The Effect of Imagery on the Waveshape of the Visual Evoked Response

In recent experiments demonstrating changes in the waveshape of the visual evoked response (VER) when a visual form is placed in the visual field[1,2], it is not clear whether the change is a direct and inevitable consequence of the patterned distribution of light on the retina in a system for which precise somatotopic localization is claimed, or whether these changes manifest the cellular activities underlying cognition. The experiments reported below suggest that cognitive processes are reflected in the VER waveshape.

Methods. Five subjects were chosen from an unselected group of 20 who had been previously studied[2]. In these subjects, the VER had been stable during repeated testing over several months and the waveshapes had been reliably changed when different geometric forms or different words were placed in the visual field. Though such changes in waveshape are constant in a given individual, they may be very different from one subject to another[1,2]: the present study is concerned with changes within individuals since changes invariant over a population have not been uncovered.

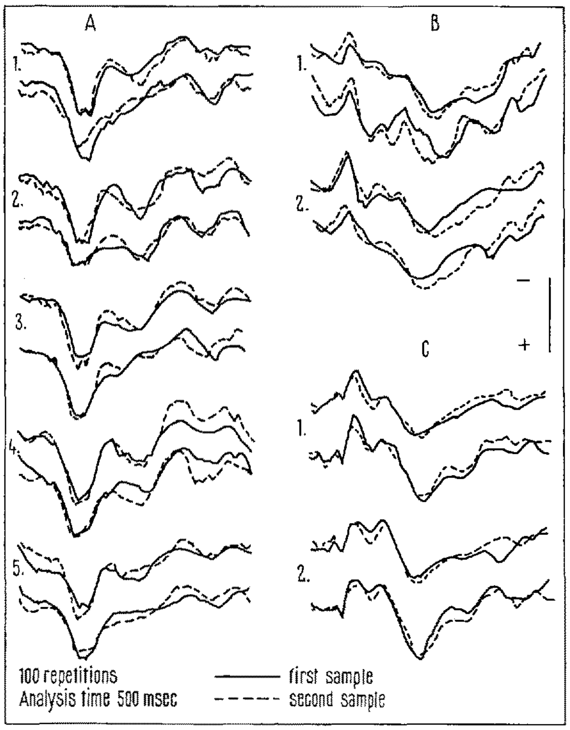
The subject sat relaxed in a contour chair in a darkened room. The VER was recorded between an active scalp electrode placed in the midline 3 cm above the inion and a right earlobe reference. Potentials were amplified by an Offner type T electroencephalograph side-tapped at the power amplifiers to provide a signal with a range of $\pm$ 3 V which was the input to an average response computer (CAT 400). Amplifier time constant settings were 0.3 sec so that the band-width of the signal ranged from about 0.5–80 cps.

In each experiment, 4 average responses were computed from multiple blocks of stimuli, each block consisting of 25 or 50 presentations of a particular stimulus. These blocks were presented in Latin square order, providing 2 replications for the average response to each of 2 types of stimuli within each experiment, while controlling for habituation, fatigue and recency. The final average waveforms were therefore computed from 100 or 200 stimuli. The stimuli were black figures drawn on white sheets of cardboard mounted on a white wall 150 cm in front of the subject: a square or a circle 64 square inches in area or the words 'square' or 'circle' equated for the area of printed letters. The stimuli were briefly illuminated by flashes from 2 Iconix cold cathode fluorescent tube flash units placed behind the subject, facing the rear of the experimental chamber. Silent flashes were produced by a square wave 20 msec in duration at 20 V and repetition rate of 1/sec. Flashes were dim: intensity at the plane of the stimulus object was 0.585 lu/m^2.

Results. Each subject participated in 1 or both of the following experiments:

(a) Replicated waveforms to a square and a circle were obtained in the manner just described. The subject was then asked to imagine, 'hallucinate' or think about a square each time the flash illuminated a circle and vice versa, and replicated waveforms were again obtained. Such control and hallucinated waveforms were then obtained in alternation as shown in Figure A. This subject was able voluntarily to modify the waveform to square by introducing and withdrawing a positive-negative sequence between 150 and 200 msec, thereby reproducing the waveform to circle. Modification of the waveforms to both square and circle is shown in Figure B from a second subject. For each subject, the experiment was repeated at least once in a separate session several days later. In all, 11 attempts were made at this experiment by 4 subjects without failure.

(b) The subject was asked to imagine a square or a circle, or the word 'square' or 'circle' each time the flash illuminated a blank field. He did not state the order in which he imagined the stimuli and this was then declared by the experimenters, from the waveforms obtained, on the basis of data recorded in previous sessions whilst looking at the actual stimuli. In 8 such experiments on 4 subjects, clear reproducible differences in waveform were produced in 5 experiments and in these the experimenter's predictions were correct. Figure C shows such differences (notably in the positive deflection at 200 msec) obtained in 1 subject whilst viewing a blank field which



Averaged evoked responses to brief flashes from 3 subjects A, B and C. Each numbered group of 4 responses contains 2 replications for the average response to each of 2 stimuli. (A) In each group the upper pair of waveforms was obtained whilst looking at a circle and the lower pair at a square. Groups 1, 3 and 5 were obtained whilst the subject perceived the stimulus actually present: groups 2 and 4 whilst subject was thinking of a square whilst viewing a circle and vice versa. (B) Upper pairs of waveforms whilst viewing a square and lower whilst viewing circle. In group 1, subject thinking of the stimulus actually present; in group 2 thinking of the alternative stimulus. (C) In group 1, all responses whilst viewing a blank field: upper responses whilst thinking of the word 'square' and lower whilst thinking of the word 'circle'. In group 2, subject actually viewing the words 'square' (upper waveforms) and 'circle' (lower waveforms). Cal. 10 μV.

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2 E. R. John, R. N. Herrington and S. Sutton, Science *155*, 1439 (1967).

were reproduced later in the same session when viewing the actual stimuli. The difference in waveshape at 150 msec when looking at the words (C, 2) and when looking at a blank field but thinking of the words (C, 1) should also be noted.

The possibility that the act of imagination introduced peripheral artifacts arising from pupillary changes or movement has not found support in these and other experiments. The outcome was not influenced in 2 experiments in which pupillary and accommodation reflexes were eliminated by homatropine and in which artificial pupils were used. Oculograms recorded between electrodes placed above and below the orbit were of low amplitude and were not influenced by the shape of the stimulus or by the act of hallucination. Tension in facial, masticatory and neck muscles is difficult to control, though subjects were asked to relax as much as possible. In experiments where tension in these muscles was deliberately and grossly exaggerated, changes in waveform were slight and restricted to the first 100 msec of the evoked response. Further, silent counting of the stimuli, eliminating feedback from vocal musculature did not alter the average waveforms.

Discussion. In these experiments, the VER waveshape corresponds to what the subject is thinking and not to what stimulus is actually present in the visual field or whether the subject is or is not 'hallucinating'. The waveform changes are not therefore likely to be due to some general process, central or peripheral, accompanying the act of imagination. Somewhat similar data have been attributed[3] to selective shifts of attention within the visual modality, but such a shift cannot account for the changes obtained in the second experiment reported here in which subjects viewed a blank field. The stimulus conditions and the flat average oculograms suggest that the central processes involved are not those generating lambda waves[4]. It therefore seems probable that the waveshape modifications described are determined by the specific cognitive processes underlying the recognition of shape, a conclusion supported by data of similar import obtained from animals carrying recording electrodes chronically implanted in various brain structures including the visual pathway[5,6].

Zusammenfassung. Unterschiede der Wellenformen, welche beim Menschen auftreten, wenn in kurzen Lichtstrahlen verschiedene geometrische Formen oder auch Wörter in das Gesichtsfeld eingeschoben werden, können auch dann in manchen Versuchspersonen erscheinen, wenn eine solche Person versucht, sich ähnliche Reize vorzustellen oder zu halluzinieren. Dabei kommt es durchaus nicht darauf an, welche geometrischen Formen im Gesichtsfeld tatsächlich vorhanden sind.

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Physiologische Untersuchungen an der innervierten glatten Muskulatur der Vogelfedern (Mm. pennarum)

Anknüpfend an frühere morphologische Untersuchungen[1] wurden jetzt die glatten Muskeln, die zwischen den Federbälgen der Vogelhaut eingespannt sind und die Federhaltung regeln, funktionell näher untersucht. Am Taubenflügel, der wegen der günstigen Lage des versorgenden Nerven für diese Versuche gewählt wurde, sind die Muskeln überwiegend so angeordnet, dass ihre Kontraktion zum Anlegen der Federn führt[2].

Methodik. Die Aktivität der Federmuskeln wurde in 20 Versuchen bei verschiedener Anordnung gemessen: (1) An der mit Urethan narkotisierten Taube wurde ein Flügel fixiert, eine gekürzte Feder wurde nahe der Wurzel angeschlungen und mit einem Spannungsmesser bei 1 bis 2 Pond Vorspannung verbunden, der versorgende Nerv wurde zur elektrischen Reizung thoraxnah freigelegt. (2) Ein isolierter, innervierter, nicht durchbluteter Hautlappen wurde in Krebs-Lösung eingebracht und die Spannungsentwicklung zwischen 2 Federn ähnlich wie bei (1) gemessen. (3) Ein zwischen 2 Federbälgen verlaufender Muskel wurde unter dem Mikroskop freipräpariert, angeschlungen, in Krebs-Lösung eingebracht und mit einem Spannungsmesser verbunden. Zur Reizung des Nerven wurden meist Sinusimpulse von 10 msec Dauer verwendet.

Ergebnisse. Figur 1 zeigt den Effekt der Nervenreizung am isolierten innervierten Hautlappen. Auf einen maximalen Einzelreiz folgt mit einer Latenz von etwa 100 msec eine kleine Kontraktion. Schon bei einer Reizfolge von 1/sec ergibt sich eine annähernd glatte tetanische Kontraktion. Bei Reizfrequenzen von 5–10/sec wird in der Regel schon die maximale Tetanusspannung erreicht. Höhere Reizfrequenzen beschleunigen nur noch den initialen Anstieg der Spannung. Als Standardreiz für die weiteren Untersuchungen wurde eine 10 sec lange Reizung mit 10 Imp/sec gewählt.

Die Kontraktion nach einer solchen Reizung verläuft in der Regel biphasisch, wie im Beispiel der Figur 2. Die zweite, langsame Phase der Kontraktion kann durch α-Rezeptoren-Blocker selektiv unterdrückt werden (Phentolamin 10^{-5} in Figur 2). Die schnelle Initialphase bleibt dabei unbeeinflusst, mitunter wird sie sogar etwas verstärkt.

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