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PERCEPTUAL FRAMING AND CORTICAL ALPHA RHYTHM

FRANCISCO J. VARELA,† ALFREDO TORO, E. ROY JOHN and ERIC L. SCHWARTZ*

Brain Research Laboratories, Department of Psychiatry, New York University Medical Center,
550 First Avenue, New York, NY 10016, U.S.A.

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Abstract—Apparent motion was used as a probe to test the hypothesis that perceptual framing is correlated to the phase of the alpha rhythm. Stimuli were presented phasically with respect to the occipital and parietal alpha cycle, and subjects were asked to judge whether the stimuli appeared simultaneous or sequential. The probability of perceived simultaneity was maximal for the positive phase of the occipital alpha cycle. Visual evoked potentials recorded during stimulus presentation were significantly different, in the late components, for the cases of perceived simultaneity or sequential motion. A brief review of previous experimental and theoretical studies of the relationship of perceptual framing to alpha rhythm is presented.

INTRODUCTION

APPARENT motion is a member of a class of phenomena which suggests that a critical period of roughly 0.1 sec is required for the completion of a temporal discrimination: a temporal frame. Thus, if two lights are shown successively with an interval of less than about 0.1 sec, they will be seen as simultaneous, or in apparent simultaneity. If this interval is slightly increased, then the stimuli will appear to be in rapid motion. If the interval is increased further, the appearance of motion becomes distinctly sequential. This phenomenon, first described by WERTHEIMER [1] has been recently reviewed by ANSTIS [2].

Many similar experimental paradigms have been studied; examples are: central masking [3], temporal numerosity [4], a spatial apparent simultaneity [5], memory scanning [6, 7], and iconic persistence of images [8, 9]. Summarizing these related non-visual phenomena, HARTER [10] concluded "... the critical periods of time at which the above phenomena occurred ranged from 50 to 250 msec, the most common value being 100 msec".

A number of different theoretical interpretations have been proposed to explain these temporal framing phenomena, variously entitled perceptual intermittency or perceptual moment [4, 10, 11, 12], travelling moment [5], quantal stage [13], iconic persistency [8], excitability cycles [14, 15], scanning cycles [16] and more recently, temporal interpolation [17]. It is often stated that certain aspects of the empirical evidence favors one particular interpretation as opposed to others. Thus, ALLPORT, [5] claims that his experiments in apparent simultaneity show that temporal framing cannot depend on the chopping algorithm proposed in the perceptual moment hypothesis; DI LOLLO [8] claims that his experiments on triple interactions of visual displays shows that cortical excitability cycles are ruled out; STROUD [18] and SHALLICE [19] state that the available evidence definitively rules out scanning cycles; EFRON [12] concludes that his evidence invalidates a quantal stage theory.

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*Author to whom correspondence should be addressed.

†Present address: Fac. de Ciencias, Casilla 653, Universidad de Chile.

In view of the empirical evidence outlined above, it is natural to assume a relationship between temporal framing and the periodic, rhythmic activity detectable in the electroencephalogram (EEG). As is well known, the electrical activity recorded from the human scalp has a spectrum with prominent activity in the frequency band between 7 and 13 Hz, the so-called alpha band (70% of total power in the occipital, parietal and posterior temporal derivations in a normal, resting adult). The alpha cycle roughly corresponds to the value of temporal framing of 0.1 sec, as reviewed by HARTER [10] and SANFORD [20].

Yet, in spite of the plausibility of this idea and of its potential importance, there is little experimental evidence which addresses this question directly. In the present report, we describe a consistent correlation between the perception of apparent simultaneity and the alpha phase at which light stimuli are presented. These results lend further support to the hypothesis that temporal framing in visual perception is correlated with the alpha cycle.

METHODS

Subjects were seated in a dark, sound-proof room, looking binocularly at two light emitting diodes (LEDs) subtending a visual field of 2°. Surface electrodes were placed at occipital (O_1 or O_2) and parietal (Pz) derivations, following the standard 10/20 system (Fig. 1). Luminances of the stimuli were adjusted so that they were dim, but bright enough to generate an average evoked potential in the occipital lead. For our conditions, this meant luminances of approximately 4 lm. The duration of both the LEDs and the inter-stimulus interval (ISI) were controlled by the experimenter (Fig. 1).

Subjects were randomly selected university students or technicians between the ages of 17 and 44 yr; three were male and two were female. Electrodes were silver cups, with resistance smaller than 2000 ohm. Linked earlobe references were used in a bipolar montage. Light emitting diodes were used to provide the stimulus because of the possibility of rapidly switching the current of an LED, thus providing a sharply defined temporal duration of the visual stimulus. Experimental sessions were usually terminated after 1 hr, since most subjects reported fatigue at this duration of testing. All electrophysiological data was recorded with the subjects' eyes open, in a dimly lit soundproofed room. All data was recorded on analog tape, and was subsequently digitized "off-line" with a PDP-12 computer. Sample rates of 512/sec were used, and the subsequent digitized data was stored on magnetic tape.

Typically an experiment began by familiarizing the subject with the task, which consisted of discriminating the temporal sequence at which the two LEDs were displayed in a series of trials. The experiment presented a number of different trials with varying ISI but fixed stimulus duration (6 msec for both LEDs in all conditions), and a fixed waiting period between the trials (2 sec). The subject was instructed to attend only to the temporal appearance of the two lights, and was asked to classify them, for each trial, in three possible categories: (1) simultaneous, (2) in apparent motion, (3) sequential. The perceived temporal appearance of these three conditions is depicted in Fig. 1(b). In our conditions, most subjects reported seeing the two light stimuli simultaneously as the ISI was decreased to about 60–70 msec.

After a subject felt sufficiently familiar with the task, the experimenter selected an ISI for which the subject reported essentially a chance level of discrimination between conditions (1) and (2) or between conditions (2) and (3). Then, without altering the ISI, the onset of the two LEDs was triggered when the alpha band component of the EEG exceeded a minimum. This alpha band component was obtained by passing bipolarly recorded EEG through a specially designed analog filter, with a pass-band of 7–13 Hz and a 40 dB/octave roll-off, which introduced a phase/delay of less than 1 msec. The output of the band-pass filter was fed into a Schmitt trigger which delivered a pulse controlling the LED's timer (Fig. 1). The experimenter could change the phase of alpha at which the Schmitt trigger delivered the starting signal for a sequence of LED displays.

The subject's classification of the temporal order of the lights was recorded for each trial, while the experimenter changed the phase at random, for a total of at least 100 trials. The ongoing EEG, the filtered EEG, and the evoked responses were stored on magnetic tape for further analysis. Subject's fatigue led to the immediate termination of the experiment. The demanding nature of the discrimination requested from the subject, as well as the lengthy procedure required to collect a significant number of data, limited the number of different alpha phase conditions that could be studied. Thus, we only compared the effects to triggering with the two extremes of the positive peak and negative trough of the alpha cycle.

The electrical data collected for each subject were processed off-line. EEG activity was recorded on analog tape, and copied to a polygraph record, which was used to eliminate those trials containing artifacts. Data were then digitized by a PDP-12 computer, averaged evoked potentials were constructed and platted, and statistical analysis was performed. For the present paper, a complete set of data were collected and analyzed for a total of five subjects.

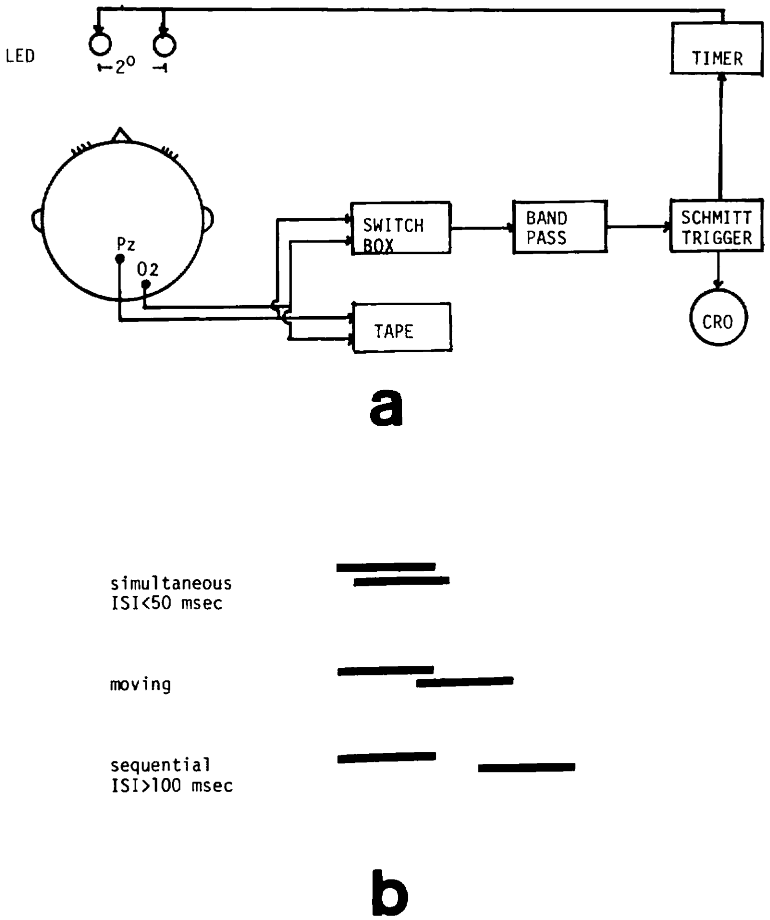

FIG. 1. (a) Experimental arrangement to study the relationship between alpha phase and perceived simultaneity of two lights (see text). (b) Perceived temporal relations between the two lights as a function of the interstimulus interval (ISI). Each line represents the time during which a light is perceived as being on. With ISIs of less than 50 msec, the two lights appear as temporally overlapping, and are thus perceived as simultaneous. When the ISI is larger than 100 msec the lights always appear as discretely separated in time, a condition termed sequential. In the intermediate regions, the lights appear to move from one position to the next or in apparent motion. The exact values of ISI for the three different conditions vary from subject to subject.

RESULTS

The main results of these experiments are shown in the graphs of Figs 2–4, which plot the probability of perceiving the two LEDs in different temporal relations for the following three different phase conditions: (1) stimulus onset locked to the positive peak of the alpha cycle; (2) stimulus onset locked to the negative trough of the alpha cycle; and (3) stimulus onset independent of the alpha cycle, that is, where the timer for the two LEDs was triggered randomly with respect to the on-going EEG. In Fig. 2 the probability of seeing the two lights as simultaneous is plotted. It is evident that in the *uncorrelated* condition there is an almost chance level of seeing the two lights as either simultaneous or in apparent motion. If the two

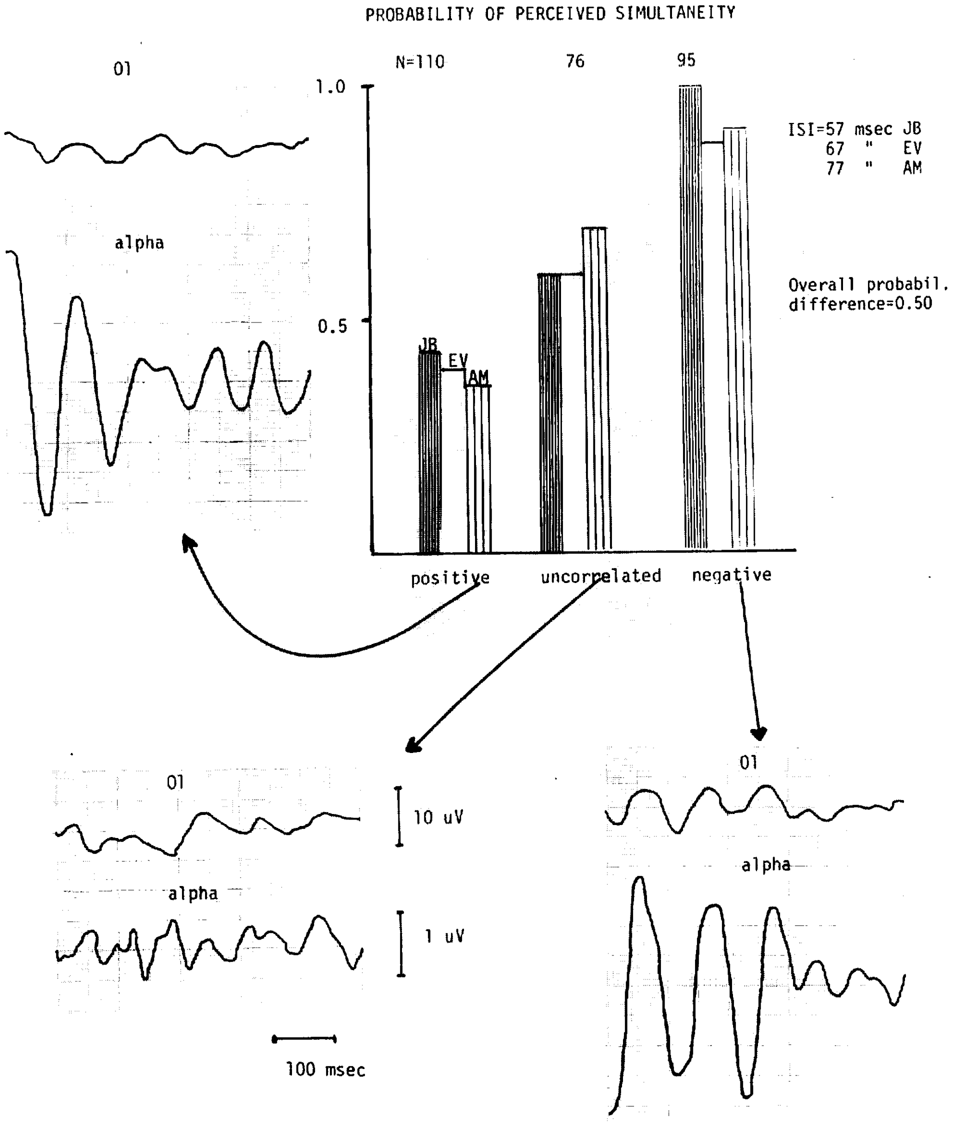

FIG. 2. Histogram of the probability of perceiving simultaneity for three subjects, whose optimum ISI is indicated to the right, together with the total number "*N*" of trials. The central histograms are responses in the absence of any correlation with the alpha phase. When the lights are triggered either with the positive peak of alpha (left) or the negative peak of alpha (right) extracted from the occipital derivation (O1), a change in probability is observed. In these experiments, the overall probability difference between positive and negative was 0.5. At the side and bottom of the page the visual evoked response for the three conditions is presented (for subject AM). The top trace for each condition shows the evoked response at the occipital pole (O1). Below each of these occipital evoked responses, the average output of the filter for the alpha band from O1 used for triggering the stimuli, is also shown. Note the change in amplification between O1 and its corresponding alpha average.

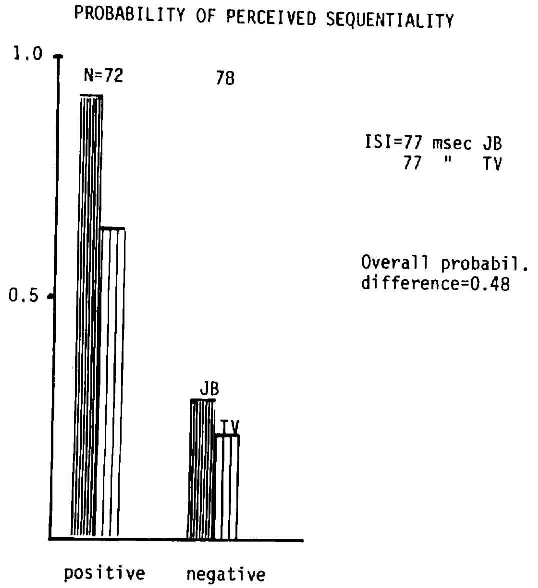

FIG. 3. Probability of perceiving sequentiality for two subjects, in the same format as Fig. 2. In this case, the probability of seeing the lights as simultaneous decreases as phase triggering changes from the positive to the negative peak of alpha.

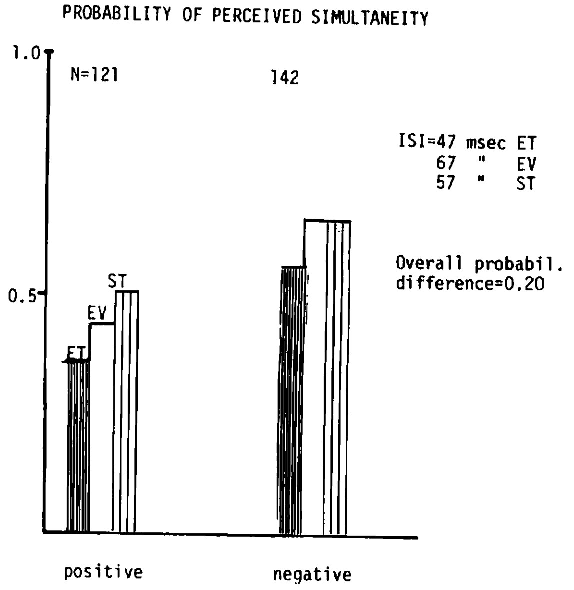

FIG. 4. Probability of perceiving simultaneity for three subjects, in the same format as Fig. 2. In this case, triggering was obtained from a parietal derivation (Pz), not an occipital on as in Figs 2 and 3.

lights were started always at the negative trough, the subjects almost invariably reported the light as simultaneous. In contrast, by simply switching this phase to the positive peak of alpha, the subject's perception was changed to one of apparent motion for the two LEDs. Optimum ISI and probabilities had a small variance across subjects, but all subjects exhibited a consistent trend as shown in Fig. 2.

In Fig. 3 the same phenomena just described is also seen for the case where the subject started with a 50% discrimination between perceiving the two lights in apparent motion or as sequential in time. As in the previous case, when the phase locking was removed from positive to negative, a significant perceptual difference was induced.

These perceptual effects can be shown to be dependent on the local activity of the occipital cortex, as shown in Fig. 4. Results from the two previous figures were obtained while the triggering was produced from the alpha filtered form the occipital (O_1) derivation. In Fig. 4 a similar design was followed, except that the alpha component of a parietal derivation (Pz) was used for triggering. It is seen that there is still a probability difference but that it is considerably diminished. Thus, the occipital alpha activity is more strongly correlated with temporal framing than the parietal alpha activity, a result which also reflects the known change of phase of alpha activity from occipital to parietal derivations.

The perceptual correlates to the EEG described above, can be put into correspondence with the average evoked potentials (AEP) collected from each subject. In Fig. 2 sample AEPs for each condition are shown. In each condition we have included the AEP for the raw EEG, and for the band-pass (7–13 Hz) filtered EEG (labeled O_1 and alpha respectively). These average responses make it clear that the triggering pulse for the starting of the LEDs corresponds well with either the negative or positive peak of the alpha component. In the uncorrelated case, the alpha component is averaged out as expected.

In Fig. 5, AEPs for different conditions are compared. In Fig. 5(a), the AEP for simultaneous lights (ISI = 0) and for light perceived as simultaneous (ISI = 50 msec) are shown, and in the bottom tract their computed difference wave is displayed. From inspection it is quite clear that these two AEPs show virtually no difference. This is supported by a *t*-test analysis, exhibiting no significant difference at the 0.01 level, also shown in Fig. 5. In Fig. 5(b), in contrast, AEPs for perceptually different conditions are compared, namely, lights perceived as simultaneous (ISI = 57 msec) and as in apparent motions (ISI = 87 msec). In this case the difference waveform does exhibit a difference, significant at the 0.01 level in the late (or P300) component. Similar results are depicted in Fig. 6, where the effect of shifting from negative to positive phase produces a perceptual change for the subject. This corresponds with a significant difference in AEPs for both conditions.

DISCUSSION

CHILDERS and PERRY [21] have reviewed the general relationship between vision and alpha-like activity. Amongst the better known of these is the fact that a brief visual stimulus can block an ongoing alpha-train, or alpha-blocking, an effect which depends on the phase at which the stimulus is delivered [22]. Further, the visual evoked response to a brief visual presentation shows changes in amplitude when presented at different phases [23]. Finally, there is an important and little explored relationship between alpha cycles and eye-movements [24]. However, in order to study the relationship between alpha and temporal

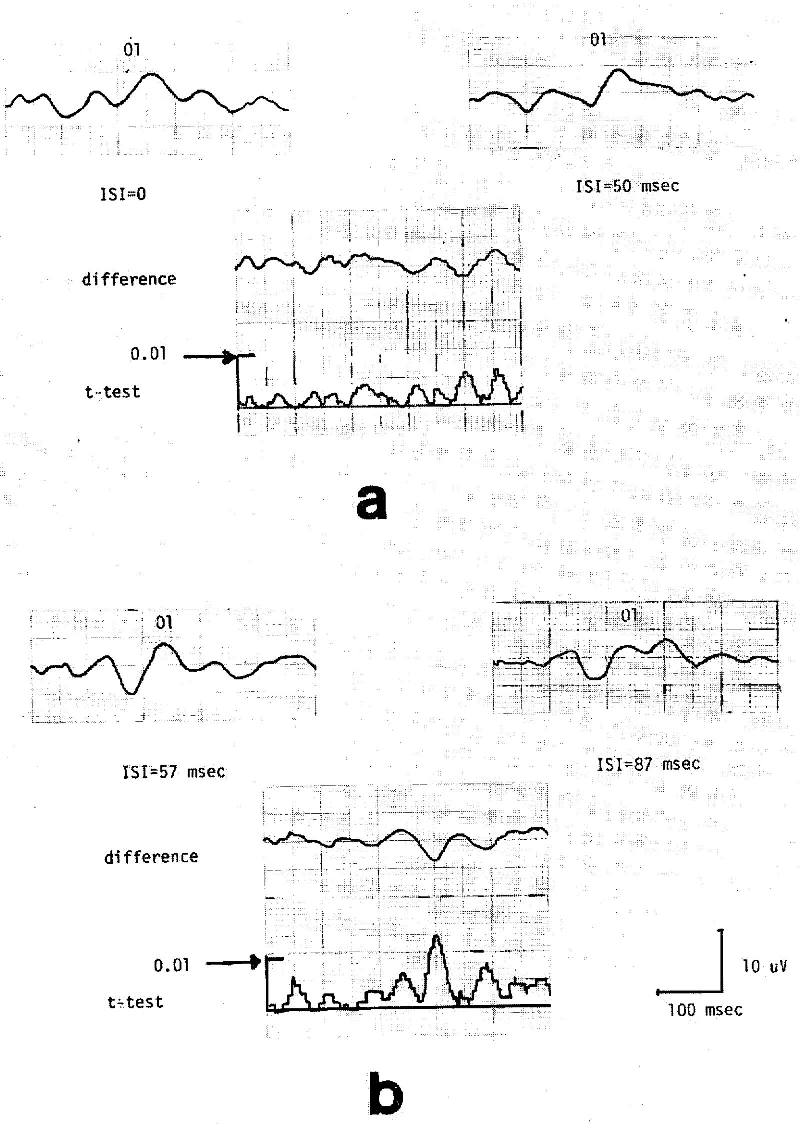

FIG. 5. (a) Comparison of the AEP obtained from two different stimulation conditions uncorrelated with EEG, which were perceptually identical for subject AM. To the left, the two LEDs were presented with no time interval between them (ISI = 0). To the right, AEPs collected while the subject saw the two lights also as simultaneous, while a substantial ISI of 50 msec existed between them. The two AEPs do not differ significantly, as shown in the two bottom traces showing the result of computing the difference waveform between them and a *t*-test for deviation from the average. A difference significant at the 0.01 level is indicated by values exceeding the indentation of the abscissae marked by the arrow. In this case, it is clear that at no point during the 500 msec of analysis do these two AEP differ above this level of significance, and thus they cannot be considered to be distinct as responses. (b) Comparison of the AEP between a condition in which the subject (ST) consistently reported seeing the two LEDs as simultaneous (ISI = 57), and one in which she consistently reported as seeing them as sequential (ISI = 87). No correlation with EEG was introduced. As in (a), the difference waveform and *t*-test for these two conditions is shown. In this case, however, there is a difference significant at the 0.01 level in the later components of the EP, in correspondence with the cognitive differences.

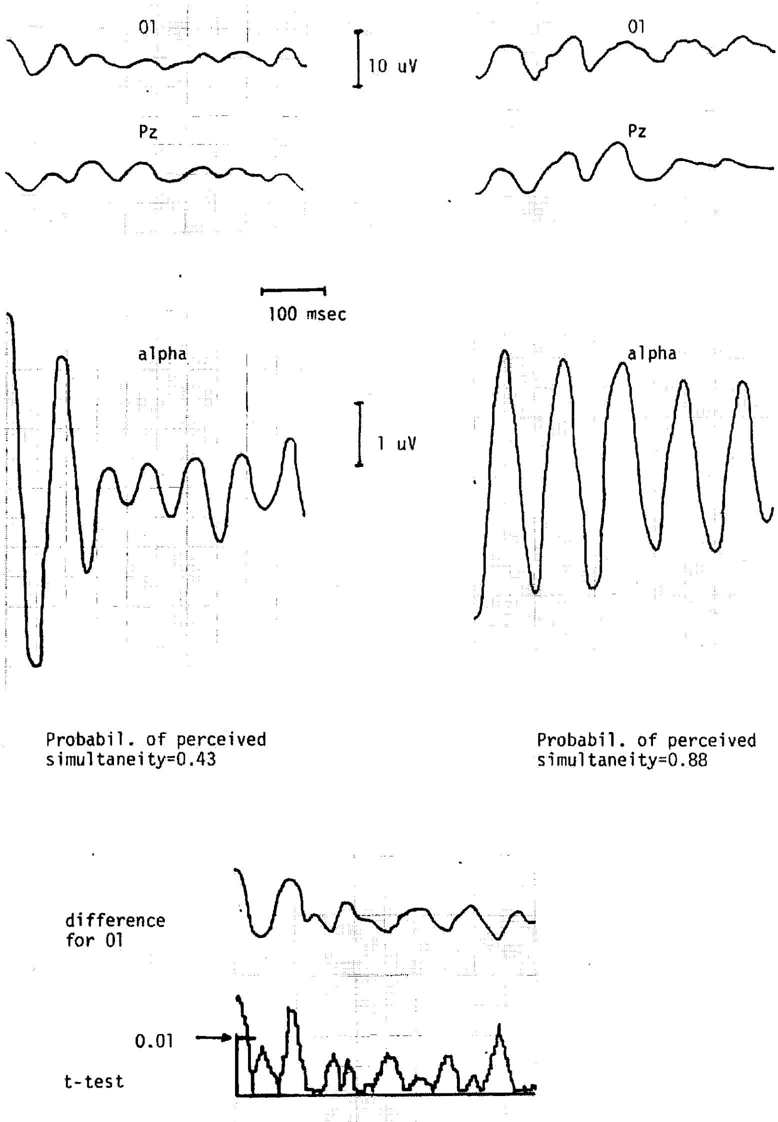

FIG. 6. Comparison of the AEPs of two stimulation conditions which were perceptually different for subject EV. To the left, the presentation of the two LEDs is triggered with the positive phase of alpha with a probability of perceiving simultaneity of 0.43. To the right triggering is done with the negative peak of alpha with a change of the probability of perceived simultaneity to 0.88. In both conditions, however, the ISI was the same at 67 msec. The AEP for the occipital (O1) and parietal (Pz) locations are shown, as well as the average output of the pass-band filter for alpha band from the occipital derivation, used for triggering. At the bottom of the figure, the difference waveform for the two occipital derivations is shown together with its corresponding *t*-test, showing significant differences at the 0.01 level primarily in the early parts of the AEP. Note also the very striking difference in the average alpha for the two conditions.

framing one must explicitly measure perceptual changes relative to the time base of alpha. Previous studies in this area can be conveniently classified under the following two categories:

(1) *Alpha frequency studies*, which are concerned with the relation between timing in behavior or perception, and changes in the power spectral content of the alpha band of the EEG. These studies only give indirect evidence for the relation between cortical rhythms and perceptual framing.

(2) *Alpha phase studies*, which are concerned with changes in behavior or perception resulting from the input of a signal at different phases of alpha. These studies provide direct evidence for the proposed relationship and can be broken into two main categories depending on whether motor reaction time or reported perception is used as a measure.

(a) *Reaction time and alpha phase.* In an early study, LANSING [14] found that the shortest reaction times were linked to light stimuli presented at a particular phase of alpha. In a later study DUSTMAN and BECK [25] confirmed these findings, although with a smaller effect than that reported by both LANSING [14] or CALLAWAY and YAEGER [26]. All of these studies do find a positive correlation between alpha phase and reaction time. However, the observed differences are generally less than the 100 msec predicted by a simple application of the alpha cycle idea (smallest value: 10 msec in DUSTMAN and BECK [25].

(b) *Reported perception and alpha phase.* Reaction time, even in its simplest form, is the outcome of a complex process which extends from the pure perceptual beginning to the actual execution of a motor act. We question whether valid inferences about perceptual framing could be drawn unequivocally from any reaction time paradigm. For the purpose at hand, it seems essential to study the relation between perceptual framing and alpha rhythm using an experimental design which deals exclusively with a perceptual phenomena whose measure is not tied to the further stages in processing which lead to the timing of a motor behavior.

It is striking that there are few results reported in the literature using a paradigm that directly conforms to the requirements outlined in 2(b) above. BOSWELL, in an unpublished Ph.D. thesis, mentioned a positive result when studying the liklihood of recognizing a letter presented at different phases of alpha [27]. He found that the number of errors was consistently lower when the flash illuminating a letter was presented at or near the zero-crossing of an alpha wave. In the only other available report, NUNN and OSSELTON [28] studied the perception of the word "danger" presented phase-locked to alpha. They took a pattern of galvanic skin response as a measure for discrimination. The correlation between stimulus presentation and alpha phase was not made electronically but by visual inspection of the EEG record, and it was concluded that there is a clear correlation between the galvanic response for discrimination and the phase of the alpha wave. Although the results of Nunn and Osselton are convincing, they provide an indirect measure of the correlation of alpha activity to perception based on a visual evaluation of the EEG. Our results provide direct evidence of the correlation of apparent motion to the phase of alpha activity, and find that the probability of perceived simultaneity is maximal when stimulus onset coincides with the positive phase of the alpha cycle.

In the studies of BOSWELL [27], and NUNN and OSSELTON [2], improved temporal discrimination was achieved in correspondence with the zero-crossing and negative peaks of alpha, respectively. These differences can be partially accounted for by difference in tasks (i.e. letter recognition, word recognition indicated by galvanic skin response, and motion perception). In addition, it must be stressed that the effects reported here, and their alpha phase correlates, are dependent on the intensities of the stimuli, as is well known from Bloch's law [29]. Under different conditions of intensity, WESTHEIMER and MCKEE [30] found low minimal values for two lights to be discriminated with respect to temporal order (20 msec), while MORGAN [17] found that 50 msec was optimal for estimating intermediate temporal position. Finally, latencies for the primary components of AEPs may vary as much as 60 msec across two log units of intensity [31]. Thus, precise *magnitude* of the interval of temporal integration of the visual system varies within certain limits, with the value of 0.1 sec being a predominant value in many experimental reports [10]. However, our study shows that there is an unambiguous correlation of perceived simultaneity to the *phase* of occipital alpha activity, and that for our experimental conditions, the greatest facilitation of perceived simultaneity was correlated with the positive peak of the alpha cycle.

Furthermore, our results clearly show a correlation between perceptual framing tasks and the average evoked response. This is consistent with the few previous reports which sought AEPs correlates of perceptual framing tasks. HARTER and WHITE [32] showed the appearance of an additional alpha-like component in the AEP every time a new item was added in their temporal numerosity experiments, although they did not deliver their stimuli phase locked to alpha when delivering a visual stimulus to measure reaction time. DUSTMAN and BECK [24] first reported the clear dominance of alpha in the AEP, also found in our study, although they did not report on the late components of the alpha channel alone. More recently, SERVIERE *et al.* [33] found clear correlation between closely related temporal pulses of light and corresponding peaks in the AEP uncorrelated to alpha phase, but no difference was visible when the subject reported simultaneity.

The neuronal basis of the relationship of alpha activity to perception has been discussed for a long time, in studies that we may classify under the following two categories: (1) *Excitability Cycles* are reflected by the periodic alpha cycle, such that afferent input to the cortex encounter periods of response facilitation and inhibition, and (2) *Scanning Hypothesis* which suggests that some form of temporal coding, or "scanning" across cortical layers is synchronized to the alpha rhythm. Neither interpretation has been proved or disproved at the present time, partially due to the paucity of data, and partly due to a lack of sufficiently clear hypotheses to be tested (see HARTER [10] for review). However, neurophysiological studies on the specific time course of synaptic events in cortical neurons have indicated that a common pattern of response consists of excitation, followed by inhibition, in a sequence which ranges from 80 to 200 msec [34]. The inhibitory component seems to mark the temporal pace of cortical events related to perception, since, for example, inhibitory (but not excitory) post-synaptic potentials are affected near flicker fusion [35]. There is substantial evidence which suggests that cortical activity is a reflection of the sequence of excitatory and inhibitory post-synaptic potentials in cortical pyramidal cells [36, 37]. VERZEANO [38] has suggested that the periodicity of alpha results from thalamic influences on pyramidal cells, resulting in the periodic movement of a wave of depolarization from deeper to more superficial cortical layers. This hypothesis is attractive, since it is well known that the different cortical laminae project differentially to intra-cortical, inter-hemispheric and thalamic targets. Thus, the connections of cortical afferent (and efferent) signals might be synchronized via the temporal course reflected in the local alpha rhythms, providing an integrative mechanism over extended regions of the brain. For two visual stimuli to be perceived as separate in time, it seems that they must occur across the temporal boundary provided by this cortical activity. Conversely, when two stimuli arrive within such cycle it seems that they are distributed simultaneously and thus are not temporally distinguished. Although the neuronal mechanisms of alpha rhythms are not clearly understood at present, our results indicate that such phasic components of the EEG are a robust enough expression of the cortical activity to be useful in the study of the physiological basis of temporal perceptual framing in humans.

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Résumé :

On a utilisé le mouvement apparent pour tester l'hypothèse selon laquelle le cadre perceptif est correlé à la phase du rythme alpha. Les stimulus étaient présentés en phase par rapport au cycle alpha occipital et pariétal et on demandait aux sujets de juger si les stimulus apparaissaient simultanément ou séquentiellement. La probabilité de la perception de simultanéité était maximum pour la phase positive du cycle alpha occipital. Les potentiels évoqués visuels enregistrés pendant la présentation du stimulus étaient significativement différents dans leurs composantes tardives, en cas de perception de simultanéité ou de mouvement séquentiel. On présente une brève revue des études antérieures, expérimentales et théoriques, sur les relations entre le cadre perceptif et le rythme alpha.

Zusammenfassung

Offenbare Bewegungen wurden als ein Stimulus verwendet um die Hypothese zu testen, daß Perzeption zur Phase des Alpharhythmus in Beziehung steht. Stimuli wurden mit dem occipitalen und dem parietalen Alpharhythmus dargeboten, und die Versuchspersonen wurden aufgefordert zu beurteilen, ob die Stimuli simultan oder nacheinander erschienen. Die Wahrscheinlichkeit der wahrgenommenen Gleichzeitigkeit war maximal für die positive Phase des occipitalen Alpharhythmus. Visuelle Reaktionspotentiale, die während der Stimulusdarbietung abgeleitet wurden, waren signifikant unterschiedlich, in den späten Komponenten, für die Fälle von wahrgenommener Simultaneität oder für das Nacheinanderfolgen. Eine kurze Übersicht früherer experimenteller und theoretischer Studien über die Beziehung zwischen Wahrnehmung und Alpharhythmus wird gegeben.