Binocular rivalry and visual evoked responses

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A subject viewed a different grating target with each eye in a binocular rivalry situation and continuously indicated with a response key which target he was seeing. Each target was illuminated with flickering light at different frequencies superimposed upon a steady background. The evoked cortical responses were tape-recorded and later analyzed by average response computer separately for each eye, seeing and not seeing. Differences in latency and amplitude of the evoked responses were found in comparing the dominant and suppressed conditions of the same eye.

In binocular rivalry, the two eyes are presented dissimilar views which cannot be fused. The result is that the observer sees alternately with each eye separately or sees a composite of elements from the two monocular views. The monocular elements which are not seen are described as suppressed. This suppression has similarities to the longer-lasting suppression in amblyopia. It is also relevant to the suppression presumed operating by certain theories in normal binocular vision.1,2

The physiological mechanisms underlying suppression and fusion are still unknown. Several recent studies of brain potentials have been made to investigate these processes. Lansing3 has used flicker stimulation of one eye and recorded brain responses with a tuned amplifier during binocular rivalry. Evoked brain responses from flicker stimulation of one eye have been averaged by computer in the studies of Van Balen4 and Riggs and Whittle.5 Evoked responses in amblyopia have been investigated by Nawratzki and colleagues.6 In the present study, evoked responses from the simultaneous flicker stimulation of both eyes have been recorded during retinal rivalry.

Method

The subject viewed two different circular targets, one for each eye, which were superimposed. The target presented to one eye contained three light and three dark horizontal bars. The target presented to the other eye was the same except the bars were vertical. The light bars were illuminated with red light. Each target was illuminated at a steady level of 3 footlamberts (ft-L) to which was added an additional illumination of 6.5 ft-L during the light phase of the flicker stimulation. The circular targets of 3 degrees diameter were surrounded by a circular white surround of 15 degrees illuminated at 0.1 ft-L. The subject viewed the targets in binocular superimposition and indicated with a three-position switch whether he was seeing horizontal bars, vertical bars, or was uncertain. Flicker stimulation was applied at slightly different frequencies in the two eyes. To
the subject the stimulus pattern in each eye periodically brightened and dimmed.

Active electrodes were placed on the occipital and parietal regions at 10 and 40 per cent of the distance along the midline between the inion and the glabella. The more anterior electrode is positive upward on the records. A ground electrode was also placed on the midline at the forehead.

The brain response, subject switch response, and two stimulus wave forms were recorded on a multichannel tape recorder. The evoked brain responses for each eye dominant and nondominant were later analysed by average response computer. Analysis was performed on the brain response adjusted to compensate for the motor response time of the subject pressing his key.

Stimulation. The visual targets were presented on a Wheatstone stereoscope (Fig. 1) with arms rotating about the center of rotation of each eye. The convergence of the arms and the interpupillary distance were adjusted for each subject. On each arm, continuous illumination was provided by a 6 v. tungsten bulb ($S_t$) shining through a half-silvered mirror ($H$). Reflected coaxially from this mirror was a second beam from a glow modulator gas discharge tube ($S_i$). Both beams were collimated by a lens ($L$), passed through a heat-absorbing filter ($HF$), red filter ($RF$, Corning 2424), and neutral density filter ($N$) when needed.

Each beam also passed through a field stop ($F$) and grating slide ($G$) containing alternate opaque and transparent bars (each 0.5 degree in width). The images of the filament of the tungsten bulb and the gas discharge light were focused at the pupil by a final lens ($L$) after reflection from the mirror ($M$). With this Maxwellian view arrangement the bar pattern was in focus at the retina. Illumination of the field stop ($F$), painted white, was by small tungsten bulbs ($S_i$). A stop ($B$) limited the extent of the illuminated surround. The head and eye positions of the subject were maintained with a biting board and forehead rest.

Each gas discharge tube was controlled by a vacuum tube. Each vacuum tube was in turn controlled by a Hewlett-Packard audio oscillator whose output was modified to square wave by a shaping device. Small samples of the input to the gas discharge tubes were used for recording the stimuli. These samples were identical in wave form and timing to a photocell sample of the light produced. The modulation was square wave with equal on and off times.

Recording. The subject’s response key consisted of two microswitches mounted together on a lightweight lever. These switches controlled batteries for putting a plus or minus DC signal on tape to control the averaging.

The cortical responses were amplified by two Tektronix 122 amplifiers in series with an attenuator between. The combination provided a gain of about 50,000. The half-amplitude band-pass was set at 0.2 c.p.s. on the low end and 1,000 c.p.s. on the high end for each amplifier. The responses were recorded at 3% inches per second on an Ampex FR100A seven channel FM tape recorder.

The motor response time of the subject after the perceived change in binocular rivalry was allowed for by averaging only those responses in which the subject switch was in one position for the entire stimulus on-cycle. This was accomplished by recording the evoked response, the subject key response, and the two stimulus wave forms on the tape recorder together with an audio channel for experimental identification. Then the evoked response signal was retrieved from the playback head and fed back to the recording head on the same tape. The second evoked response channel was thus delayed 1.43 seconds.

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Fig. 1. Wheatstone stereoscope. Right arm only is shown. $S_i$, glow discharge tube; $S_t$, tungsten filament bulb; $H$, half-silvered mirror; $L$, collimating lens; $HF$, heat-absorbing filter; $N$, neutral density filter; $RF$, red filter; $G$, grating; $F$, field stop; $S_i$, surround-illuminating bulbs; $B$, surround limit; $L$, final lens; $M$, mirror; $RE$, $LE$, right and left eye of subject. (U.S. Army photograph.)
Positive potential when dominance switch is in selected position

Pulse coincident with light on

Pulse coincident with dominance switch changing from selected position

Pulse coincident with light off

Fig. 2. Logic diagram for analysis timing control. (U.S. Army photograph.)

from the rest of the tape signals. The computer trigger pulse was delayed 0.8 second by a Tektronix 161 pulse generator and 162 wave form generator, before which time the decision was made by the digital logic circuitry whether to average that response. If the dominance switch was in the correct position for the entire on-cycle of the stimulus, the tape was then averaged from the delayed signal channel with the computer synchronized with the on-point of the stimulus for that eye.

The decision-making apparatus received only two signals at a time. One was the stimulus wave form from either the right or left stimulus. The other was either the zero plus or zero minus square wave output of the subject key. This apparatus was made up of two parts (Fig. 2). One was a level detector and pulse former which would produce a pulse synchronous with the light stimulus on or off level change. The second part was used to gate the pulse from the first part. The second part consisted of a flip-flop with the "set" fed by an AND gate and the "reset" by an OR gate. The DC AND gate received a positive level coinciding with the dominance switch being in the proper position and it received a pulse coinciding with the on-point of the light stimulus. Thus the subject switch had to be in the proper position before the turn-on of the stimulus could set the flip-flop. The OR gate allowed a pulse when the subject switch changed position or the stimulus light went off. The output of the flip-flop, when set, energized a fast action relay which gated the pulse former. The level detector and pulse former was adjusted to give a pulse when the light stimulus went off. If the flip-flop stayed set until reset by the stimulus going off, the 3 milliseconds' delay of the gating relay opening was just enough to let the pulse through before the circuit was broken. This pulse was delayed 800 milliseconds before triggering the averaging computer. This delay plus the length of the on-time of the stimulus cycle subtracted from the 1.43 seconds' delay of the signal channel meant that the computer sweep began between 130 and 200 milliseconds before the on-point of the stimulus, depending on the total on-time of the stimulus. The analysis time of 0.5 second thus covered approximately the first 300 to 400 milliseconds of the on-period of the stimulus. The stimulus periods were checked and found not to vary significantly during the course of the experiment. The stimulus on-point for the records was arrived at by putting a photocell signal through the brain response channels and recording that on the computer.

The tape recordings were analyzed four times by an average response computer, Mnemonotron CAT 400. The four analyses were for: (1) response to the right eye stimulus when the right eye is dominant, (2) response to the right eye stimulus when the left eye is dominant, (3) response to the left eye stimulus when the left eye is dominant, and (4) response to the left eye stimulus when the right eye is dominant.

As the responses are averaged from the tape record of the simultaneous functioning of both eyes, the degree of control inherent in this procedure is great. If one eye is misaligned, the effective brightness of the stimulus to that eye is decreased. If this produces a smaller response when that eye is suppressing, it also produces a smaller response when the same eye is dominant. Hence the effects of misalignment or other stimulus artifacts are cancelled out and cannot account for the differences between dominant and suppressed evoked potentials from the same eye.
Results

In Fig. 3 are presented the results of 3 separate runs each for 3 normal subjects. These are selected as typical of 25 runs in 4 subjects over a 3 month period.

In most runs the response in the dominant condition had a shorter peak latency and/or a larger amplitude than the non-dominant response from the same eye. Subject T. L. (Fig. 3A) illustrates the situation where one or both differences held. Some possible exceptions occurred where the nondominant response was so small or lacked a clearly defined positive peak so that accurate latency comparisons could not be made. For Subject C. C. (Fig. 3B), the dominant response consistently had an earlier peak latency, this difference often being quite large (50 milliseconds or more). In some runs, however, the non-dominant response was of larger amplitude than the dominant response. In the case of Subject H. L. (Fig. 3C), the dominant response was always larger than the non-dominant response, this difference usually being very pronounced. Latencies for H. L. were less consistent.

In 13 further runs using different conditions for stimulus luminance, the results were consistent within the same subjects. The same pattern of differences (dominant response being earlier and/or larger than the suppressed response in the same eye) held up in spite of unbalancing stimulus luminances which shifted total dominance time toward one eye.

The gratings presented to the two eyes were also reversed, so that the eye previously viewing the horizontal grating now viewed the vertical, and vice versa. The pattern of evoked responses remained dependent on dominance and not on grating orientation.

Discussion

Clear differences are found in the visual evoked responses of the present experiment between the dominant and suppressed eye conditions. The differences appear either in a shorter peak latency or a larger amplitude evoked response from the dominant condition. In previous studies Van Balen and Lansing have found reductions in response amplitude of the suppressing eye during rivalry while Riggs and Whittle found no differences. As these previous investigations recorded the response from only one eye at a time, it is possible that reduction of one eye's response could also have been correlated with simultaneous reduction of response from the other eye with changes in attention or other factors. The present experiment provided a control for this in that the separate responses from each eye were recorded simultaneously. The results are similar to the earlier findings of Van Balen and Lansing in which differences were found between the dominant and suppressed eye conditions. The results of the rivalry experiments show similarities to the findings of an experiment on amblyopic eyes by Nawratzki and colleagues. They found responses from stimulation of the amblyopic eye to be both lengthened in latency and reduced in amplitude in comparison to the normal eye.

There seems to be little doubt that the cortical evoked responses do differ between the dominant and suppressed eye conditions in a retinal rivalry situation. The significance of this fact is more obscure. The effects on the evoked response (reduction of amplitude, lengthening of latency) are similar to that produced by a decrease in stimulus luminance. The apparently inconsistent pattern found in one subject (C. C.) where a sharply reduced peak latency was associated with a reduced amplitude has also been reported occurring at high stimulus luminances. As stimulus luminance is increased, response latency is consistently decreased, while response amplitude may show reversals. Further research on this problem using many different stimulus luminances upward from visual threshold may show whether dominance consistently affects the response in the same manner as increased luminance. As simultaneous measures of
Figs. 3A, 3B, and 3C. Three groups of 4 records for each of 3 subjects. Each record is the summation of 512 responses for one eye in one dominance state. D, dominant; nD, suppressed. Stimulus onset is coincident with the beginning of each record. (U.S. Army photographs.)
Fig. 3B. For legend see opposite page.
Fig. 3C. For legend see p. 382.
both eyes functioning are used in the present experiment, the effects of dominance cannot be attributed to some stimulus artifact reducing effective luminance to one eye alone.

The factor of the subject's attention to the visual stimulus has been shown to affect the evoked response by Chapman and Bragdon. They find that stimuli of equal intensity, some of which have relevance to a task which the subject is asked to perform, produce differences in the evoked response depending on their relevance. The present results suggest that the effect on the evoked response from the suppressed eye in retinal rivalry is like the effect of reduced attention in only one eye. Further research is needed to determine if an active inhibitory process is involved.

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REFERENCES