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BEREITSCHAFTSPOTENTIAL DURING THE ACQUISITION OF A SKILLED MOTOR TASK

by

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Abstract

The Bereitschaftspotential (BP) (Kornhuber et al, 1965) is a slow negative cortical EEG wave that precedes voluntary movement. The preparation for the movement, measured indirectly by the response speed and accuracy, and the certainty with which the movement is performed, are positively related to BP amplitude and duration. Typically, BP research has used very simple, abrupt movements, that require no learning and which change little over the duration of the experimental session. One study has investigated the BP preceding a skilled movement, and although larger amplitudes were found with the skilled task, there were no changes in the accuracy of task performance over time (Papakostopoulos, 1976). The present study was designed to investigate changes in the size and cortical distribution in the BP during the acquisition of a skilled motor task.

Twelve right handed, experimentally naive subjects were recruited from a university population. Scalp electrodes were placed at Fz, Cz and two lateral placements, 5 cm lateral and 2 cm posterior to Cz (C3" and C4"), all referred to linked mastoids. EOG was monitored from an infraorbital lead. The EEG was amplified by Grass 7P1 A, DC amplifiers and collected

on-line by an HP 2116B computer. A series of six button presses in a specified pattern constituted the motor task. Subjects were instructed to press the series every 20 sec. as quickly as possible, but with no errors. Forty-five trials of this response were collected from each subject. Electrical activity was recorded 4 sec. prior to the motor response and continued 2 sec. after its initiation.

The electrophysiological data were averaged in groups of five consecutive trials, yielding nine averages per subject. Response times for the first through sixth series of button presses was measured for each of the 45 trials. Area measures of the resultant BPs and the response times were subjected to analyses of variance and multivariate analyses of covariance, with the response time as the covariate.

Significant response time, electrode and trial (over the nine sequential averages) main effects, and electrode by time interactions were found. The multivariate analyses of covariance showed a consistent relationship between the response times and the size of the BPs. The response times decreased steadily over the first 20 trials, reaching asymptote for the final 25 trials. The BP increased in size at all electrode placements over the first 20 trials; during the last

25 the BP recorded at Fz and C4" decreased, while the BP at Cz and C3" remained relatively constant. The BP increased progressively in size over the electrodes Fz, C4",C3" and Cz.

This study demonstrates that the size and cortical distribution of the BP are systematically related to improved proficiency of a motor response with learning. The skilled movement is performed faster, more efficiently and with less hesitancy as learning progresses. The results also support previous studies which found the certainty and preparation for response related to the size of the BP.

The importance of the frontal cortical areas in the organization of movement has been related to the subject's conscious involvement and attention with the task (Kelso & Stelmach, 1976; McCallum, 1976). Maintenance of a skilled response requires less involvement than does the learning of a motor skill. After learning the frontal BP decreases while the BPs proximal to the motor projection areas of the responding musculature fail to decrease, supporting this interpretation.

Acknowledgments

I wish to thank my committee members; particularly Barry Beyerstein for the critical reading of the manuscript; John Dickinson for support and advice in the field of motor skills; and Chris Davis whose support, confidence and theoretical orientation made this thesis possible. A special thanks goes to Ray Koopman for his time and enthusiasm for the Aspex plots and the invaluable smoothing program; and Howard Gabert for his oft-needed technical help and advice over the years.

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Introduction

The Bereitschaftspotential

Although movement-associated cortical electrical potentials in man were first reported by Bates in 1951, it was not until fourteen years later that the slow negative wave preceeding movement was first discovered (Kornhuber et al., 1965). The Bereitschaftspotential (BP) or readiness potential (RP) was found to precede voluntary movements. However, the BP was correlated with intentional engagement in the required task and a single movement was not always preceeded by the same size BP. These results led Kornhuber et al. to conclude that the BP was related only indirectly to the motor process.

Movements that are passive or involuntary are not preceded by BPs (Papakostopoulos et al., 1974; Sumitsuji, 1975); nor are responses in reaction time paradigms lacking a warning stimulus (Oikawa et al., 1972). BPs have been recorded prior to hand, finger, foot, arm and saccadic eye movements, speech and the tensing of a single motor unit (Vaughan et al., 1968; Jones & Beck, 1975; Becker et al., 1973; Grozinger et al., 1975; Tanji & Kato, 1971). Although the waveform is morphologically similar in all reported studies (including research with monkeys (Vaughan et al, 1969)) the topography, amplitude and duration vary considerably.

The physiological basis of the BP has not yet been established. Vaughan et al. (1968) suggest that the BP arises from localized cortical sources no larger than the generators of the corneoretinal potentials. Many researchers have found cortical negative slow waves to accompany increased neuronal activity and dendritic depolarization (Fuster & Alexander, 1971; Sheafor & Rowland, 1974; Rebert, 1973, 1976). Although slow potentials have been recorded from subcortical areas such as the thalamus, caudate nucleus and amygdala, a clear functional relationship has not been found for intracerebral slow waves (Rebert, 1976). The investigation of the genesis of slow potentials continues in areas of physiology, neurobiology, neurochemistry and psychophysiology. The sensitivity of the BP to experimental manipulations and psychological states suggests, however, that an adequate explanation of the physiological basis may still be quite distant.

One of the first controversial issues in the BP literature concerned the possibility of identifying subclassifications of the BP. Some researchers separated the BP into several component waves but attempts to replicate these failed to produce general agreement. Suggested component waveforms were: a slow negative rise starting .5 to 2 sec prior to the response (BP or N1), a small positive wave 150-80 msec prior to the response (P1), a steep negative rise 100-50 msec prior to the response (N2) and a large positive wave following the response (P2) (Gilden et al., 1965; Vaughan et al., 1968; Deecke et al., 1969; Kornhuber et al, 1965; Gerbrandt et al, 1973). The only component that researchers have linked to the motor command has been N2, yet even this is not unanimously supported (see Gerbrandt et al, 1973; Papakostopoulos, 1975). Furthermore, the smaller waves (P1 and N2) have not been consistently found within or across studies, which severely limits further investigation and classification. Consequently, recent studies have focused attention primarily on the larger waves, BP or P2 (Delaunoy et al., 1976).

The exact cortical distribution of the BP is also uncertain Usually, the BP is largest over the motor cortex, decreasing precipitously both anteriorly and posteriorly. Over the central sulcus it is largest at the vertex decreasing laterally, but most often asymmetrically. The majority of studies has found the BP to be larger over the hemisphere contralateral to the muscle group employed in the response; although this effect is weak or absent in left-handed subjects and when subjects respond with their non-dominant hand (Kornhuber et al., 1965; Gerbrandt et al., 1973; Vaughan et al., 1968; Kutas & Donchin, 1974; McCallum, 1976). Deecke et al., (1969) and McAdam & Rubin (1971) however, found the BP to be symmetrically distributed in right-handed subjects responding with their dominant hand. When the responding musculature is not lateralized as in eye movements the BP is bilaterally symmetrical (Becker et al., 1973; Vaughan et al., 1968). Vaughan found the BP to be largest over the area of the motor cortex associated with the responding musculature during foot, arm and hand, and mouth movements. The distributional differences, however, were found only between grossly disparate muscle groups, as various hand and finger movements did not produce reliably different spatial distributions. Earlier studies found the BP to be larger precentrally (anterior to the Rolandic fissure) (Vaughan et al., 1968; Deecke et al, 1969), whereas more recent studies have found the BP larger postcentrally (Gerbandt et al, 1973; Papakostopoulos, 1976). The explanation for this discrepancy is not readily apparent, as the four studies used similar electrode placements and response movements.

Researchers have also sought to discover systematic changes in the BP which covary with movement parameters. Evidence from independent studies has been steadily accumulating however, which strongly suggests that the BP is not simply a motor potential. The claim of Vaughan et al., (1968) and Gilden et al. (1965) that the BP is a cerebral or physiological correlate of specific movements is being superceded by claims that the BP represents a more general readiness or preparation to perform a task (McAdam & Seales, 1969; Jarvilheto & Fruhstorfer, 1970). Kutas & Donchin (1974) found BP amplitude to vary directly with increases in the force of the response, yet Wilke & Lansing (1973), Hazeman et al. (1976) and Donchin & Kutas (1976) failed to corroborate this finding. Tanji & Kato (1971) trained subjects in the volitional discharge of single motor units. They found BPs preceding the contraction of a motor unit to be equal to those preceding the movement of the entire muscle. The authors made no interpretations concerning the preparation required for the respective responses, as both were easily performed, but the results clearly demonstrate the stability of the BP despite the great diversity of movement parameters.

Hazeman et al. (1976) reported that speed of response had no effect on the BP, although Becker et al. (1976) reported slow movements to be preceded by BPs of greater amplitude and duration than were ballistic movements. Becker et al speculated that more preparation was required for slow, well-controlled movements and this interpretation has been supported by other researchers. Loveless & Sanford (1974) reported the amplitude of the wave preceding a response to be proportional to the level of preparatory set, as inferred from the speed of the reaction time. McAdam & Rubin (1971) used response accuracy as a measure of preparation to respond and found larger BPs with accurate responses. Their subjects' post-response estimates of accuracy were positively related to the actual accuracy obtained. The more certain the subjects were about response accuracy or the better prepared they were to respond, the larger the BP. Ford et al (1973) investigated BPs with qualitatively different button presses. Pressing a skin-contact button, which required more preparation than a standard push-button, was preceded by BPs of increased amplitude and duration.

A confounding variable in the study of Ford et al (1973) however, is post-response feedback or stimulation. Their subjects received more sensory feedback concerning the accuracy of their response from the skin-contact button than from the standard button. It has been well documented that feedback from, or contingencies placed upon, the movement affect the BP amplitude and duration. If the voluntary response triggers a stimulus or another task, the accompanying BP is of greater amplitude and duration than if the response effects no change in the subject's environment (McAdam & Seales, 1969; Dincheva & Harding, 1975; McCallum, 1976; Taylor, 1976). Also, as the level of task involvement increases, corresponding increases in the BP are found with the frontal areas making relatively greater contribution (McCallum, 1976).

Research with BPs to date has used simple repetitive movements, with little attempt to investigate the development of a specific movement or skill. Only one study has been reported in which the voluntary response could be considered a skilled movement. Papakostopoulos (1976) had subjects trigger a moving dot on an oscilloscope which they were instructed to stop when it reached the middle of the screen. They triggered the trials with their left hand and stopped the trace 40-60 msec later with their right hand. Stopping the trace was judged a skilled movement. The total number of errors did not decrease with practice, although the variability of the responses decreased. The amplitude of the BP was greater over the right hemisphere than over the left (as it was with a single left-handed response), although the skilled task was performed with the right hand. This would imply that the general preparation to start the trial was greater than the preparation to respond within the trial. However, conclusions regarding the lateralization of the BP are difficult to make under these conditions, as the subjects' use of both hands in somewhat different responses probably confounds the results. In all conditions the BP was larger postcentrally than precentrally and was largest at Cz only during the skilled task condition. BPs preceding correct responses were larger than those preceding incorrect responses, further supporting the thesis that BPs are more appropriately interpreted as a measure of certainty and preparation to make a response.

Motor Skills

Problems with the study of Papakostopoulos (1976) largely surround the definition of a skilled task. There was no increase in the number of correct responses, yet Papakostopoulos discusses the results in terms of developing and improving skillful performance. In order to discuss the development of a skill, there should be an objective measure of improvement in the performance of the skill. Papakostopoulos' subjects were not learning a response as much as selecting the response on cue. Research in the field of motor skills, however, has shifted from an emphasis on product, or the selection of responses, to an emphasis on processes occurring while people learn to make skilled responses. For better integration of Bp research with the field of motor tasks, a response which can show clear improvement in performance with practice should be chosen as the voluntary movement.

The performance of a skilled task gives rise to several sources of feedback and recently much research has centered on the role of feedback in skilled movements. Studies of motor skills often require the subject to practice a single response, allowing no visual or external feedback. Such studies have found that as the subject attempts to learn the task, the responses become less variable, but not more accurate (Seashore & Bavelas, 1941; Newell, 1974). When subjects receive feedback from proprioception and vision, they are able to accurately estimate the precision of their response after the movement. By varying their responses, subjects can correct errors on subsequent trials and performance of the skilled task improves. (Schmidt, 1976; Adams, 1971, 1976). Under such conditions information from the experimenter regarding the correctness of the response becomes increasingly redundant. As the skill is acquired the sequence of movements becomes structured and no longer requires direct visual control. This implies that although several sources of feedback are beneficial to skill acquisition, redundant portions can be dropped once the proper movement has been established (Keele & Summer, 1976). Under conditions of ample feedback the skilled movement can rapidly approximate a response described in an instructional set. A high correspondence has been found between instructions to the subject delineating the required reponse and the actual response performed (Bouisset & Lestienne, 1974). This study also found the most effective instruction to achieve this end to be one emphasizing response speed.

During the acquisition of a serial task, speed and accuracy are not independently acquired; each is a critical factor of the response and improvements of both proceed simultaneously. However, the instructional set given to a subject influences the relative change in these two aspects of a task. Instructions emphasizing either speed or accuracy of response decrease variability in the responses, but increase respectively errors or reaction time (Fitts, 1966). The importance of these two aspects to a study should be assessed and specific instructions given to the subjects. A lack of instructions regarding speed and accuracy yields greater variability in the data and less fast and less accurate responses.

As elements are added to a serial task the period required to master it lengthens and attentional requirements for the response increase. Klein, & Posner (1974) report that simple discrete movements demand no attention except at initiation, but that attentional demands throughout a serial movement increase with the level of accuracy required. A decrease in attention produces a decrease in response accuracy and improved performance is accomplished only with the allocation of additional attention (Klein, 1976; Pew, 1974). The attentional demands of a repetitive serial task diminish only after the sequence is learned and response uncertainty decreases. Also, a movement that a subject is prepared to make involves more attention and is performed better than an unanticipated movement. This suggests that attention is related to the preparation to respond and to the accuracy of the response with obvious implications for BP research.

The internal organization or planning of a movement prior to its initiation have been assumed to require such functions as preselection and feedforward (Teuber, 1964; Kelso & Stelmach, 1976). It also has been suggested that the principle role of the frontal structures is to permit monitoring of movements in an anticipatory manner. This activity would be expected to be maximal in the frontal areas prior to an intentional movement. During the acquisition of a motor skill, these aspects of preparatory brain activity are more crucial than during the maintenance of a learned response. If this processing occurs primarily in the frontal structures, then that area should be more involved during the acquisition of a skilled response than during the repetition of an acquired task.

Research in the area of motor skills often parallels the research with BPs yet few studies have made these parallels explicit. Pew (1974) views goal-oriented, self-initiated movements as the highest order of movement in a multi-level theory of skills. Non-skilled self-initiated movements have been studied by BP researchers; goal-oriented motor skills have been studied by motor performance, learning and control theorists. Research that can interrelate knowledge from both fields is necessary if a fuller understanding of the mechanisms involved in motor skills is to evolve.

Current Study

This thesis was designed to investigate the BP and its cortical distribution during the acquisition of a skilled, serial motor response. Improvement in the speed of the response over trials was established as the measure of skill acquisition. Pilot research had shown that the task could not be mastered immediately. Yet it was simple enough that response performance reached asymptote within 15-30 trials with no feedback from the experimenter.

A standard condition, consisting of 15 single button presses, was conducted both before and after the skilled task condition to determine if any systematic changes occurred in the BP as a function of the duration of the experimental session. No difference in the BPs from the two standard conditions was predicted.

It was expected that the BP would increase in size during learning, particularly over the frontal areas, and then diminish after acquisition. An initial rise in the BP was predicted as response preparation and accuracy increased; the frontal area was expected to change more rapidly to reflect the anticipatory planning of the movement (Teuber, 1964; Kelso & Stelmach, 1976). After acquisition of the response the subjects' attention and involvement with the task and hence the recorded BPs were expected to decrease (Pew, 1974; Klein, 1976; McCallum, 1976). As subjects were responding with their dominant hand lateralization of the BP was also expected (Gerbrandt et al., 1973; Kutas & Donchin, 1974). Finally, it was predicted that the BP preceeding a single button press would be much smaller than the BP preceeding the skilled task, as the latter would require much more preparation and attention (McAdam & Rubin, 1971; Klein & Posner, 1974).

Method

Subjects. Six male and six female paid subjects (19-31 years of age) were recruited from the psychology department at Simon Fraser University. All were right-handed and all were naive as to the purpose of the study.

Apparatus. Non-polarizable Beckman silver silver-chloride electrodes were used to gain sufficient stablility for DC recording. The EEG signals were amplified by Grass 7P1 A DC amplifiers, with a roll-off of 3dB at 50 Hz. The single trials were collected and digitized (1024 points per sweep) by a Hewlett Packard 2116B computer and stored on-line on magnetic tape. After each trial the record was displayed immediately on a CRT and accepted for storage unless an artifact, such as an eye movement, was present. In case of contamination by an artifact the trial was rejected and the subsequent artifact-free trial accepted in its stead.

Data collection was controlled by a program, written by H. F. Gabert, P. Eng., that allowed the subject to initiate the trials. The program collected data from the ongoing record during the period 4 sec prior to and 2 sec following the initiation of the subject's response.

Procedure. Electrodes were filled with EKG Sol electrode paste one hour preceding application, allowing the paste/electrode interface to stabilize. After the skin had been cleaned with alcohol and abraded, the EEG electrodes were affixed to the subject's scalp with collodion soaked gauze at Cz, Fz and two lateral placements, five cm lateral and two cm posterior to Cz (C3" and C4") (Papakostopoulos, 1976). An infraorbital EOG electrode and two mastoid electrodes were held in place with electrode collars. The EEG and EOG electrodes were referred to linked mastoids. The impedance between any two electrodes was less than 5K ohms for all subjects.

The subjects were seated in a large comfortable chair in an electrically shielded room, and given a small metal box (12.5 x 10 x 8cm) which they held on their laps. The box contained two rows of three buttons each, with 2 cm between adjacent buttons. A force of 1050g was required to depress the buttons the necessary 5 mm for switch closure. Subject's right arm rested on the arm of the chair and was supported with a pillow to minimize involvement of the forearm when responding. All subjects used their right hand throughout. They were instructed to refrain from blinking and moving their eyes, particularly during the few seconds before and after a response. Subjects were asked to respond approximately every 20 seconds, but were requested not to count or use a watch as some variability in timing was desirable.

Between trials, the subject's finger rested on the first button ensuring that the first movement initiating the trial was identical across trials and conditions. The first or standard condition required the subject to make a single button press. The subjects were instructed to respond sharply as they would in a reaction time task. During this condition the subjects were given feedback, via an intercom, regarding spacing of their responses (i.e., whether there was either too little or too much time between trials) and eye movements (whether they were blinking or moving their eyes during trials). Subjects generally required very little feedback during the session.

After collecting fifteen trials of the standard condition, instructions for the experimental condition were given. The subject was shown a pattern of button presses, which included all six buttons with no repetitions (Figure 1). The pattern was demonstrated three times by the experimenter but subjects were allowed no practice. Subjects were asked to repeat the series as quickly as possible always returning to the first button upon completion. The requirement of maximizing speed without sacrificing accuracy was stressed. Subjects were told that the spacing of responses and control of eye movement would be the same as in the preceding condition, but that the duration of the experimental condition would be longer. Forty-five trials were collected. The subjects were then informed that the standard condition was to be repeated. The earlier instructions were reiterated, and a final fifteen trials collected. Upon completion of the session the subjects were debriefed.

Data Analysis

The data from each standard condition were averaged across the fifteen trials. In the experimental or skilled task condition, data from sets of five consecutive trials were averaged, yielding nine averages for each channel for each subject. The first second of data from each trial was taken as the baseline before averaging.

Area measures were calculated over three sections of each average as depicted in Figure 2. The sections were defined as follows: 1. the 2 sec period prior to the response; 2. minus to plus 50 msec from the response; 3. the 2 sec period following the response. In each section any area bounded by the curve below the baseline was subtracted from the area of the section above the baseline. This method of area determination takes into consideration all data points within a specified section, rather than looking at only negative data points and ignoring those which fall below the baseline. The first of these area measures is related to both the amplitude and duration of the BP. The usual method of determining duration, fitting a linear regression line from the peak of the BP to baseline by hand and eye, was deemed inappropriate for two reasons. The slope of the BPs in this study was rarely linear, and the method itself is susceptible to experimenter bias. The amplitude at the response has been the most common measure in previous research. The peak area measure was computed to allow comparison with other studies. The third or post-BP section was included to measure any changes in area during the perfomance of the skilled task as that performance improved. Although the response initially required more than 2 sec to complete, by the 20th trial subjects usually finished within the 2 sec section.

The duration of the response from the first through sixth series of button presses, and the time between the first and second button presses, was measured for all 45 trials. Response time over the series of six presses was averaged in sets of five, to correspond with the EEG averages for the analyses.

FIGURE 1 Pattern of button presses for skilled task

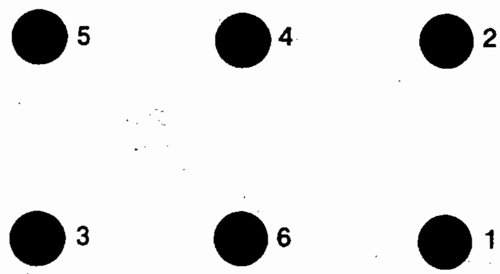
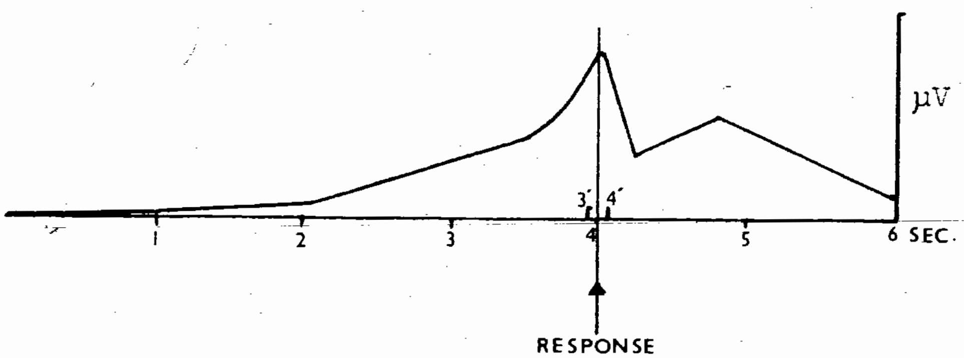


FIGURE 2. Area measures under the curve:

1. 2 to 4 sec.
2. 3′ to 4′
3. 4 to 6 sec.



The EEG data across conditions were analysed using a one within, two between analysis of variance (subjects(6) within sex(2), crossed with conditions(3) and electrodes(4)) for each of the two BP area measures. For the skilled task the EEG data were analysed using analyses of variance in a one within, two between design (subjects(6) within sex(2), crossed with electrodes(4) and trials(9)) for the three area measures; and four multivariate analyses of covariance, using the reponse time as the covariate. For each average there were four sets of measures, one for each electrode, but only one response time necessitating a multivariate analysis of covariance for each electrode. The response times were subjected to a one within, one between analysis of variance (subjects within sex, crossed with trials).

The 45 single trials of the skilled task for each subject and each electrode were plotted using the 'Aspex' program. This is a computer graphics program modelled on 'Symvu' which generates three dimensional line-drawing displays of data. The program utilizes grid matrix data (in this case points within trials by trials over time), interpolates between data points, yielding spatially continuous data. A program for two dimensional smoothing of data (within and across trials) was written by R. F. Koopman. The program employs either polynomial or fourier smoothing and the degree of smoothing can be specified independently across and within trials. This initial treatment of the data was an essential prerequisite for use of the Aspex program, due to the noise in EEG single trial data.

Results

An analysis of variance was conducted for each of the BP measures to test for differences among the two standard and the skilled task conditions. No significant condition main effect was found for the BP measure 2 sec prior to the response (F=1.391, df=2/20, p>.05); whereas, the peak measure was significantly larger during the skilled task than during the two standard conditions (F=42.782, df=2/20, p<.001).

The averages across subjects for the skilled task, for the nine trial blocks and four electrodes illustrate the general trends in the data (see Figure 3a; Figure 3b shows a single subject's data of the skilled task condition). The influence of skill acquisition on the BP was investigated using three analyses of variance, one for each of the dependent area measures. The analyses of variance (summarized in Tables I, II and III) found significant trial and electrode main effects and a trial by electrode interaction for the area measure 2 sec prior to the response and the peak area measure. Significant electrode main effect and a trial by electrode interaction were found for the area measure 2 sec following the response. No significant change over the trial blocks was found for this measure. The electrode main effects were attributable to the

FIGURE 3a BPs averaged across subjects for the nine trial blocks of the skilled task

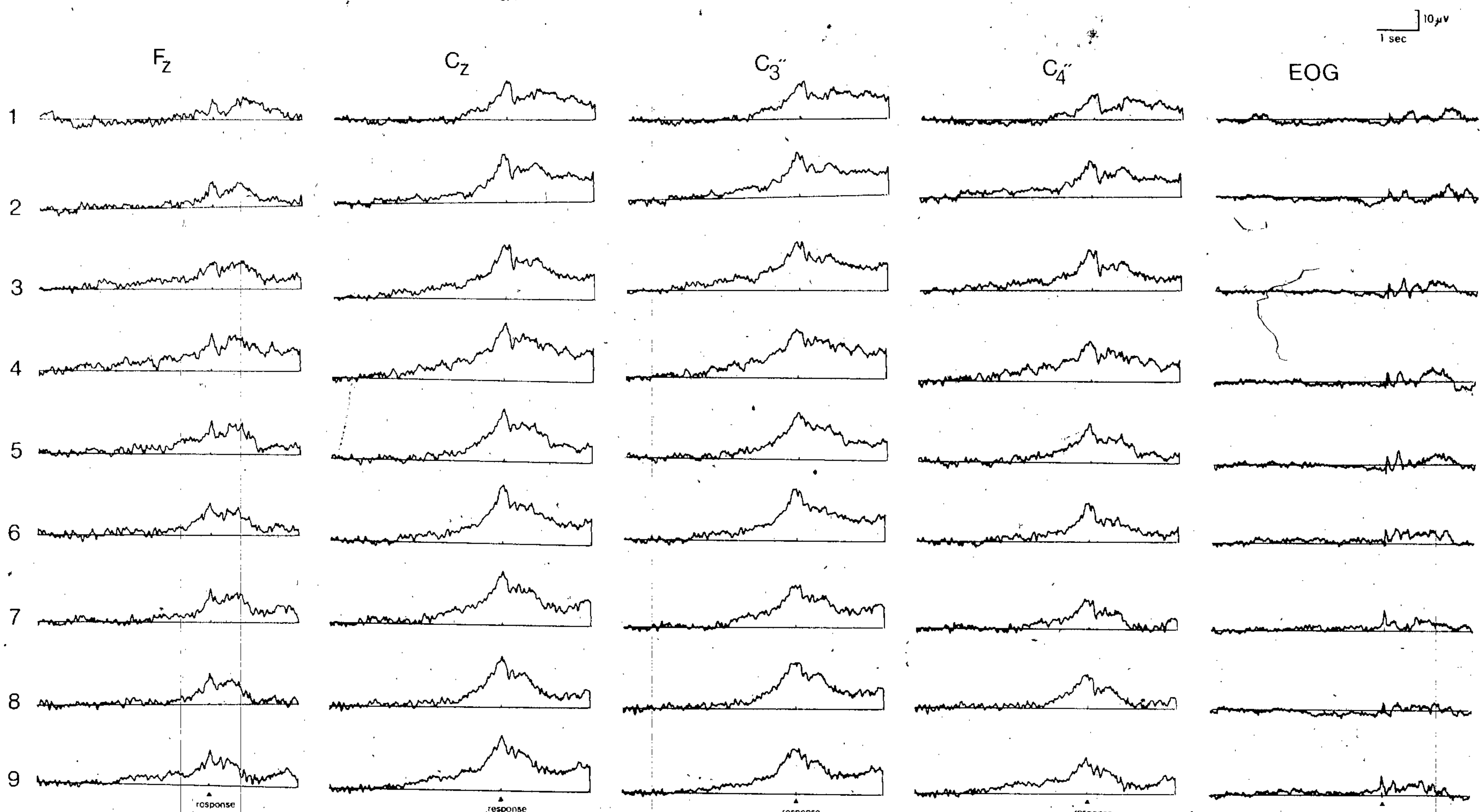


FIGURE 3b BPs for one subject for the nine trial blocks of the skilled task

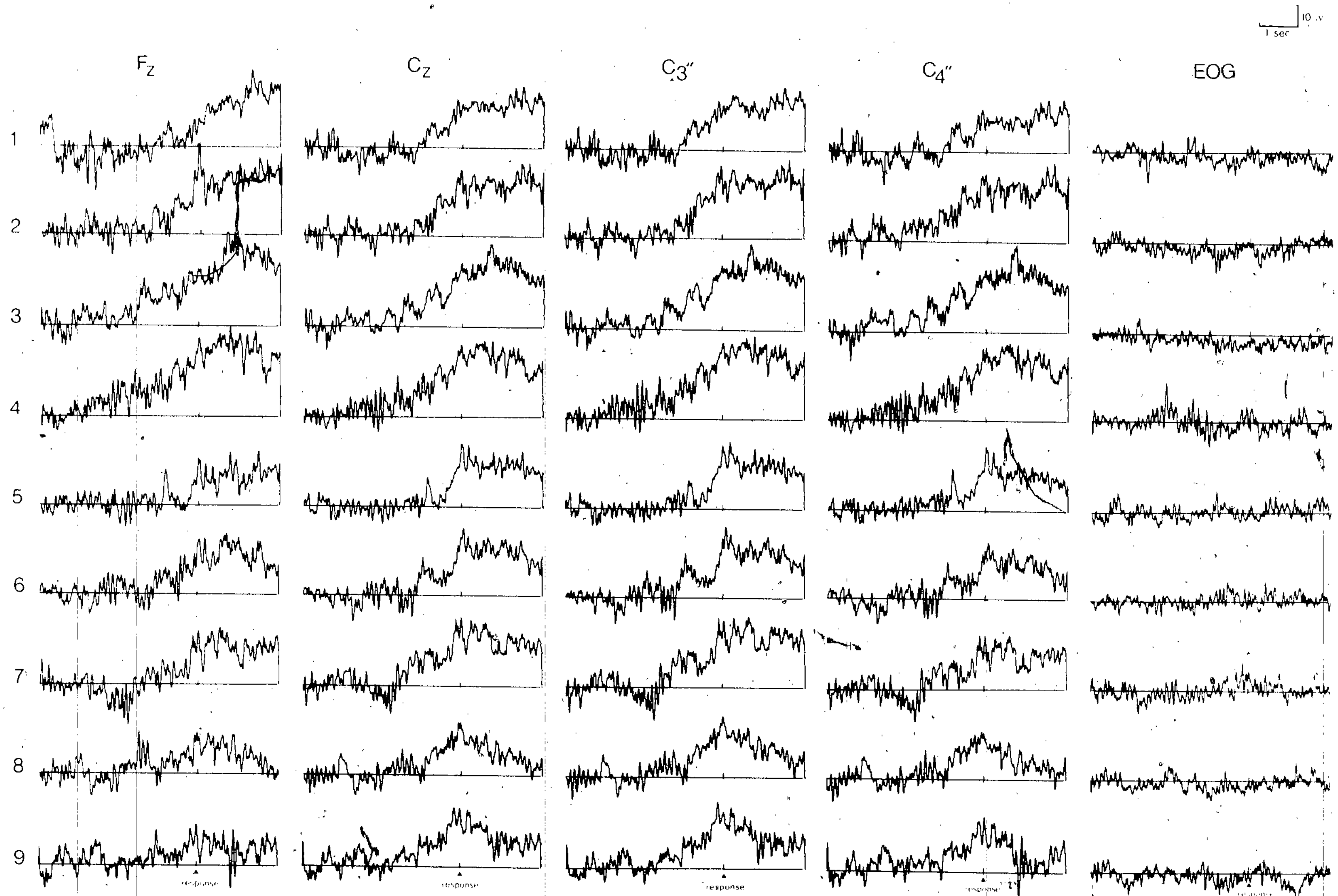


Table I

Summary of the Analysis of Variance
for area measure 2 sec prior to response

Source	Error Term	df	MS	F	p
X (Sex)	S(X)	1/10	54.2	.0469	ns
T (Trials)	ST(X)	8/80	451.0	2.3425	<.05
E (Electrodes)	SE(X)	3/30	1450.7	12.6444	<.001
XT	ST(X)	8/80	311.8	1.6193	ns
XE	SE(X)	3/30	229.5	2.0002	ns
TE	STE(X)	24/240	37.0	1.9073	<.005
XTE	STE(X)	24/240	11.7	.6027	ns

Table II

Summary of the Analysis of Variance
for peak area measure

Source	Error Term	*df*	*MS*	*F*	*p*
X (Sex)	S(X)	1/10	20.7	.0613	ns
T (Trials)	ST(X)	8/80	34.4	2.7489	<.025
E (Electrodes)	SE(X)	3/30	370.4	17.0198	<.001
XT	ST(X)	8/80	23.3	1.8594	ns
XE	SE(X)	3/30	20.1	0.9215	ns
TE	STE(X)	24/240	6.3	2.7642	<.001
XTE	STE(X)	24/240	1.0	0.4562	ns

Table III

Summary of Analysis of Variance
for area measure 2 sec following response initiation

Source	Error Term	df	MS	F	p
X (Sex)	S(X)	1/10	4880.4	0.3765	ns
T (Trials)	ST(X)	8/80	434.8	1.2221	ns
E (Electrodes)	SE(X)	3/30	3478.8	8.9441	<.001
XT	ST(X)	8/80	599.2	1.6843	ns
XE	SE(X)	3/30	448.9	1.1541	ns
TE	STE(X)	24/240	77.0	1.8845	<.01
XTE	STE(X)	24/240	20.9	0.5101	ns

constant amplitude differences among the electrodes. Across subjects and trials the size of the BP increased from Fz, to C4", to C3", to Cz (see Figure 4). The greatest difference in the BP measures was between Fz and the other three electrodes ($F=20.36$, $df=1/30$, $p<.001$). . The BP at C3" was not significantly larger than that at C4" ($F=3.85$, $df=1/30$, $p<.1$) although the trend was in the expected direction. For the last area measure, 2 sec following the response, both Fz and C4" were of much smaller area than were Cz and C3" ($F=25.86$, $df=1/30$, $p<.001$) (see Figure 5). The trial main effects were due to a steady increase in the area, at all electrodes for the first 4 averages (or 20 trials), and then some decrease, on average, over the last 4 averages (or 20 trials). The interaction effect at the measure 2 sec preceeding the response, was due to differences between the electrodes during the last 5 averages. At C4" and Fz the BP decreased steadily for 3 to 4 of these last 5 averages while at Cz and C3" the size dropped initially and then rebounded for one to two averages. At all electrodes there was an increase in the size of the BP during the last average (see Figure 6). The interaction effect at the BP peak measure was due to similar, although somewhat less marked changes (see Figure 7).

FIGURES 4 & 5

AREA MEASURES

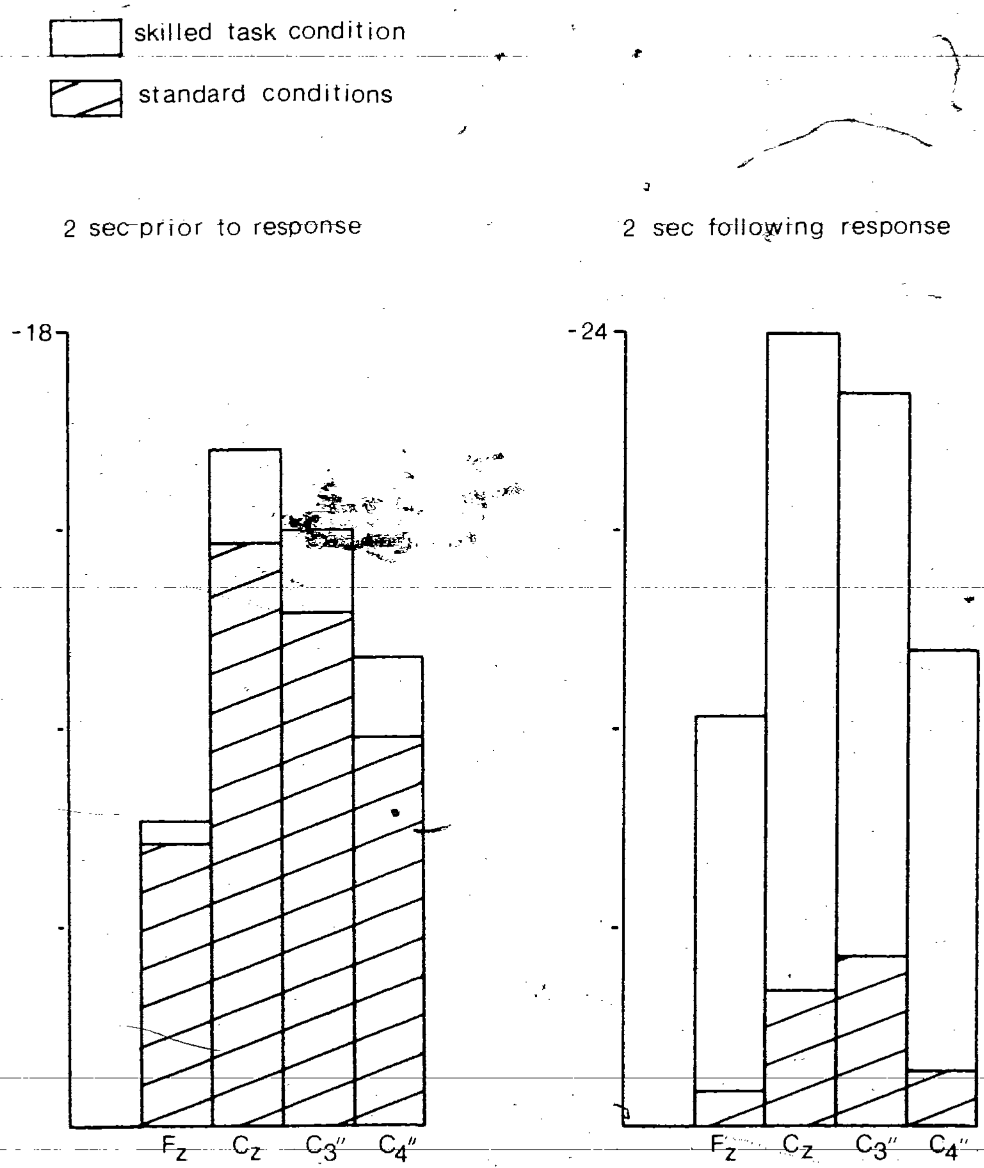


FIGURE 6

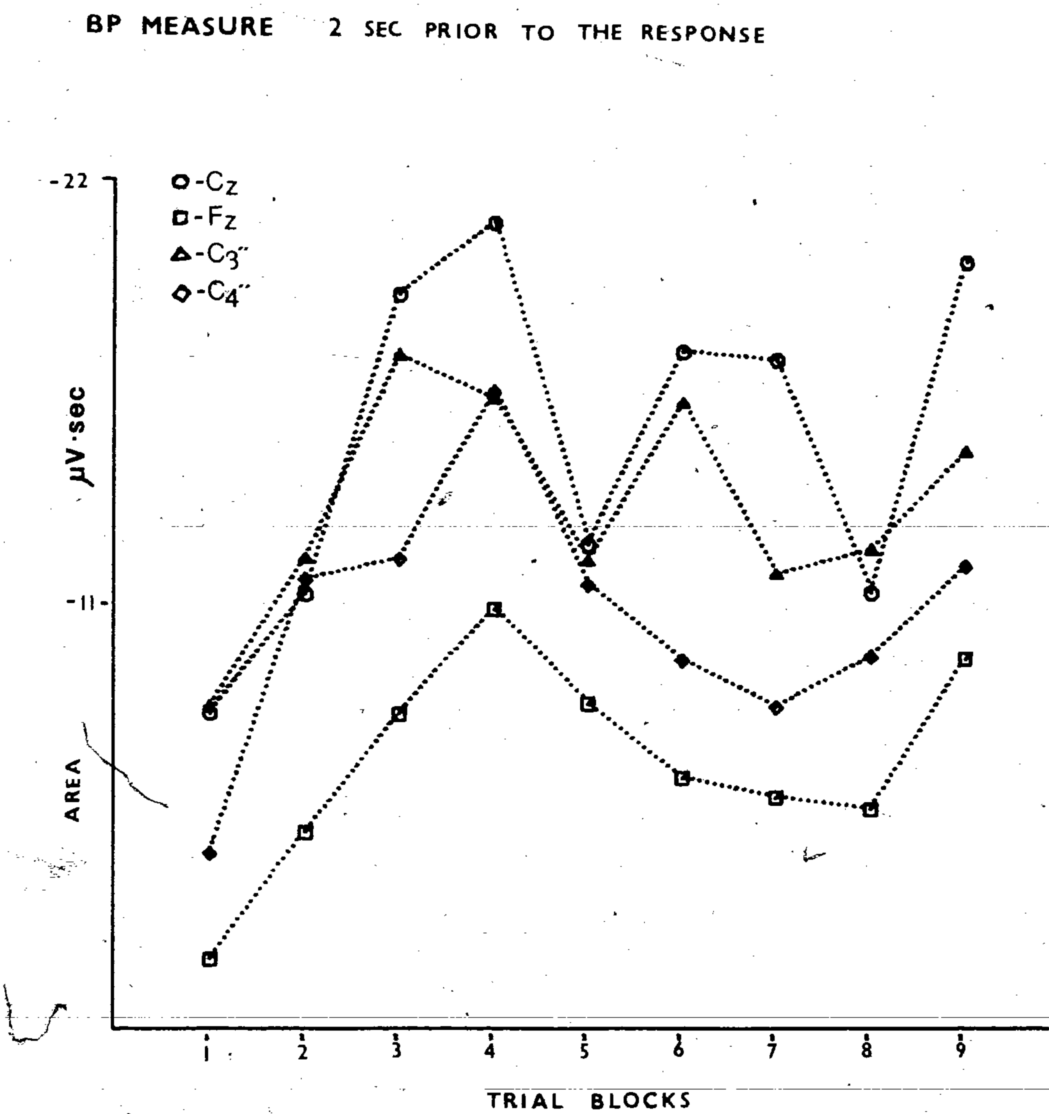
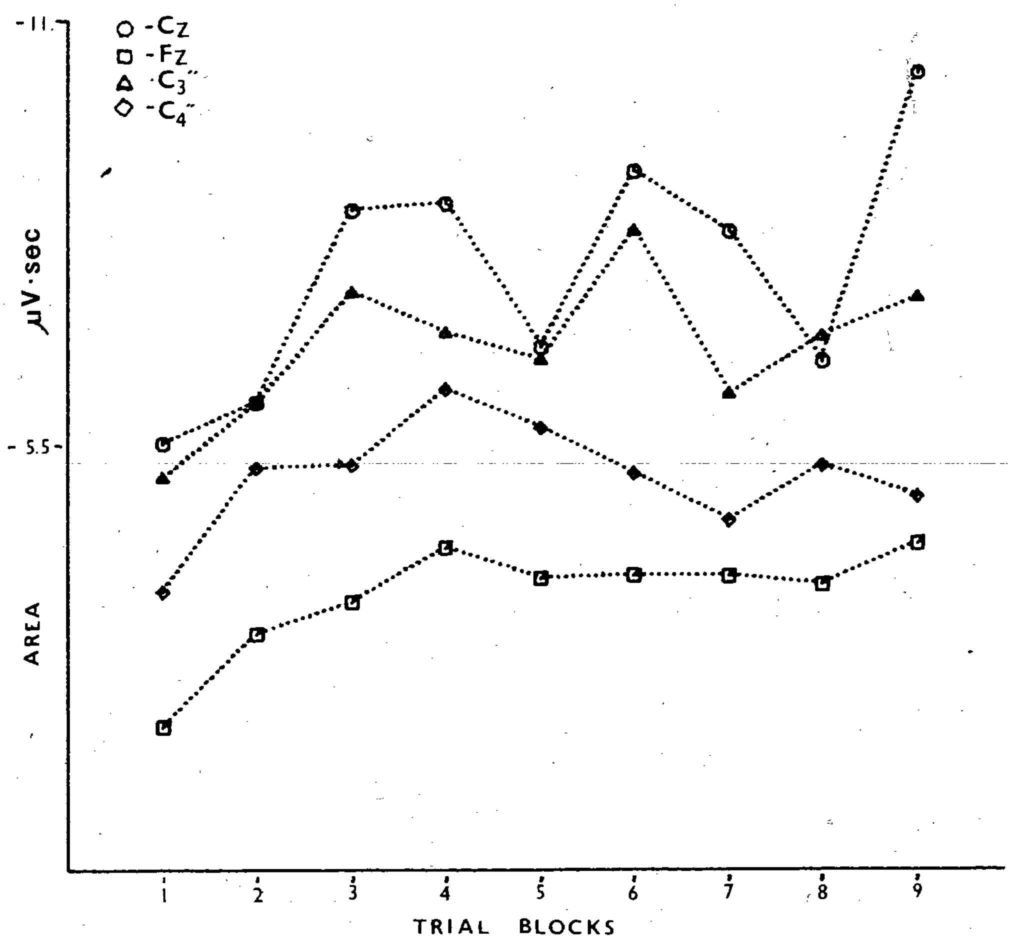

BP MEASURE 2 SEC PRIOR TO THE RESPONSE
-22
-11
AREA μV·sec
-Cz
-Fz
-C3"
-C4"
1
2
3
4
5
6
7
8
9
TRIAL BLOCKS

FIGURE 7

PEAK MEASURE



The response time over the series of six button presses decreased for all subjects over trials (F=28.42, df=8/80, p<.001) reaching asymptote at about the 20th trial or fourth average. (see Figure 8). Figure 9 shows the response times between the first and second button presses over the 45 trials; they follow the same pattern as the total response times.

No significant trial main effects were found with the multivariate analyses of covariance; Fz (F=1.06, df=32/281, p>.05), Cz (F=1.26, df=32/281, p>.05), C3" (F=1.60, df=32/281, p>.05) and C4" (F=1.25, df=32/281, p>.05). This shows that when the EEG data from the trials were adjusted for response times the trial effect drops out. This demonstrates a consistent relationship between the changes in the BP and the improvement in the response times over trials.

The plots produced by the 'Aspex' program offer clear visual representation of the trends in the single trial data (see Appendices A and B).

FIGURE 8

Response time over the series of six button presses

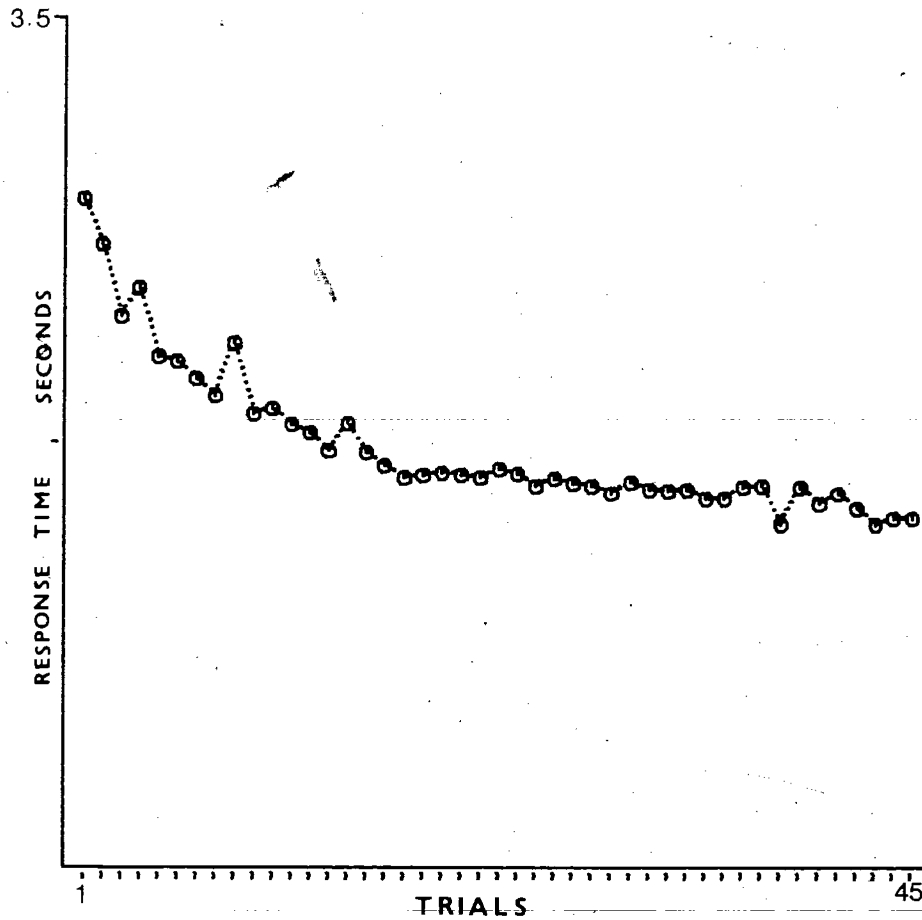
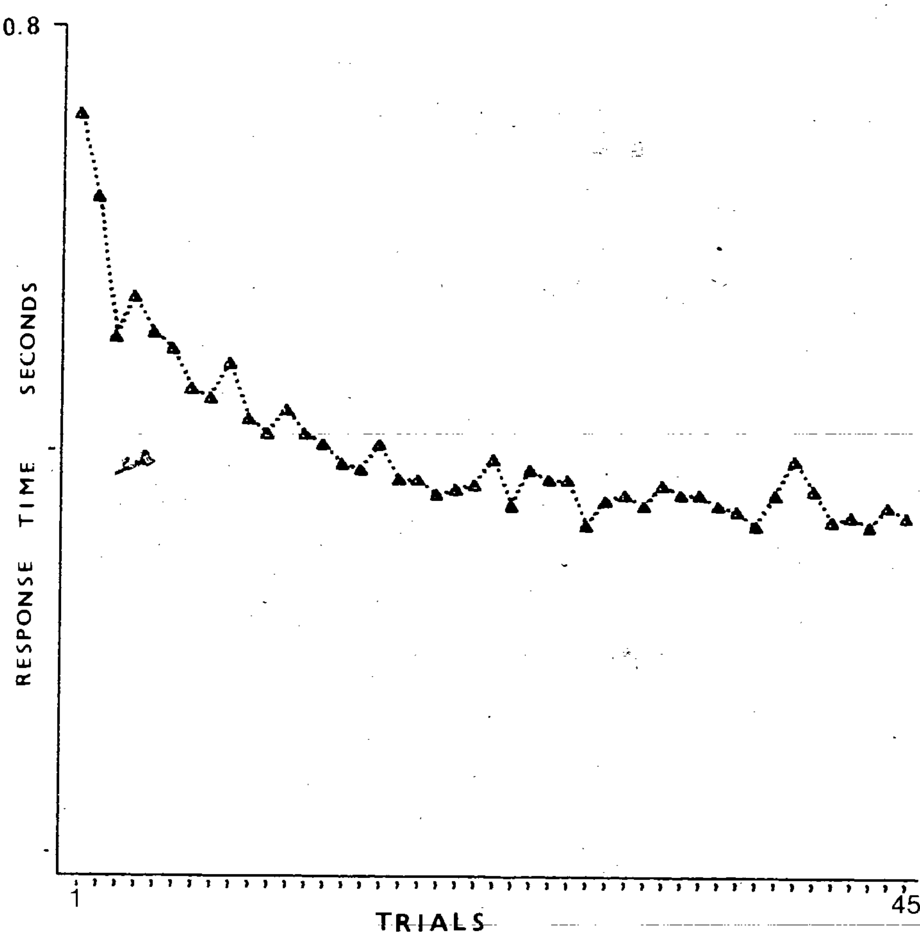


FIGURE 9

Response time between first and second button presses



Discussion

The results offer strong support for the hypothesis that the size and cortical distribution of the BP change with the acquisition of a skilled motor task. The magnitude of the BP at all electrode locations increased steadily over the trials in which the response time was decreasing; i.e., during the acquisition of the response. The two essential requirements of the study were found for all subjects. First, a clear learning effect of the motor skill and second, no significant differences between the two standard conditions, indicating that systematic changes in the BP were not a function of the duration of the experimental session.

As subjects acquire a skilled response their response accuracy should improve. An increase in accuracy and preparation to respond has already been related to increased size of the BP (McAdam & Rubin, 1971; Ford et al., 1973; Loveless & Sanford, 1974; Papakostopoulos, 1976). In all previous research, however, the measures of certainty, preparation and accuracy have been dichotomized. The subject's responses were not learned but selected and then performed either correctly or incorrectly. With the learning of a motor skill gradual changes in certainty and preparation would be expected to parallel gradual improvement in performance accuracy. Subjects in the present study were fully aware of the increase in the precision of their performance over the experimental session. Thus, the systematic increases in the BP area concurrent with the steady improvement in response performance, adds further credibility to the theory that the BP reflects preparation and certainty of the subject to respond. The results do not support the alternate contention that the BP is merely a physiological correlate of movement. During acquisition, the only response parameter known to change systematically was the speed with which the serial task was performed. Hazeman et al. (1976) found no variation in the BP with speed of response, and although Becker et al. (1976) did find such a change, the BP was smaller with responses performed quickly than with slow responses.

It was expected that the area of the BP two sec prior to the response would be larger preceeding the skilled response than before the single button press. The demands placed upon the subject in terms of preparation, preselection and attention during a skilled task far outweigh those necessary for a simple movement. Also, greater amounts of information must be monitored after perfomance of a skilled task compared to an unskilled task; an increase in post-response feedback has been shown to increase BP amplitude and duration (Dincheva & Harding, 1975). There was no significant difference, however, between the standard conditions and the skilled task condition for this measure.

The explanation for this result may rest in the large variations in the size of the BP within the skilled task condition. For the first one or two trial blocks of the skilled task the BP was smaller at all electrode placements than it was during the standard condition. On subsequent trials it was larger than the standard conditions except for one or two trial blocks after learning (see Table IV). According to the hypothesis presented in this study these results would imply less accuracy and preparation for the performance of the response during the initial 5 or 10 trials of the skilled task than for the standard response. When the skilled response is acquired and uncertainty decreased the corresponding BP is larger than in the standard conditions. The decline on some trials after learning could be attributed to decreases or lapses in the subjects' attention. Klein (1976) and Pew (1974) found attentional demands of a serial task to diminish after the task sequence had been learned.

Table IV

Bp area measures 2 sec prior to the response
for standard conditions and skilled task trial blocks

	Fz	Cz	C3"	C4"
Standard I	-6.43	-12.10	-11.62	-8.05
Skill Task 1	-1.83	-8.17	-8.32	-4.53
Skill Task 2	-5.08	-11.26	-12.17	-11.64
Skill Task 3	-8.16	-18.98	-17.40	-12.17
Skill Task 4	-10.86	-20.85	-16.28	-16.47
Skill Task 5	-8.42	-12.53	-12.09	-11.51
Skill Task 6	-6.50	-17.51	-16.18	-9.52
Skill Task 7	-6.00	-17.29	-11.76	-8.33
Skill Task 8	-5.68	-11.29	-12.38	-9.62
Skill Task 9	-9.57	-19.82	-14.89	-11.98
Standard II	-6.46	-14.32	-11.55	-9.49

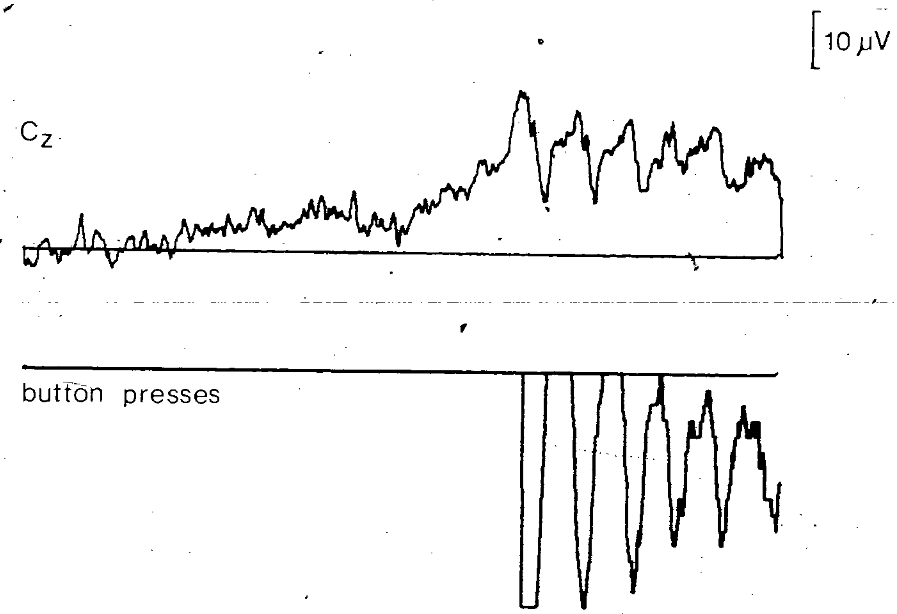
The significantly larger peak measures in the skilled task condition appeared, from visual inspection, to be concomitants of increased negativity of the slope of the BP preceeding skilled movement. In the standard conditions the slope of the BPs was usually linear, in accordance with previous studies which employed simple movements. In the skilled task condition the slope was quadratic or cubic. Unfortunately a method for objectively measuring non-linear slopes was not available. From this study it is impossible to determine whether the apparent difference in slope between the conditions is a function of the learning required for the skilled task or of the duration of the skilled task.

It was expected that the role of the frontal areas in organizing motor output and in monitoring output and feedback would be reflected in qualitatively different changes in the frontal BPs than those in the BPs from over the motor cortex. The electrode by trial interaction is attributable to differences only after the response had reached asymptotic levels. The frontal BP increased at the same rate as the vertex and lateral BPs during acquisition. After response acquisition, the frontal BP, in contrast to those from C3" and Cz, decreased steadily. With practice the performance of a response tends to become automatized lessening both attentional demands and the amount of feedback requisite for maintenance of the response (Klein, 1976; Keele & Summer, 1976). Probably the subject's involvement in the task also decreased after the goal of fast, accurate responses had been achieved, which would predict a reduction in frontal BPs (McCallum, 1976).

The most perplexing anomaly of this study however, was the failure to detect changes during learning in the frontal BP that could be differentiated from changes occurring in the BPs over the motor strip. The importance of the frontal areas in the organization of movement prior to its initiation has been well documented (Teuber, 1964; Kelso & Stelmach, 1976) and some measure of this was expected at Fz. Possibly insufficient sensitivity of the macroelectrode was to blame, or too posterior a placement. Alternatively, the organization of movement in terms of preselection and feedforward may not be timelocked to the response as other processes are, perhaps ocurring minutes before the response; or may be intrinsically more variable in its occurrence and duration. If either of these was the case, the methodology used for measuring the BP would be inappropriate for detecting such changes in frontal activity related to learning a skill. However, as the skill was acquired and response variability decreased the anticipatory activity in the frontal areas may also become more consistent, timelocked to the response and measurable.

The relative size of the BPs in relation to their cortical distribution was congruent with expectations and with most other research in the field. The BP was largest at Cz, larger over the motor cortex than frontal areas and tended to be larger contralateral to the responding musculature. The divergence between C3" and C4" after learning (see Figure 6) suggests that the less attention a movement requires the more specific to the motor projection area the BP becomes. This offers an explanation of the maintenance of large BPs close to the motor projection area even after acquisition when BPs recorded from more remote locations decreased. In concurrence with this, McAdam & Rubin (1971) suggested that their finding of non-lateralized BPs was a function of the exacting attentional demands placed upon their subjects. The decrease at C4" during the actual performance of the task, independent of learning, could reflect less processing of motor commands and sensory feedback than at C3". Even during this period, however, the potential was largest at Cz suggesting continued general preparation and not solely the relaying of motor commands. In one subject a series of small waves reminiscent of BPs occurred in this interval; one preceeding each successive button press (see Figure 10). This subject responded more slowly than average, although the effect was not notable in other slow responders.

FIGURE 10 BP and the series of six button presses averaged over trials 16-30 of the skilled task. subject CH



Continued negativity after the initiation of the response is not generally reported in the literature, as a large positive wave (P2) usually follows the response within 200-300 msec. (One exception to this is the study by Timsit-Berthier (1973) of the relationship between post-response negativity and psychoses). This discrepancy between the present study and the existing literature is likely due to the duration of the serial response. In other BP research P2 follows the initiation of the response, but the responses have been simple, short movements, such that the P2 also follows the termination of the response. As the subjects acquired the skilled task and the response duration shortened this post-BP negativity tended to decrease, although the effect was not significant.

The response performance improved and the BP area measures increased over the first twenty trials. After the response reached asymptote the BP decreased at Fz and C4" while remaining relativly large over the motor projection area. These systematic changes over the 45 trials of the skilled task yielded a significant trial main effect for the BP area measures. The multivariate analyses of covariance demonstrated that when the variance contributed by the response times to the BP measures was taken out of the area measures, the significant trial main effect was no longer found. This suggests a sound relationship between the acquisition of the skilled task and the observed changes in the BP. Although the data suggest a causal relationship, whether changes in the BP are necessary for changes in performance cannot be determined from this study. The BP may be one of many electrophysiological signs that correlates with improved performance in a motor skill; this does not claim that it is an essential component of motor skill acquisition.

In this study, however, the BP reflects the level of motor skill learning, and after learning, possible changes in attention. Potentially, it could be used to distinguish between movements that require central attentional mechanisms for initiation and performance and those that do not. It clearly would be easier to employ a measure such as response time if one was only interested in whether a subject learned a motor skill. But, if one is interested in the mechanisms involved in the acquisition of skills and in motor skill performance after acquisition, the BP could add a valuable dimension to the research.

Appendices

The following Aspex displays were plotted using the parameters listed below:

Altitude=20 degrees above horizontal
Azimuth=350 degrees, clockwise from center front
Interval=2, only every other diagonal is drawn
Across trial smoothing=5 Hz, a low pass filter of 5 Hz
Within trial smoothing=15 Hz, a low pass filter of 15 Hz

As Aspex program the plots positive values above baseline, the EEG data were inverted, such that negative values became positive and positive values negative. In Appendix A the parameter 'Minimum=0' was employed such that all data points below baseline (i.e., those that were originally positive) were not plotted. This improves the clarity of the plot in terms of the BP and the systematic changes in the waveform over trials.

Appendix A

The EEG data from four subjects plotted using the Aspex program with the following parameters in effect:

Altitude=20

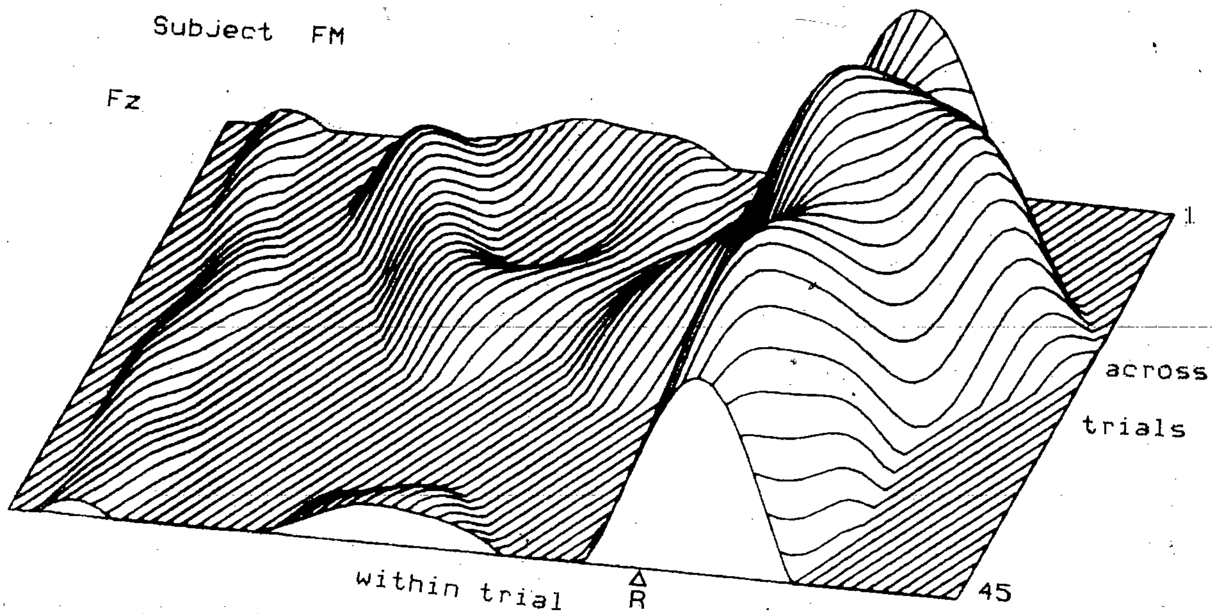
Azimuth=350

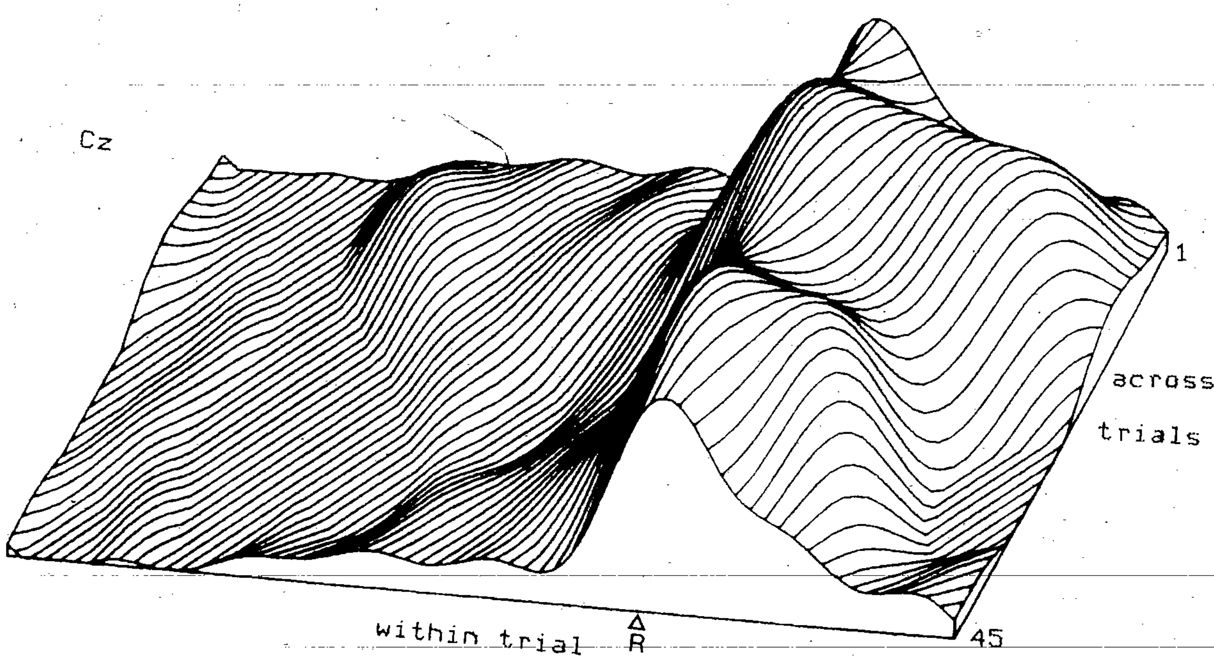
Height=3

Inputscale=3.5

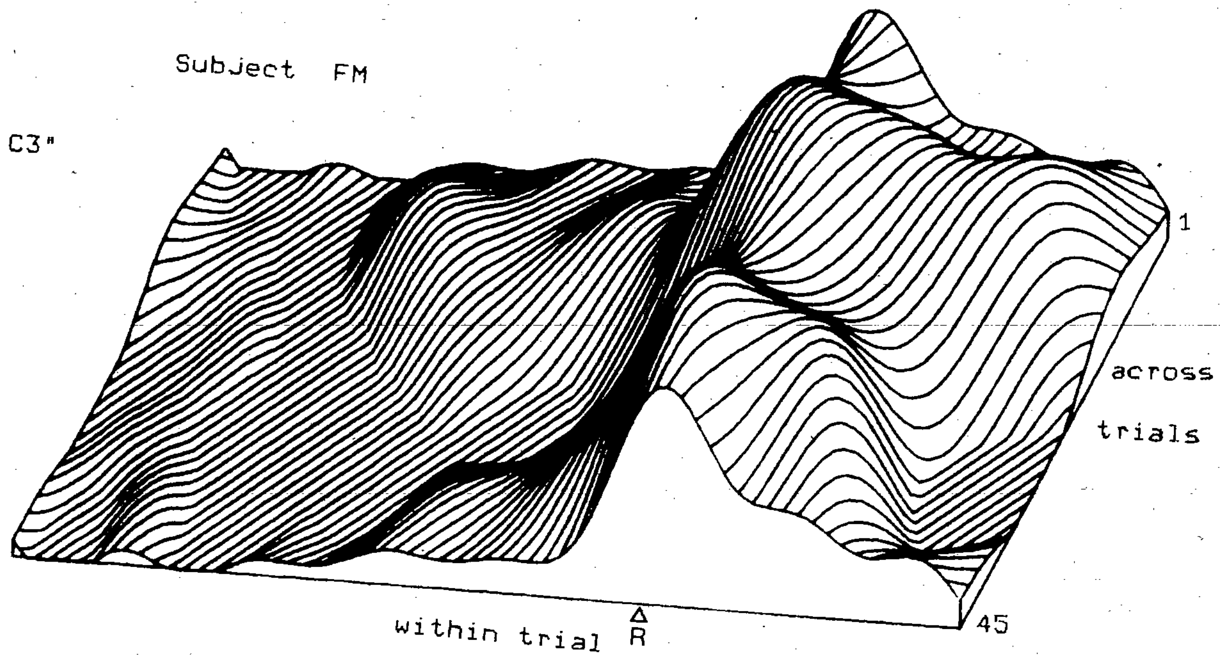
Minimum=0

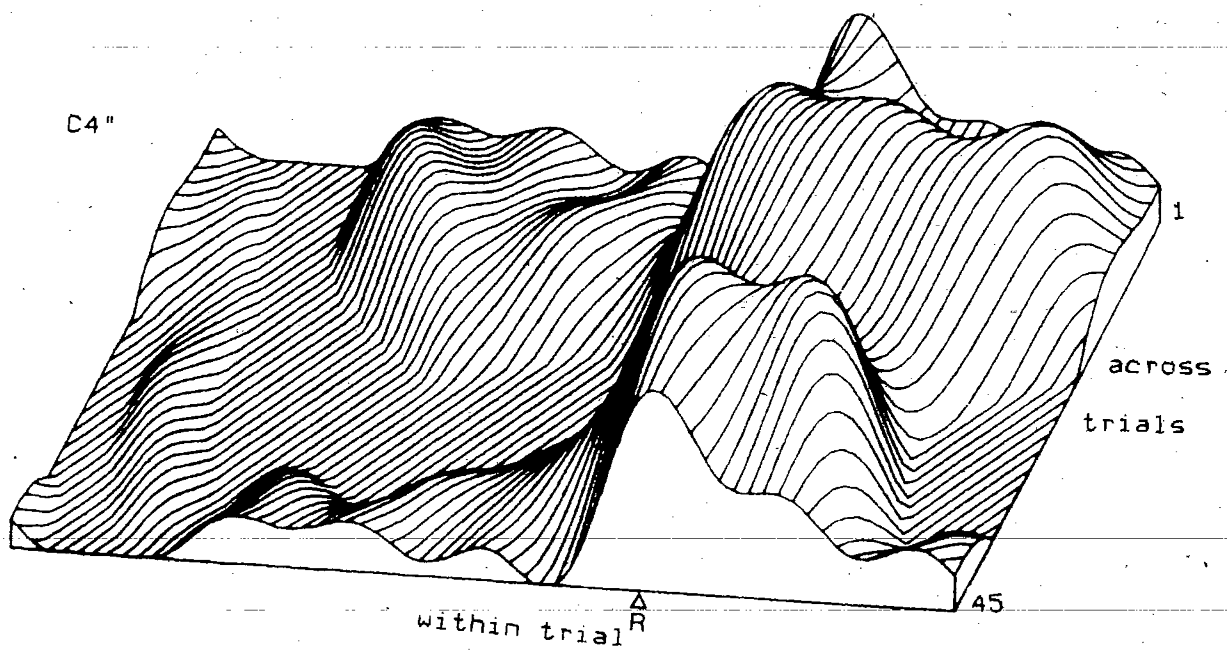
Interval=2

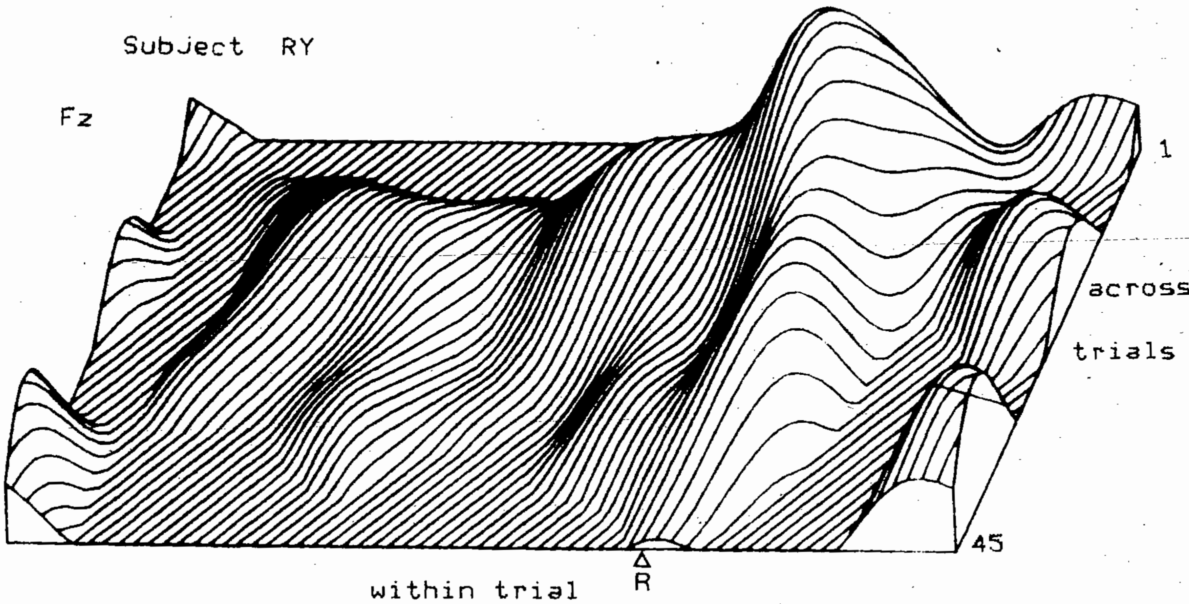

Subject FM
Fz
1
across
trials
within trial
R
45

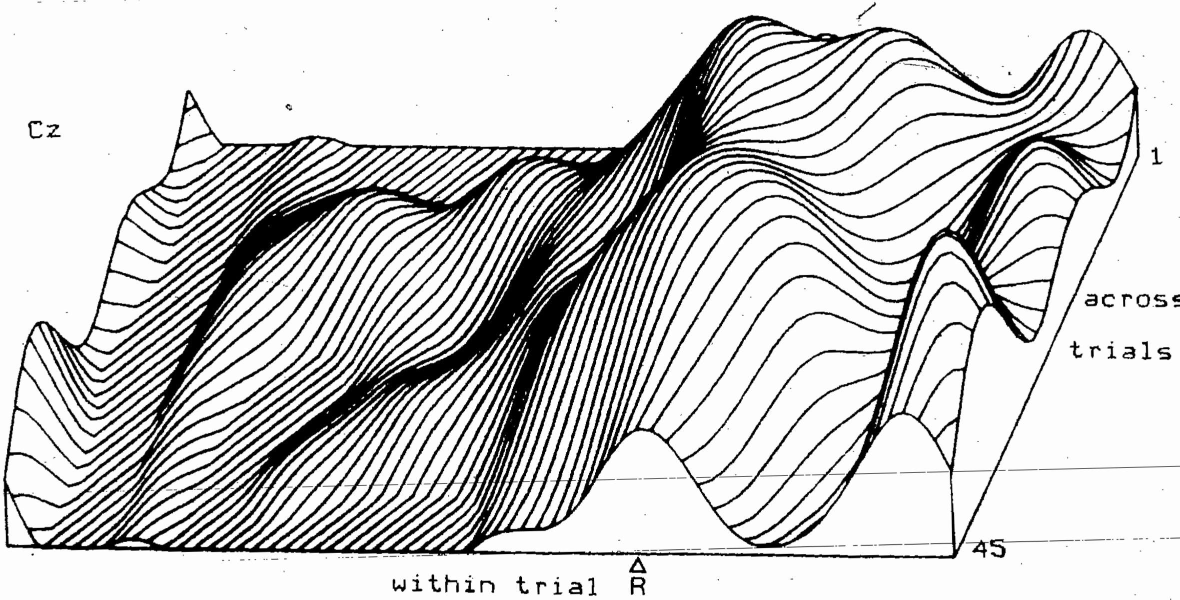

Cz
1
across
trials
within trial
R
45

Subject FM

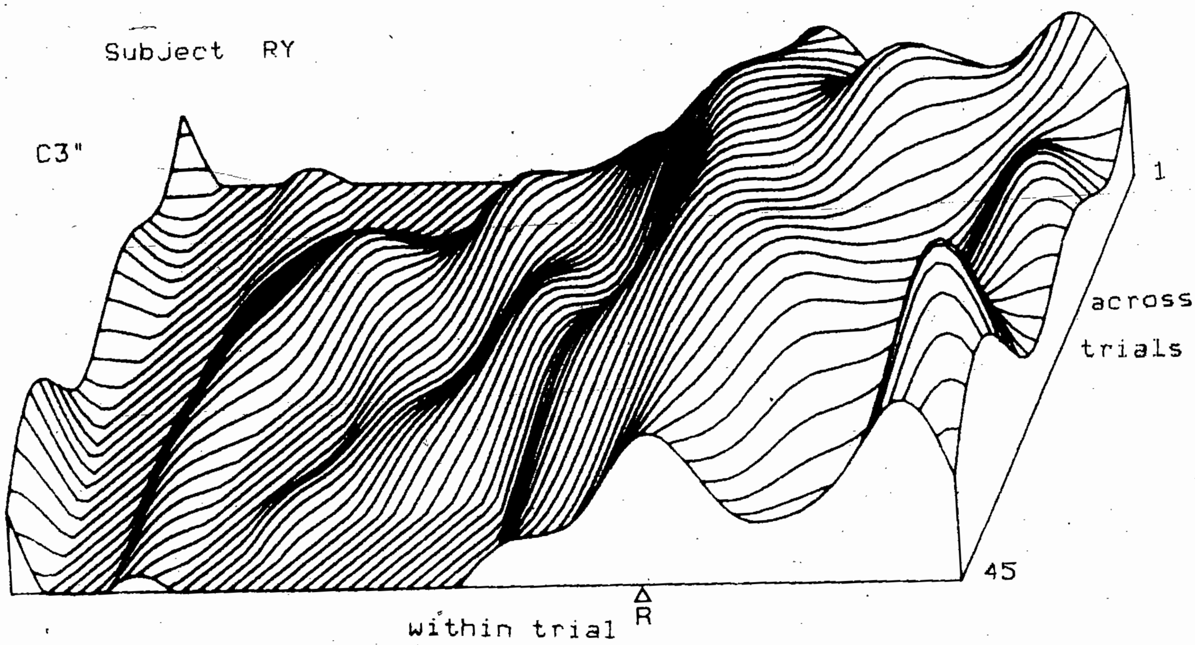

C3"
1
across
trials
45
within trial
R

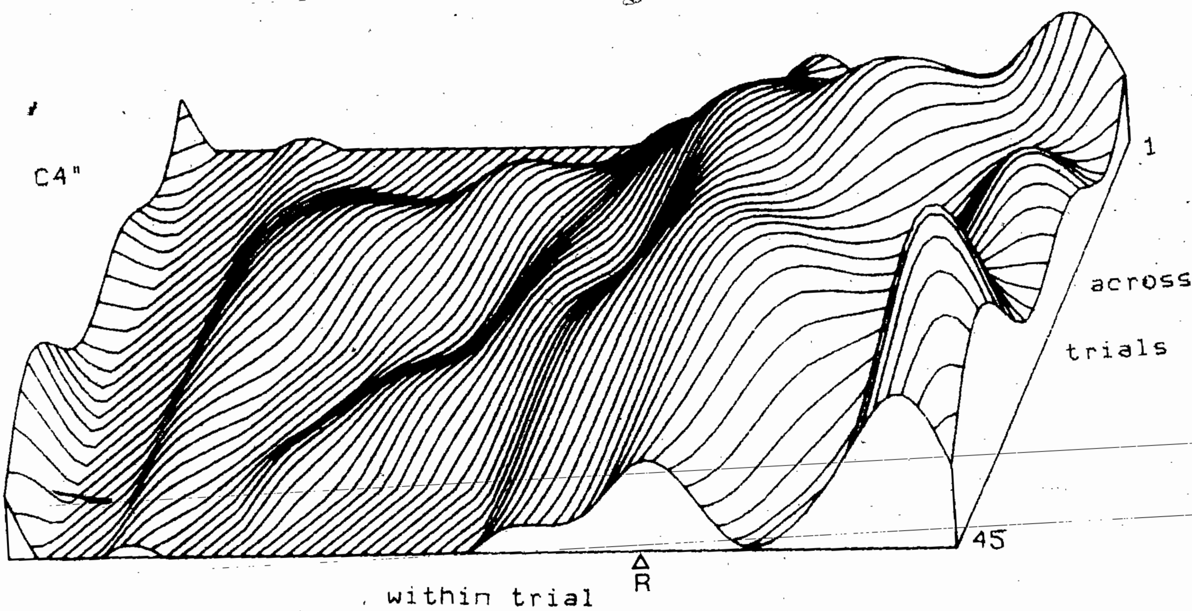

C4"
1
across
trials
45
within trial
R


Subject RY
Fz
1
across
trials
45
within trial
R

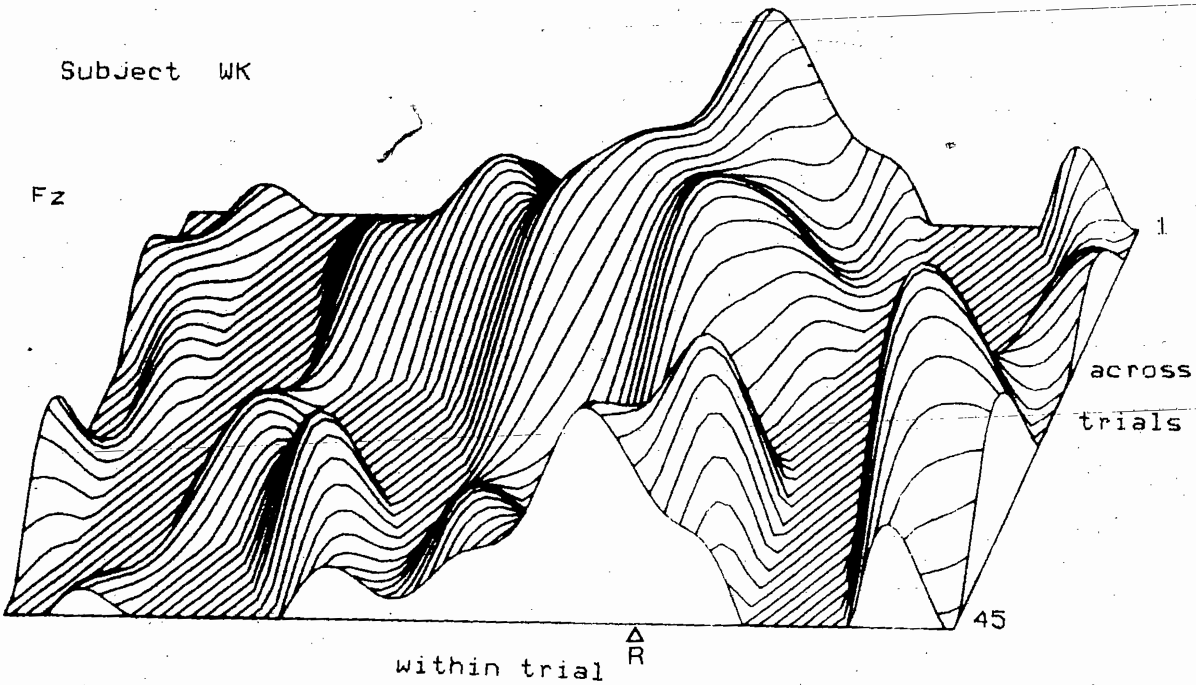

Cz
1
across
trials
45
within trial
R

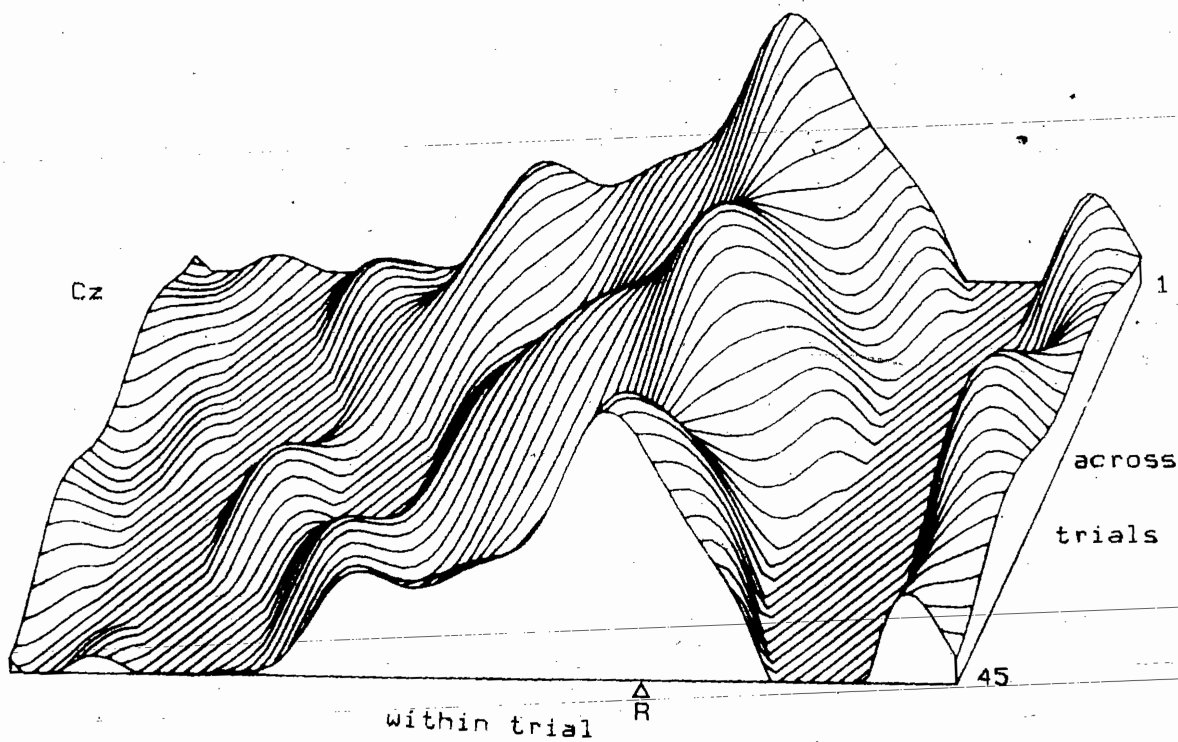
Subject RY


C3"
1
across
trials
45
within trial
R

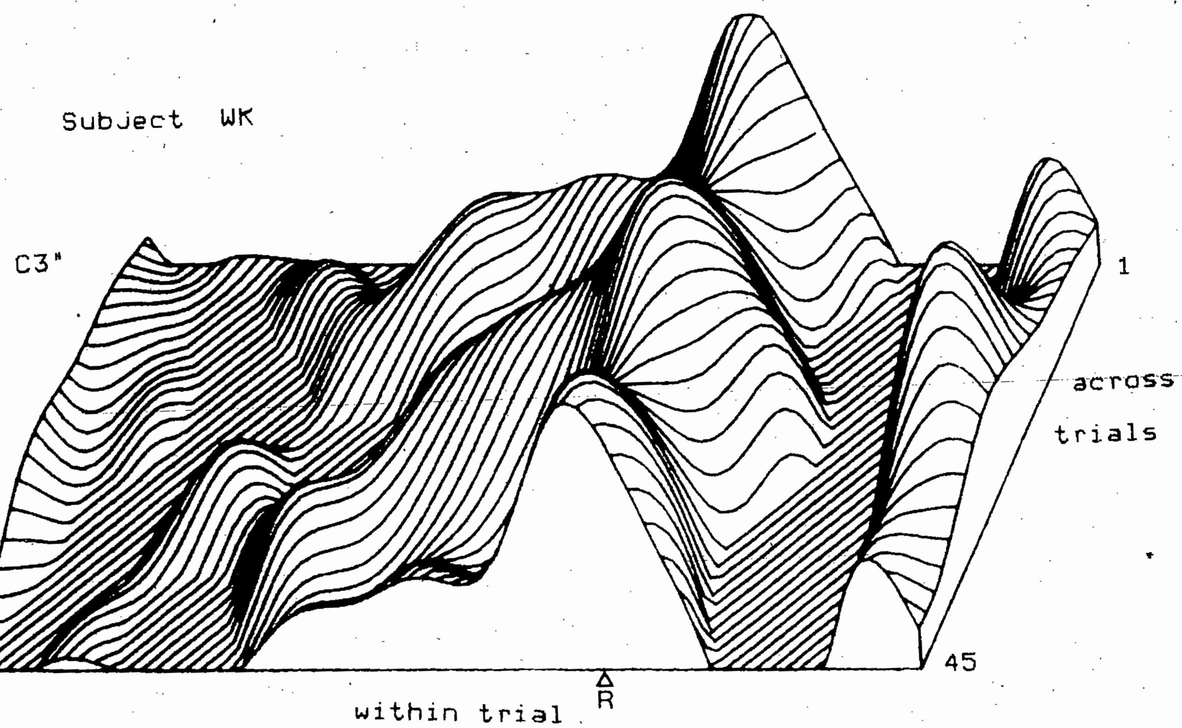

C4"
1
across
trials
45
within trial
R

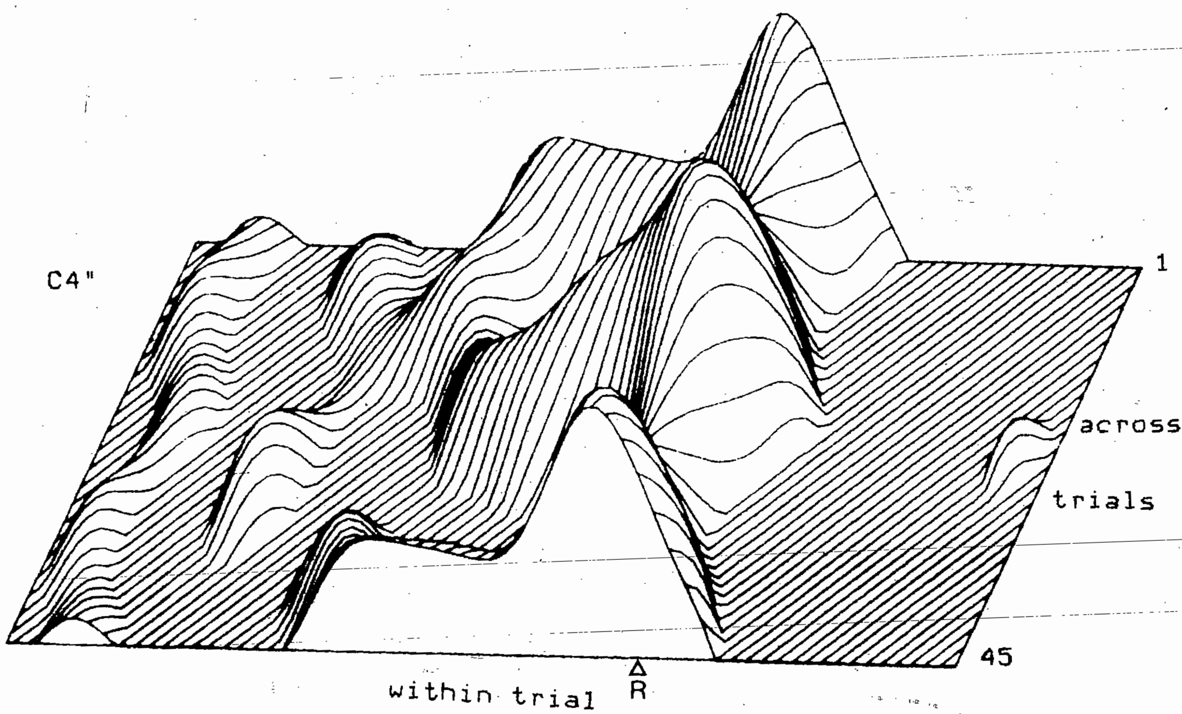
Subject WK


Fz
1
across
trials
45
R
within trial

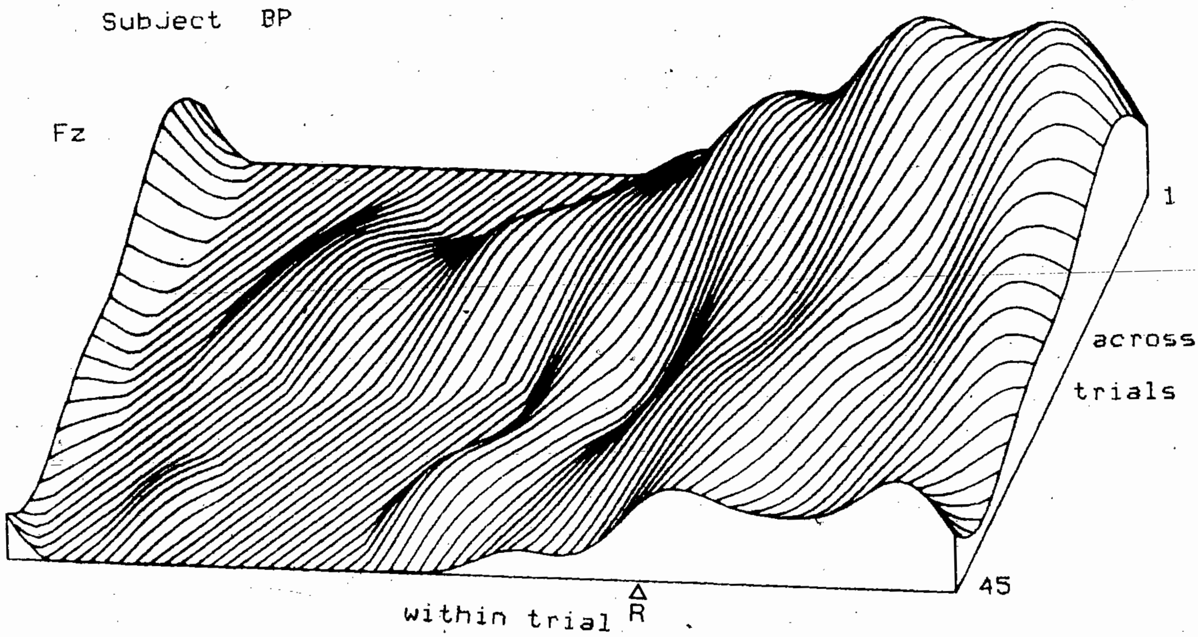

Cz
1
across
trials
45
R
within trial

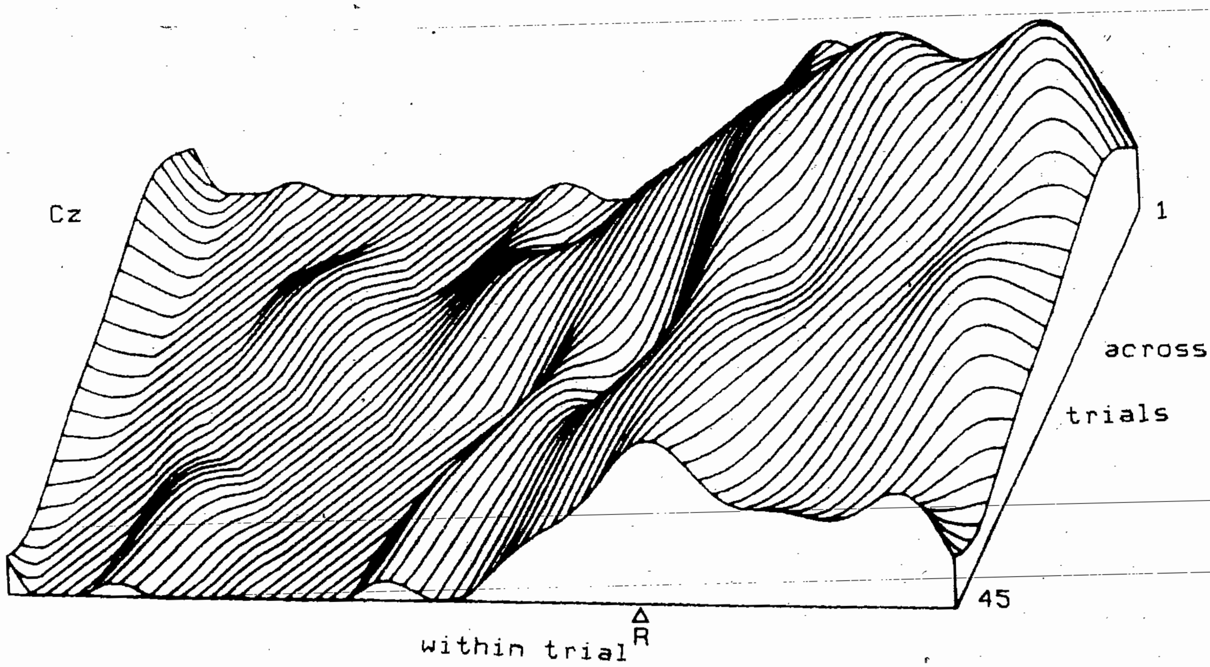
Subject WK


C3"
1
across
trials
45
within trial
R

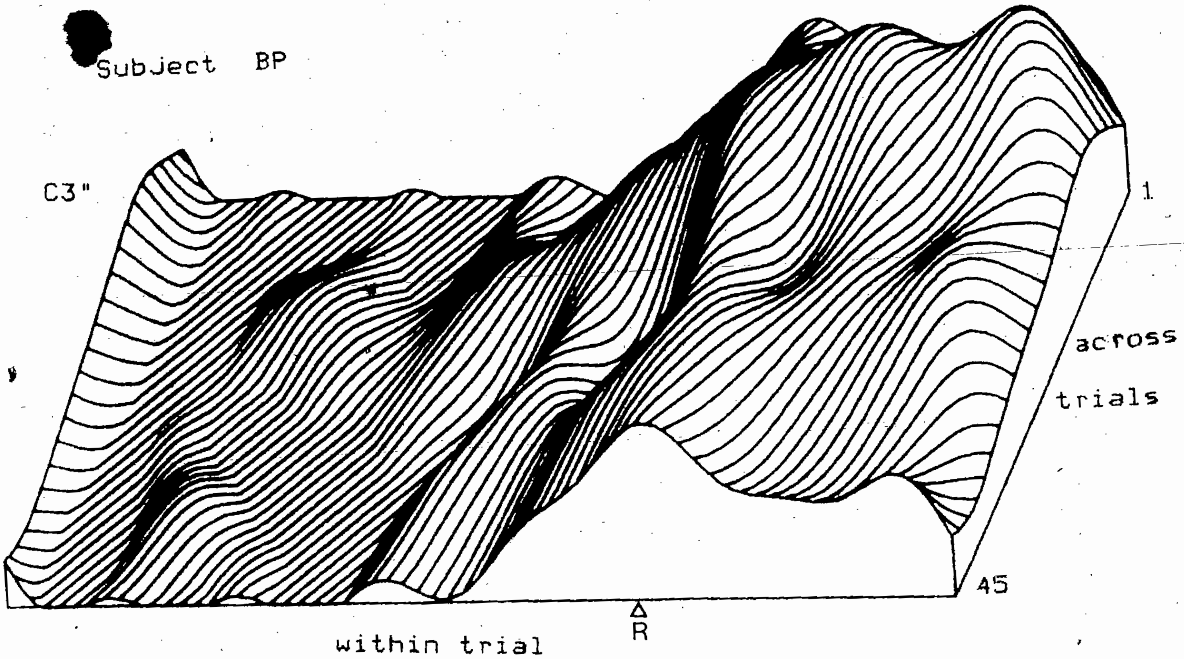

C4"
1
across
trials
45
within trial
R

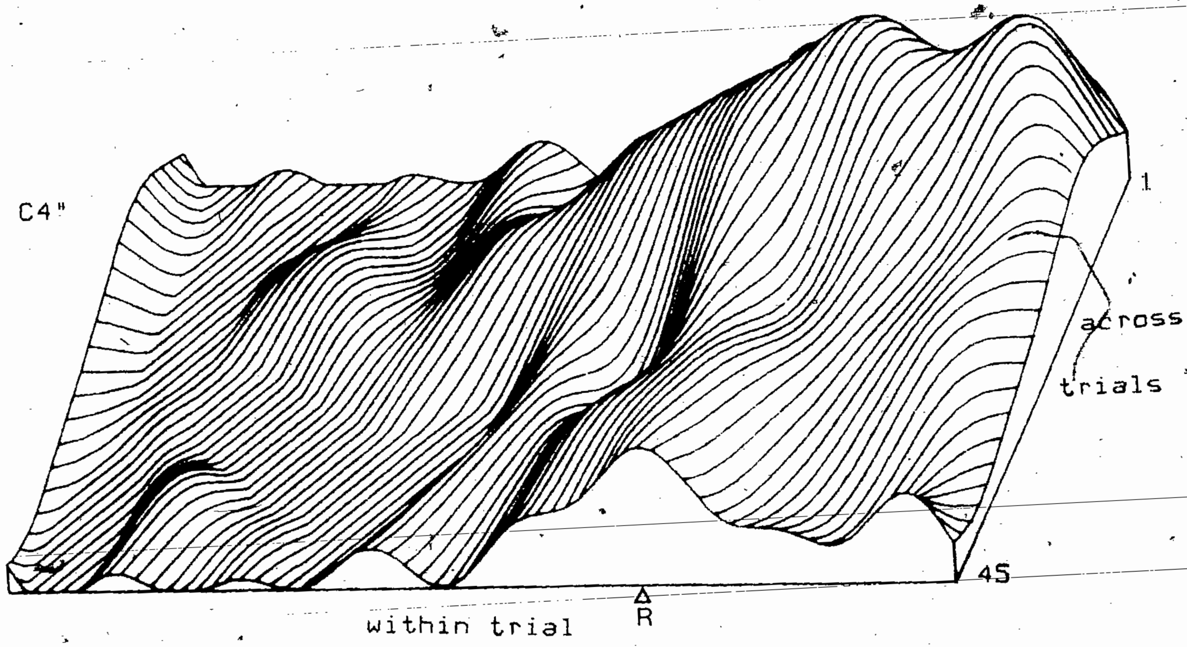
Subject BP


Fz
1
across
trials
45
within trial
R


Cz
1
across
trials
45
within trial
R

Subject BP


C3"
1
across
trials
45
R
within trial


C4"
1
across
trials
45
R
within trial

Appendix B

The EEG data from four subjects plotted using the Aspex program with the following parameters in effect:

Altitude=20

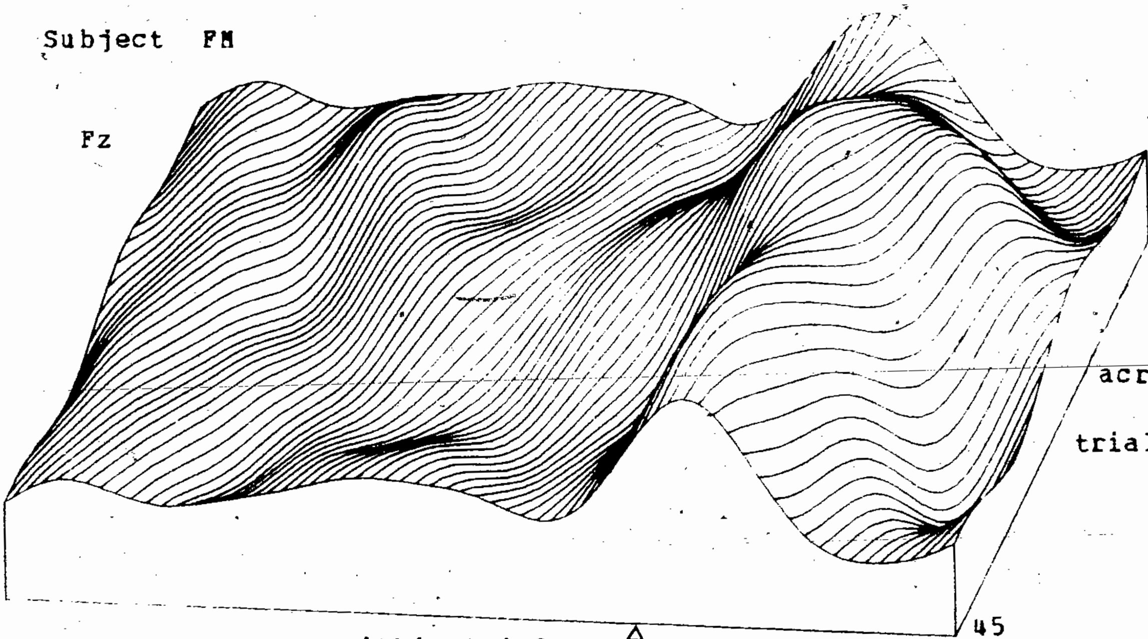
Azimuth=350

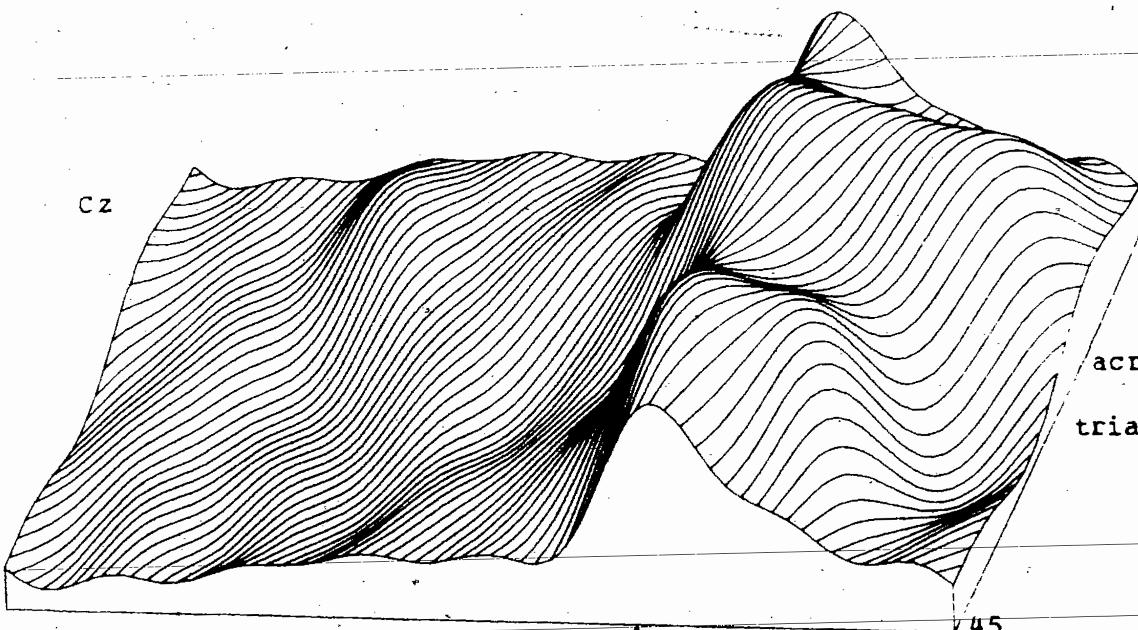
Height=3

Inputscale=3.5

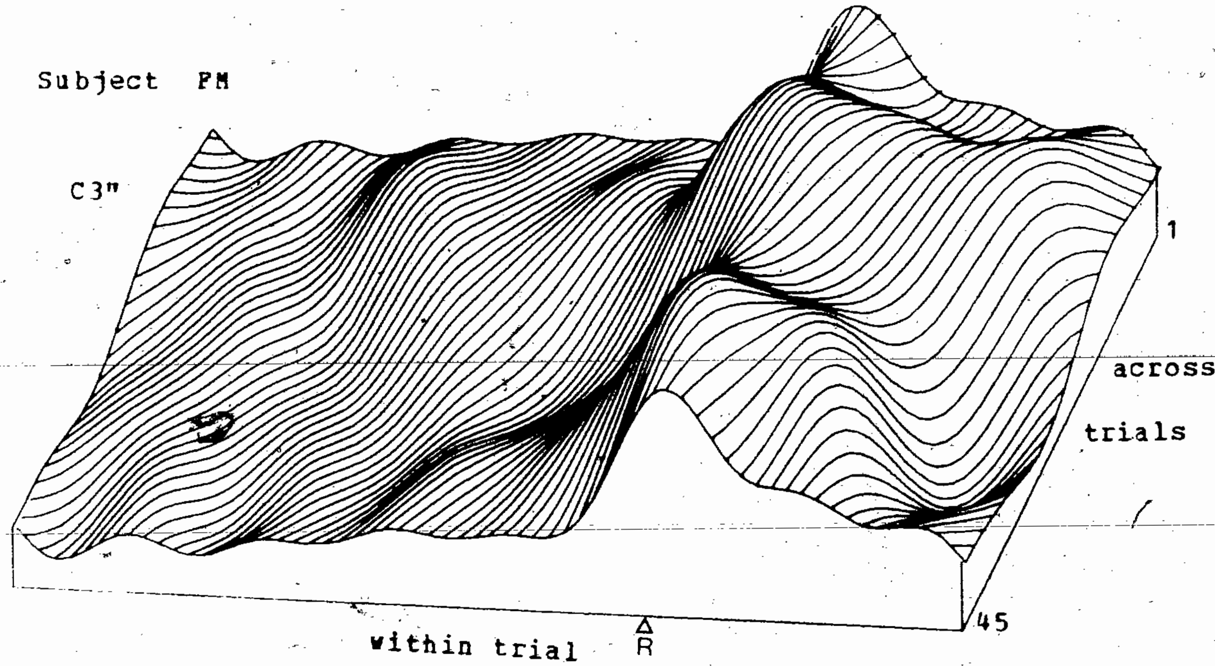
Interval=2

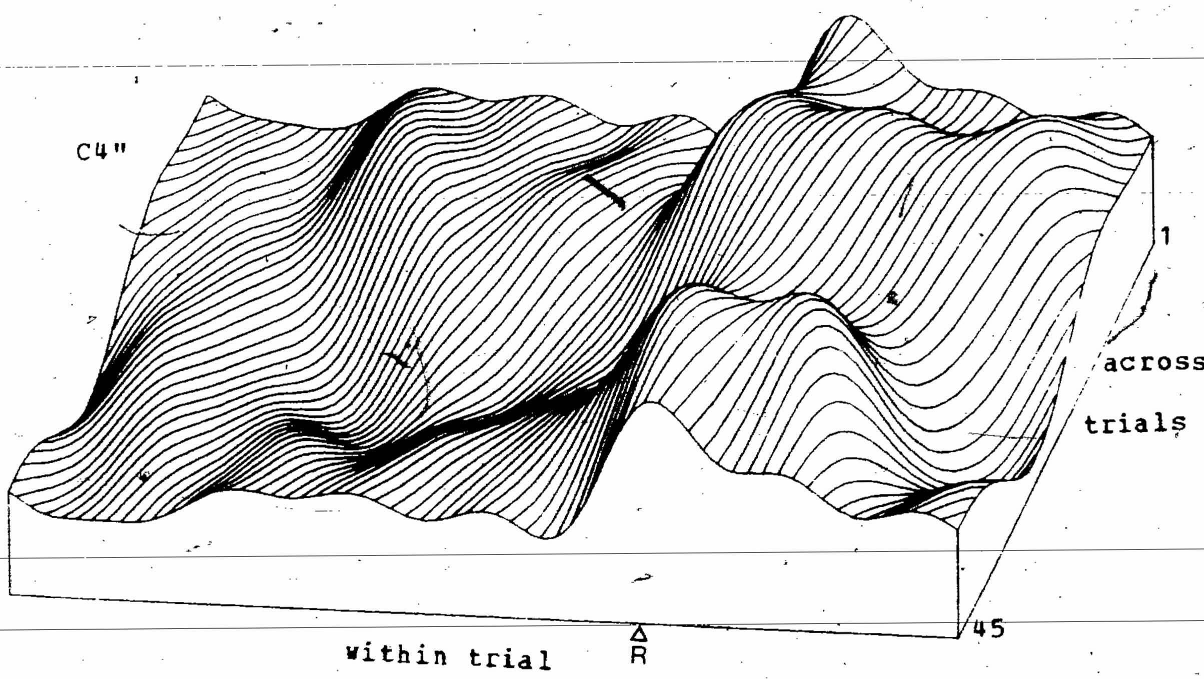
Subject FM


Fz
1
across
trials
45
within trial
R

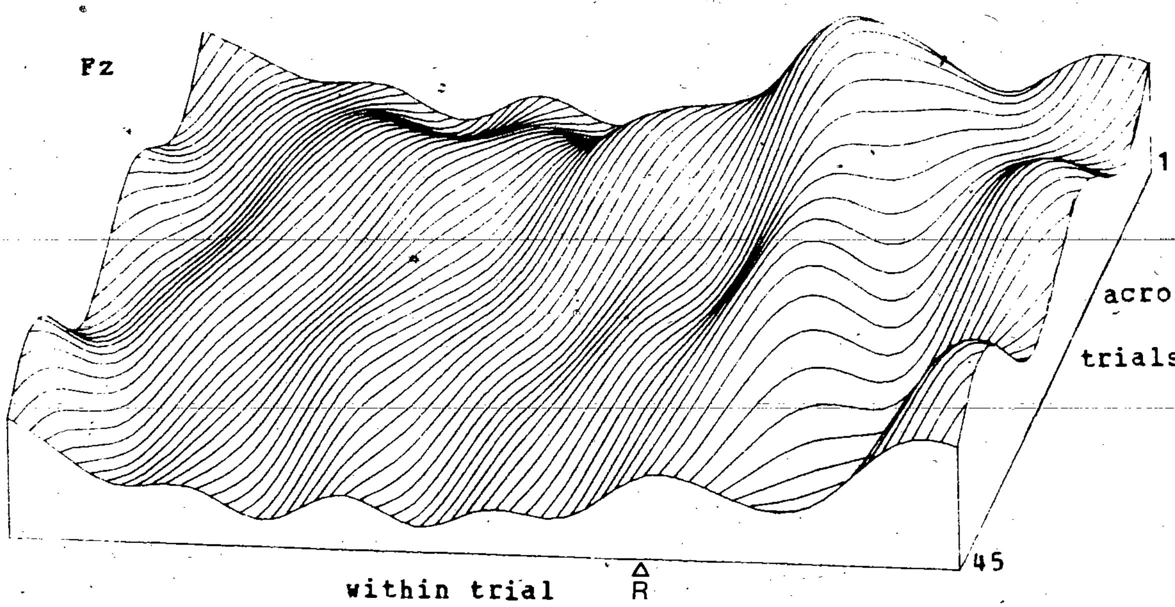

Cz
1
across
trials
45
within trial
R

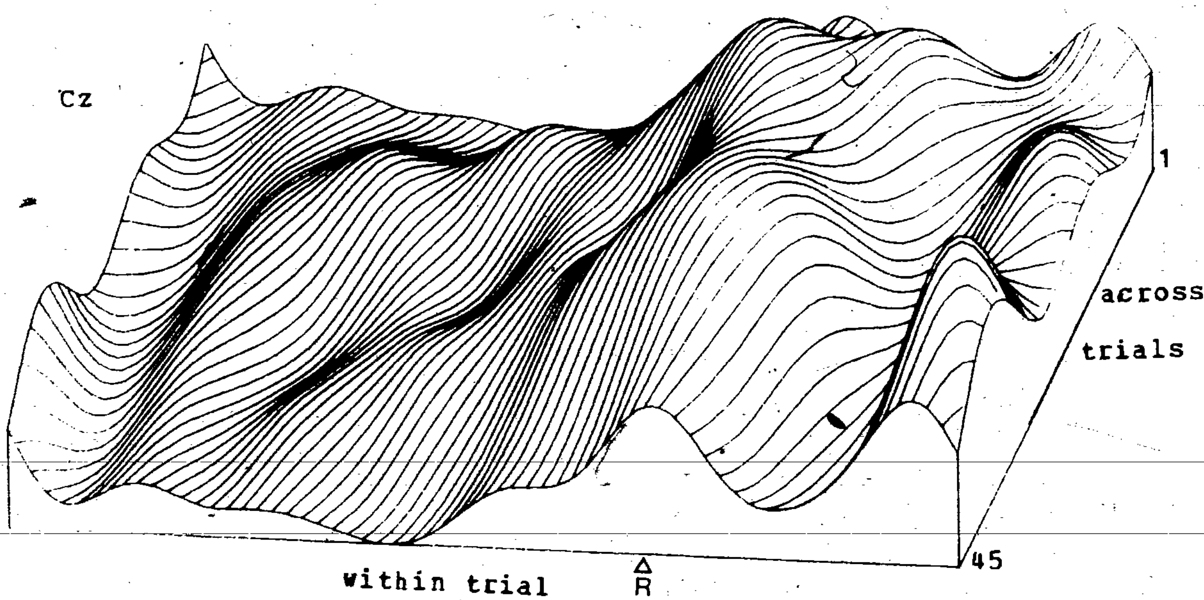
Subject FM


C3"
1
across
trials
45
within trial
R

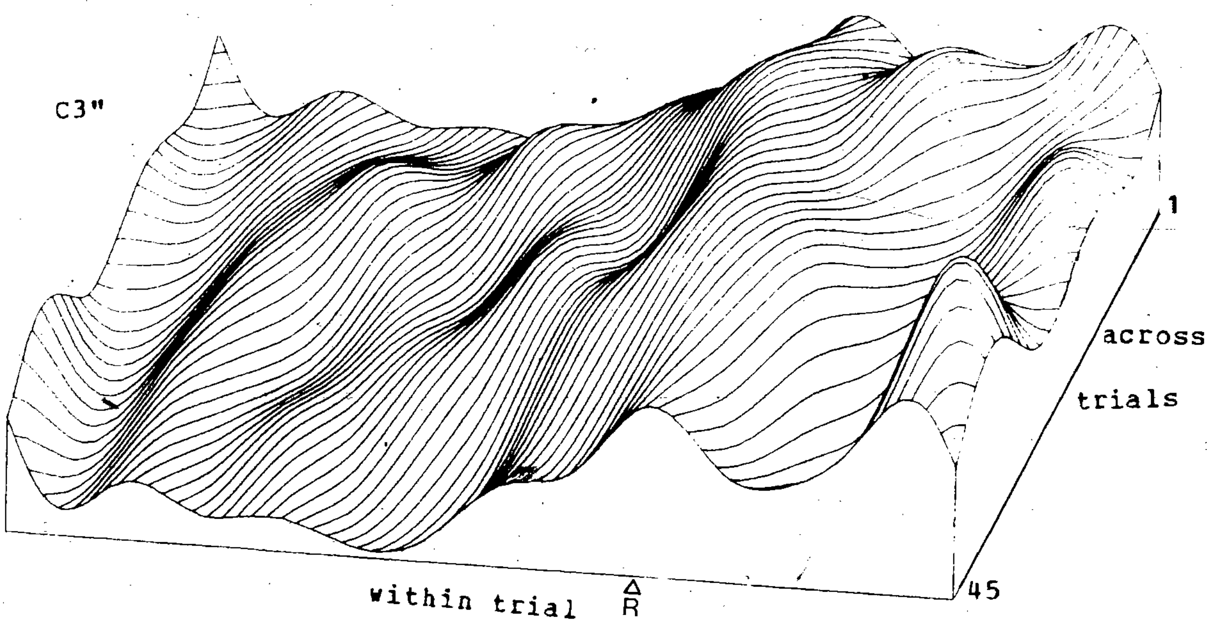

C4"
1
across
trials
45
within trial
R

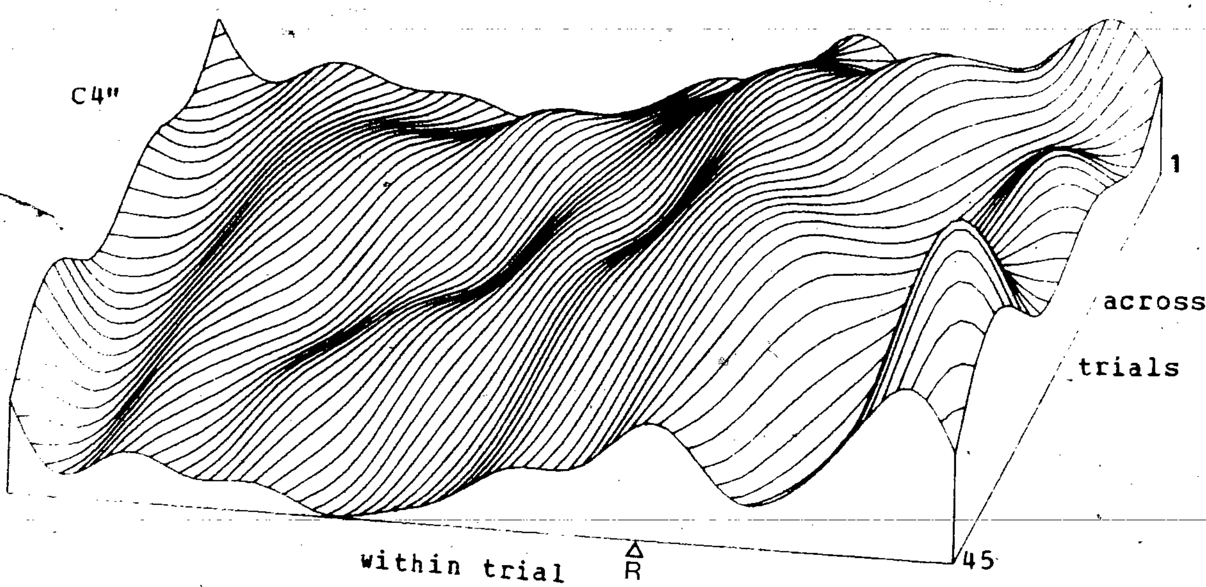
Subject RY

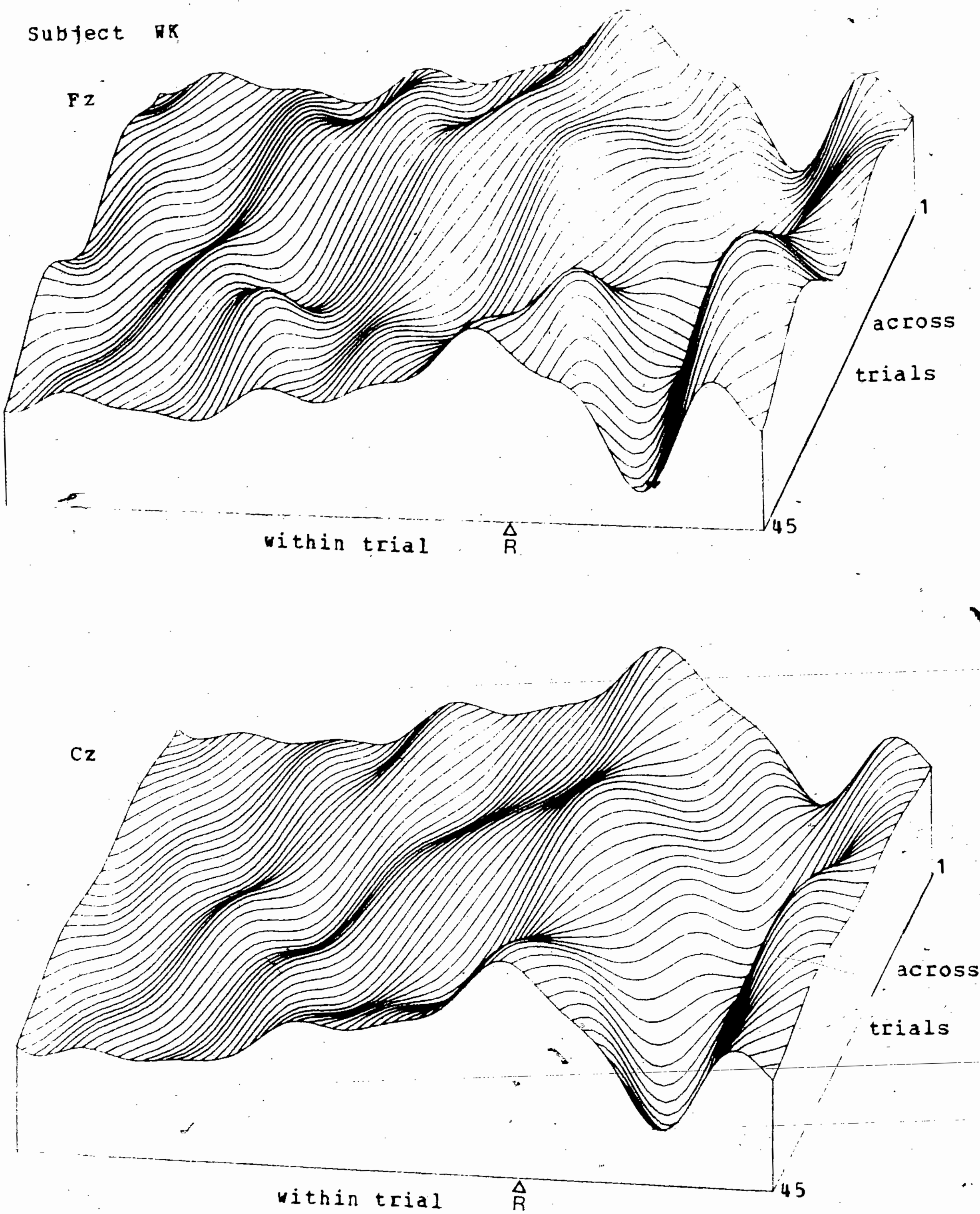

Fz
1
across
trials
45
within trial
R

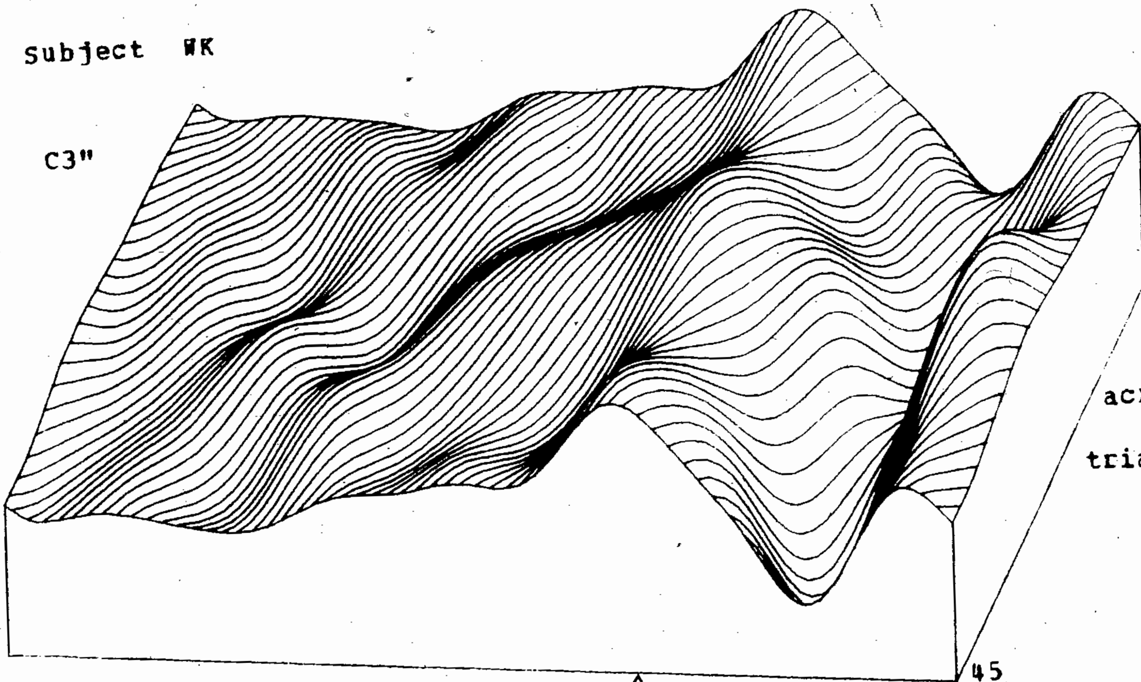

Cz
1
across
trials
45
within trial
R

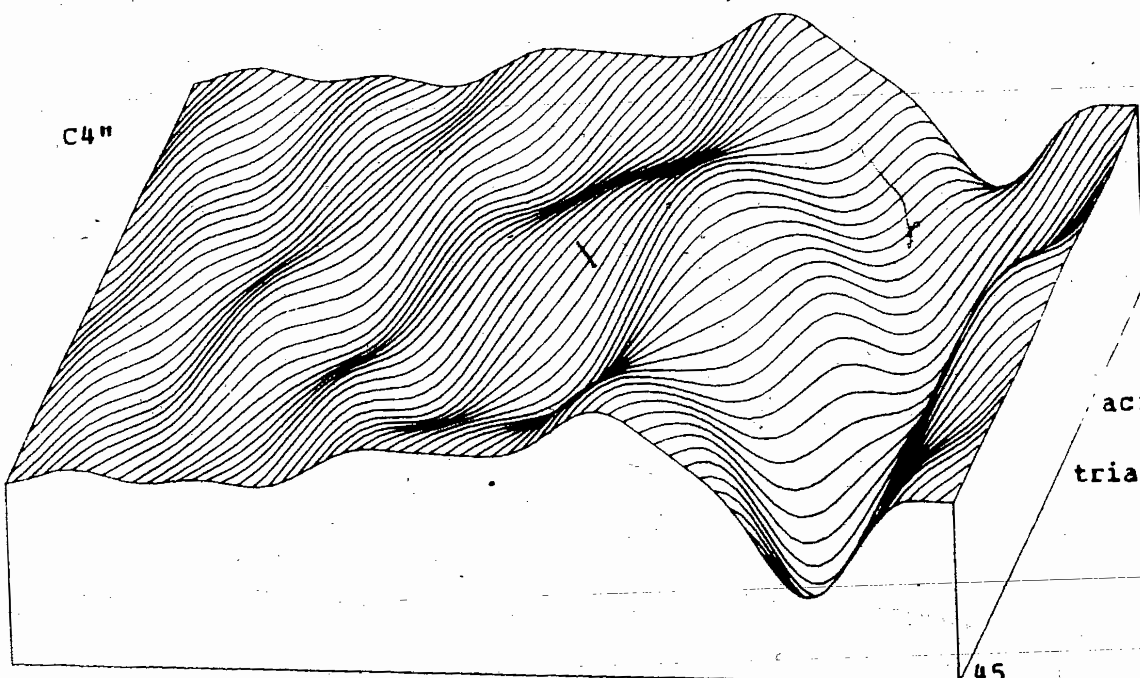
Subject RY


C3"
1
across
trials
45
within trial
R

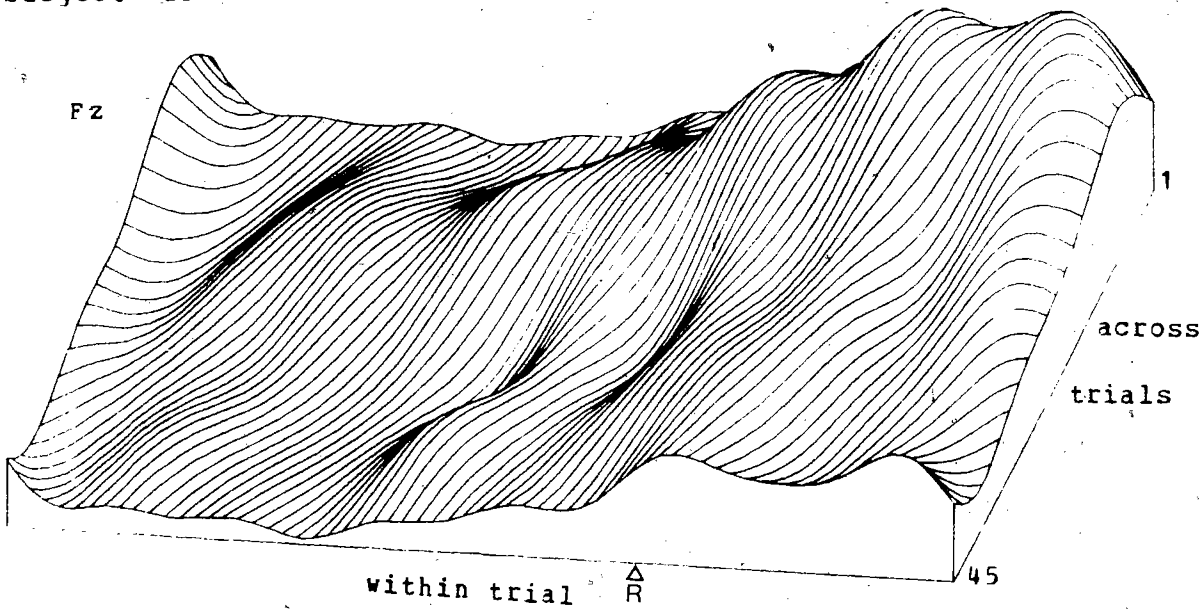

C4"
1
across
trials
45
within trial
R

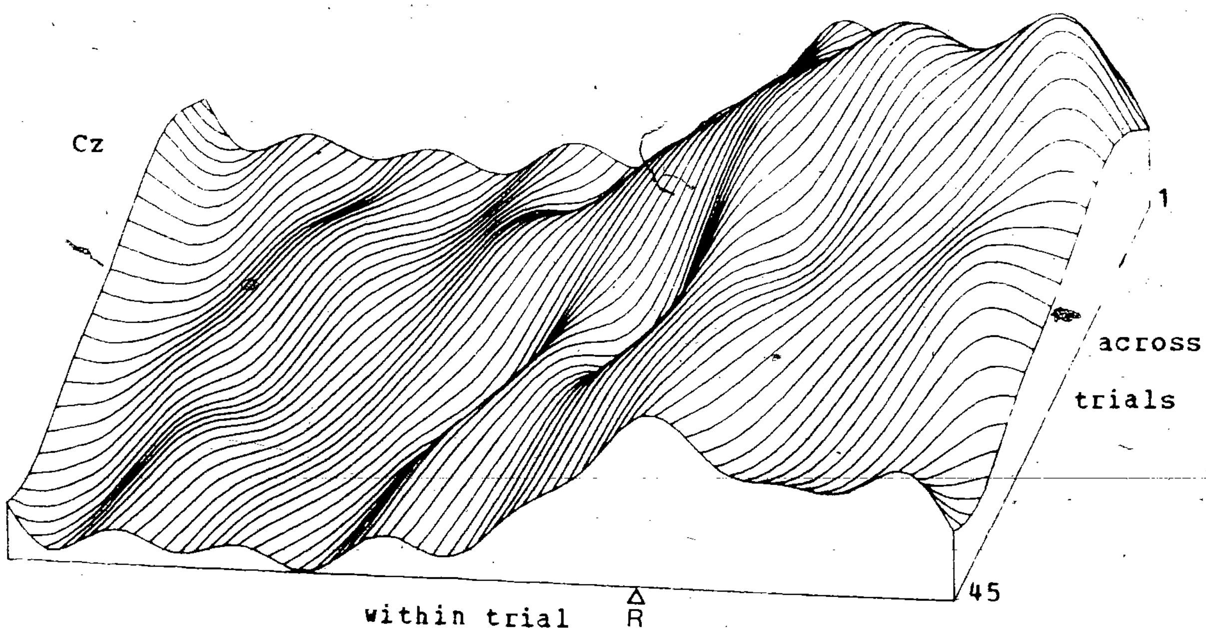

Subject WK
Fz
1
across
trials
45
within trial
R
Cz
1
across
trials
45
within trial
R


Subject WK
C3"
1
across
trials
45
within trial
R

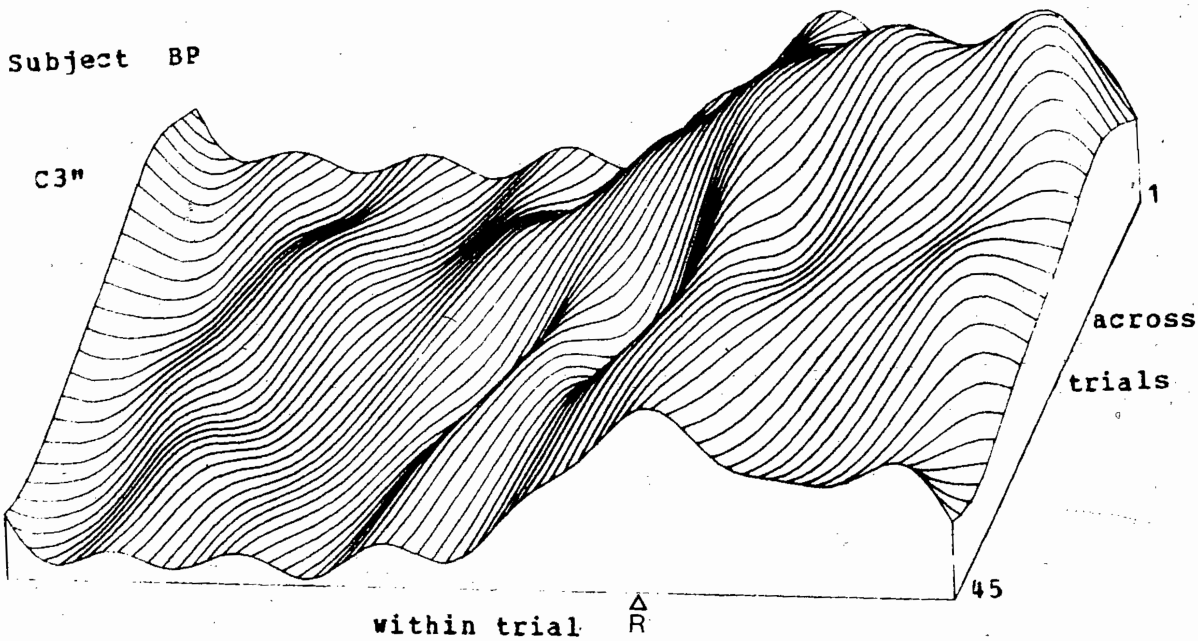

C4"
1
across
trials
45
within trial
R

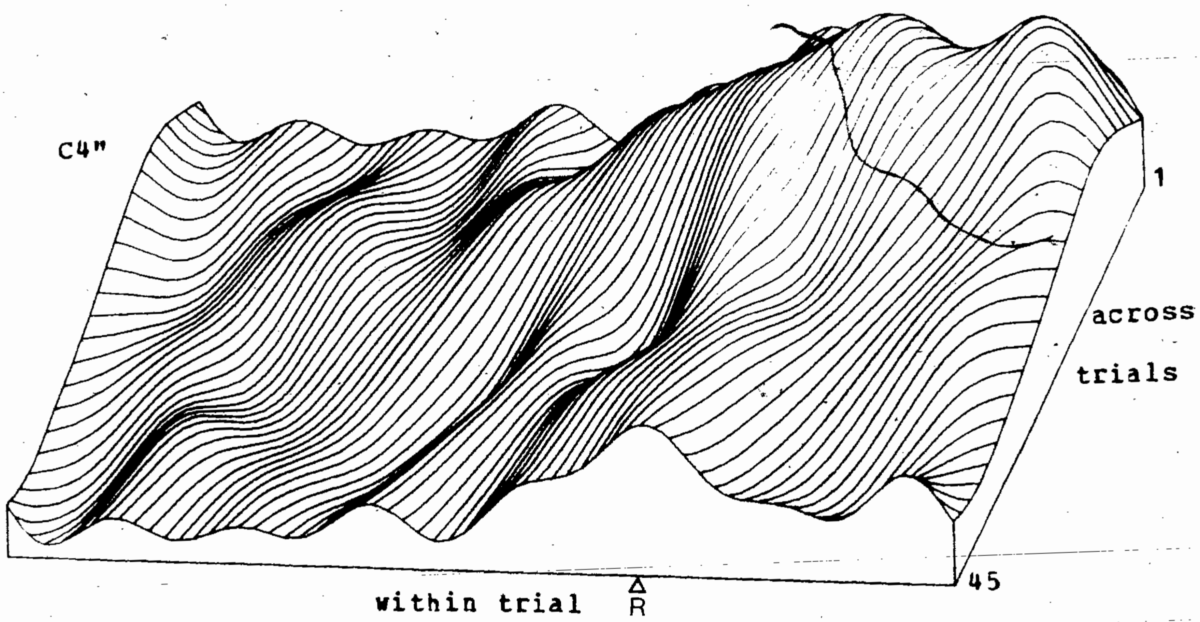
Subject BP


Fz
1
across
trials
45
within trial
R


Cz
1
across
trials
45
within trial
R

Subject BP


C3"
1
across
trials
45
within trial
R


C4"
1
across
trials
45
within trial
R

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