural circuitry which, in the engineering sense, is redundant.

In sum, the Sherrington effect is large indeed. In our view, it is sufficiently large to permit an unequivocal inference of interaction. The study of such interaction lies obviously more within the province of study of the physiologist than of the psychologist.

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NOTES

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