Electroencephalography and clinical Neurophysiology, 83 (1992) 236–247

EEG 91011

Anterior brain electrical asymmetries in response to reward and punishment *

Stanislaw S. Sobotka, Richard J. Davidson and Joseph A. Senulis

Department of Psychology, University of Wisconsin-Madison, Madison, WI 53706 (U.S.A.)

(Accepted for publication: 2 April 1992)

Summary A variety of recent research indicates that when subjects are induced to experience certain negative emotions, there is greater suppression of alpha power in the right than left frontal region, while during the experience of positive emotion, alpha power asymmetry in this region shows the opposite pattern. We have conceptualized this asymmetry as reflecting specialization for approach and withdrawal processes in the left and right frontal regions, respectively. In this experiment, reward and punishment contingencies were directly manipulated to produce approach and withdrawal emotional states. In addition, subjects responded to imperative stimuli using either an approach response (finger press) or a withdrawal response (finger lift). EEG was recorded from multiple scalp locations. During the foreperiod prior to the response to the imperative stimuli, the EEG was extracted, Fourier-transformed and power computed in the theta, alpha and beta frequency bands. In addition, the contingent negative variation (CNV) was derived from the identical epoch. Reward trials were associated with greater left frontal alpha power suppression than punishment trials, while during the latter trials, there was greater right-sided frontal alpha power suppression than during reward trials.

There was also some evidence to indicate that withdrawal responses were associated with greater right-sided alpha power suppression in the temporo-parietal region compared with approach responses. Power in the theta and beta bands did not systematically vary with condition. The CNV was larger during trials on which subjects responded quickly compared with slow trials, but did not differentiate between reward and punishment contingencies. The findings support the hypothesis that approach-related processes can be differentiated from withdrawal-related processes on the basis of asymmetrical shifts in alpha power in the frontal region. They also indicate that the CNV and spectral power estimates from the identical epochs reflect different neural processes.

Key words: Brain electrical asymmetries; Negative emotion; Positive emotion; Contingent negative variation

Approach and withdrawal behavior represent fundamental behavioral reactions that are observed at many levels of phylogeny (e.g., Schneirla 1959). Recently, Davidson and his colleagues have conceptualized emotion-related cerebral asymmetries as components of a lateralized approach and withdrawal system. Specifically, positive affect which is approach-related has been found to be accompanied by increased left-sided anterior frontal activation, while negative affect which is withdrawal-related is accompanied by increased right-sided frontal activation (Davidson et al. 1990b; see Davidson and Tomarken 1989 for review). A growing body of evidence using a number of diverse measures converges on a similar conclusion (see Leventhal and Tomarken 1986; Silberman and Weingartner 1986, for reviews).

Previous research on the effects of phasically aroused emotion on measures of hemispheric activation have relied upon standardized mood induction procedures (e.g., Tucker et al. 1981) or the presentation of emotionally evocative visual stimuli (e.g., Davidson et al. 1990b) to arouse emotion in the laboratory. Unfortunately, the emotion generated by the use of such procedures may be only loosely related to the activation of approach and withdrawal behavior. Moreover, the stimuli used in such procedures are typically relatively long (i.e., on the order of minutes) and are likely to produce considerable variability in subject responses. If the electrophysiological measures are integrated across the entire time period during which the stimulus is presented, such indices are likely to reflect periods during which the target emotion is present, as well as periods during which other irrelevant emotions are occurring and periods during which no emotion is present. Although methods exist to circumvent many of these problems (see Davidson et al. 1990b), formidable obstacles remain in the study of regional electrophysio-

Correspondence to: Prof. Richard J. Davidson, Ph.D., Department of Psychology, University of Wisconsin, 1202 West Johnson Street, Madison, WI 53706 (U.S.A.).

* This research was supported by NIMH Grants MH40747 and MH43454 and by an NIMH Research Scientist Development Award (MH00875) to Richard J. Davidson. S. Sobotka was supported by a Fulbright-Hays Award. S. Sobotka is now in the Department of Physiology, University of Rochester School of Medicine.

logical changes associated with approach and withdrawal-related emotion.

Reward and punishment contingencies have more consistently been linked to approach and withdrawal tendencies than standardized laboratory emotion elicitors. Specifically, organisms are likely to approach cues that are followed by reward and to withdraw from cues that are followed by punishment. Accordingly, in this experiment, we specifically manipulated reward and punishment contingencies and examined changes in brain electrical activity immediately following the presentation of the cues which signaled reward and punishment. Because of the nature of the task which the subjects performed, we were able to achieve a tighter time-locking between stimulus events and measures of brain electrical activity than in most other studies of EEG changes associated with emotion.

This experiment also included a simple, frank manipulation of the required motor response. In one condition, an approach response was required — subjects had to approach and press a key. In the other condition, subjects began each trial with their finger already depressing the response key. Upon seeing the imperative stimulus, subjects were required to withdraw their finger from the key. This manipulation was included to determine if approach or withdrawal motor behavior by itself would be associated with different patterns of anterior brain asymmetry. In addition, we wished to determine if the reward and punishment contingencies would interact with the motor response type. In particular, is the combination of reward trials and approach responses associated with the most pronounced left frontal activation and punishment trials and withdrawal responses associated with the most pronounced right frontal activation?

These questions were tested in an experiment in which the major dependent measure was changes in power in the alpha band extracted by Fourier transform from short segments of ongoing EEG. The method is based upon an extensive series of studies done by Davidson and his colleagues which have used the same methods in a number of different paradigms (Davidson 1988, 1992; Davidson and Tomarken 1989). Using the EEG in this way, decreases in power in the alpha band are thought to be indicative of increases in activation (e.g., Shagass 1972). Recently, Davidson et al. (1990a) have reported that decreases in power in all frequency bands are associated with activation. However, greater task-dependent variation is present in the alpha band and changes in this band consistently show the most robust differentiation among tasks in the waking state. In the present study, in addition to examining changes in alpha power, we also examined task-related changes in theta and beta power. Regional brain activity was analyzed in the 4 sec period between the presentation of a stimulus which denoted whether the trial was a potential reward or punishment trial and the presentation of an imperative stimulus to which the subjects were required to respond. We predicted that punishment trials would be associated with greater right-sided frontal activation compared with reward trials. We also examined whether the manipulation of movement type (i.e., approach versus withdrawal) systematically influenced the asymmetry of brain activity just prior to response execution. In addition to examining the effects of our experimental variables on EEG power in different frequency bands, we also examined the contingent negative variation between the warning and imperative stimuli. In this way, we could directly compare the effects of our experimental manipulations on these two classes of dependent measures.

Methods

Subjects

Fifteen college students (7 males and 8 females) ranging in age between 18 and 25 years served as subjects. They received extra credit points for their participation. As will be explained below, subjects also had the opportunity to win money over the course of the experiment. Only right-handed individuals were included. Handedness was assessed with the Edinburgh Handedness Inventory (Oldfield 1971). Subjects were required to use their right hand on a minimum of 11 of 13 items. In addition, all subjects were required to have normal visual acuity (with correction, if needed).

Procedure

The subject was comfortably seated in an acoustically shielded room. The subject was seated 75 cm in front of a 14 in. computer monitor. Subjects were presented with a multiple trial task which involved both reward and punishment contingencies. All trials consisted of the same basic structure (see Fig. 1). All stimuli were presented against a black background. Each trial began with the presentation of a red fixation point (0.15°) in the center of the screen. After a random time interval that varied between 2 and 4 sec, an arrow (3° wide × 5° high) was presented for 1 sec. On approximately half of the trials, the arrow was presented in the up position and on the remainder of the trials the arrow was presented in the down position. The order in which these trial types occurred was randomly determined, separately for each subject. Four seconds following the presentation of the arrow stimulus (during which time the fixation point re-appeared), a square (2° × 2°) was presented in the center of the screen for 1 sec. This was the imperative stimulus to which subjects were required to respond (see below). Two seconds following the offset of the square, a feedback stimulus (3° × 5°) was presented for 1 sec

which provided subjects with information about their performance on that trial. An inter-trial interval (ITI) of 2 sec then occurred, after which the fixation point was illuminated for the next trial. Throughout the trial sequence, the fixation point was illuminated during all times when another stimulus was not present, except during the 2 sec ITI. Other than the fixation point, all other stimuli were white.

There were two types of trial: "reward" trials during which the arrow was in the up position and "punishment" trials during which the arrow was in the down position. The direction of the arrow denoted whether the subject could potentially win or lose money on that trial. The outcome on each trial was based upon the subjects' reaction time to the imperative stimulus. There were two possible outcomes on each trial. For reward trials, subjects could either win money or have no change in their earnings. For punishment trials, subjects could either lose money or have no change in their earnings. The amount of money which was won or lost on each trial was always \$0.25.

Each subject took part in two identical experimental sessions, each lasting about 1.5 h. Subjects were told that they would receive \$5 at the beginning of each session which represented their starting sum of money in the game they were about to play. Subjects were instructed that they could win additional money as well as lose money from the \$5 starting amount. They were also told that the amount of money they ended up with during the game would be theirs to keep.

During one-half of the session, subjects were instructed to make a button press response (i.e., approach) to the imperative stimulus. During another half, subjects were instructed to make a button lift response (i.e., withdrawal) to the imperative stimulus. Order of approach and withdrawal trial blocks was counterbalanced across the two sessions. Half the subjects began with approach trials and half with withdrawal trials. For trials on which approach responses were required, subjects had the index finger of their right hand lightly touching the response button and upon seeing the imperative stimulus, they were required to press the button as fast as possible. For trials on which withdrawal responses were required, subjects began the trial with the button depressed (with the same finger) and upon seeing the imperative stimulus, they were required to lift their finger from the button as fast as possible. Each half of the session began with a block of 10 practice trials during which the subject did not play for money. Following the practice trial block, there were 5 blocks of 20 trials each. Between blocks there was a 3 min break. In the middle of the session there was about a 10 min break. Thus, there were 100 trials per movement condition (approach/withdrawal) during each session. The entire experiment therefore consisted of a total of 400 trials, half of which were reward and the other half punishment. Of the 200 reward and punishment trials, half of each required an approach response and the remainder required a withdrawal response.

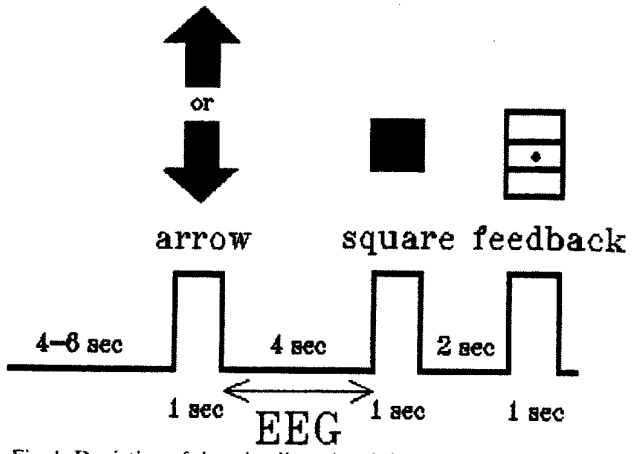

Fig. 1. Depiction of the stimuli used and the timing sequence of each trial.

An IBM PS/2-60 computer acquired reaction time data. The computer calculated median reaction time for each trial block. For subjects to win money in the reward trials, they were required to have a reaction time which was faster than the median reaction time from the previous block. On the basis of pilot data from this task, we used a starting reaction time of 220 msec as the criterion for the practice trials. The criterion for the first block of real trials was calculated from the practice trial data. Subjects were not told that the criterion reaction time values for a given block were determined on the basis of their performance during the prior block. Mean earnings per session was \$8.45.

The basic structure of the feedback stimulus is illustrated in Fig. 1. The stimulus consisted of a 3-box ladder with a dot contained within 1 of the 3 boxes. On reward trials, the dot could appear in either the top or middle positions. A dot in the top position denoted that the subject responded faster than the criterion for that block and therefore \$0.25 was earned. A dot in the middle position denoted that the subject was slower than the criterion and therefore no money was earned. On punishment trials, the dot could appear in either the middle or bottom positions. A dot in the bottom position denoted that the subject responded slower than the criterion for that block and therefore \$0.25 was taken away. A dot in the middle position denoted that the subject was faster than the criterion and therefore avoided any loss of money. Subjects were given the amount of money they earned in each session after that session. At the beginning of the study subjects' were acquainted with the task by the experimenter and then once more by instructions presented

on the computer monitor. The subject was asked to fixate his/her eyes on the fixation point and not blink during the trials.

At two different times during each session, subjects were asked to rate different aspects of their emotional state. They were asked to make these ratings after the first 5 trial blocks (at the midpoint of the session) and then again at the end. They rated the following 4 questions on 1–9 point intensity scales, with 1 denoting that they did not experience the emotion at all and 9 indicating that the emotion was experienced extremely intensely:

(1) How happy were you when you saw the arrow turned up?

(2) How sad, distressed or angry were you when you saw the arrow turned down?

(3) How happy were you when your reaction was fast enough and you gained money?

(4) How sad, distressed or angry were you when your reaction was too slow and you lost money?

EEG recording and data reduction

EEG activity was recorded from 14 standard sites: F3, F4, F7, F8, T3, T4, C3, C4, O1, O2, Pz, Cz according to the 10/20 system and from the following non-standard locations: TP3, TP4 located in the middle of the distance between points T3-P3 and T4-P4. All sites were referred to linked A1-A2 [1] (see Senulis and Davidson 1989). EEG was recorded with a lycra cap (Electro-Cap, Inc.). All impedances were below 5 kΩ, and the impedances of homologous electrodes were within 1 kΩ. EOG was recorded from the external canthus to the supra-orbit of one eye. The side on which EOG was recorded was varied between sessions, with half the subjects starting with electrodes on the left side and half with the opposite configuration. This procedure was followed to eliminate any systematic differences in attentional bias produced by asymmetrical electrode location across subjects.

All signals were amplified with a Grass Model 12 Neurodata system, with high and low pass filters set to 0.01 Hz and 100 Hz, respectively. An additional 24 dB/octave low pass filter (Rockland Model 432) set to 55 Hz was used to prevent aliasing. The output of the amplifiers was digitized at a frequency of 200 samples/sec by a Nicolet Pathfinder and stored on digital magnetic tape for off-line analysis. Triggers corresponding to the different events within the trial sequence were stored along with the data. These triggers were generated from the video input signal to the monitor to insure their accuracy.

The period during which EEG was examined was between the end of the arrow stimulus which denoted the trial type and the imperative stimulus (period length = 4 sec) in response to which subjects made a button press (see Fig. 1). The EEG data were visually examined off-line by an experimenter who was blind to the condition from which the data were obtained and only those 4 sec periods during which no eye movement or blink artifact were present were accepted for further analysis. Approximately 10% of the trials were rejected because of artifact. These trials were rejected prior to any EEG analysis. The EEG activity from each trial was transformed to the frequency domain by Fast Fourier analysis and log power density (in $\mu V^2/Hz$) was calculated in alpha (8–13 Hz), beta (13–25 Hz) and theta (4–8 Hz) bands. Our hypotheses were based upon changes in the alpha band only since our previous findings have consistently demonstrated more reliable task-related effects in this band compared with other bands (e.g., Davidson et al. 1990a,b). In these studies, alpha power is interpreted to be inversely related to activation (see also Shagass 1972). We decided not to examine EEG activity in delta band (1–4 Hz) because of the likely presence of artifact in this band.

In addition to examining the EEG in the frequency domain, the CNV was also assessed. CNV amplitude was determined by measuring a baseline voltage during the 250 msec period before the presentation of the arrow stimulus and subtracting this voltage from the averaged value of the last 250 msec of the 4 sec foreperiod interval prior to the presentation of the imperative stimulus. The effects of the experimental variables on CNV were examined using the same analytic strategy as was used for the EEG.

The visual stimuli were presented on an IBM 8513 monitor and controlled by Micro Experimental Laboratory (MEL; Schneider 1988) software. The computer (IBM PS/2-60) which presented the stimuli also acquired subjects' reaction time and controlled the Nicolet Pathfinder during data acquisition.

Results

Behavioral and self-report data

A 2 × 2 × 2 ANOVA was performed on the reaction time data with movement type (approach/withdrawal), valence (arrow up/arrow down) and outcome (win/lose) as factors. It should be noted that on the up

[1] Although Nunez (1981) has suggested that linking the ears may attenuate the magnitude of brain electrical asymmetries, recent findings from 3 independent studies have not found any support for this claim (Senulis and Davidson 1989; Andino et al. 1990; Miller et al. 1991). Even if linking the ears does slightly attenuate the magnitude of observed asymmetry, this would work against us finding significant shifts in asymmetry within subjects between reward and punishment conditions. Recent studies from our laboratory that have directly compared several different referencing montages within the same subjects in response to standardized tasks have found consistency across references (e.g., Davidson et al. 1990a; Henriques and Davidson 1990).

arrow trials, if the subject responded sufficiently quickly, s/he actually won money; however, on the punishment trials when the subject responded sufficiently quickly, s/he avoided the loss of money. We refer to both of these trial outcomes as "win" for this analysis. This ANOVA was first run with Sex also included as a factor. Since no main effect of sex or interactions with sex were found, the data from both sexes were combined. The results of the ANOVA revealed, as expected, a highly significant effect for outcome (F (1, 14) = 127.0, $P < 0.0001$). Importantly, there were no significant differences in reaction time between the positive and negative valence trials (arrow up vs. arrow down). No additional main effects or interactions were present in these data. The reaction time data for each condition, split by win vs. lose are presented in Fig. 2.

There were 4 questions asked about subjects' emotional reactions to different components of the task. These 4 questions were completed twice per session. The responses across all 4 administrations of the questions (twice per session, for two sessions) were averaged for each subject. The first and second questions asked about positive and negative affect experienced in response to the arrow stimuli which denoted whether the trial was a potential reward or punishment trial. The third and fourth questions asked about positive and negative emotion respectively, experienced in response to feedback denoting a win (in response to arrow up trials) vs. feedback denoting a loss (in response to arrow down trials). A 2 × 2 ANOVA was performed on the questionnaire responses with trial component (arrow stimulus/feedback stimulus) and valence (positive/negative) as factors. This ANOVA revealed a highly significant main effect for trial component (F (1, 14) = 30.36, $P < 0.0001$). This effect is a function of slightly, but consistently more intense emotion reported in response to the feedback stimuli compared with the arrow stimuli. No significant main effect was obtained for valence, nor was the interaction significant. The lack of a significant main effect for valence is important since it indicates that the intensity of positive affect in response to arrow up trials and to winning was comparable to the intensity of negative affect reported in response to arrow down trials and losing. The means for the questionnaire data are presented in Fig. 3.

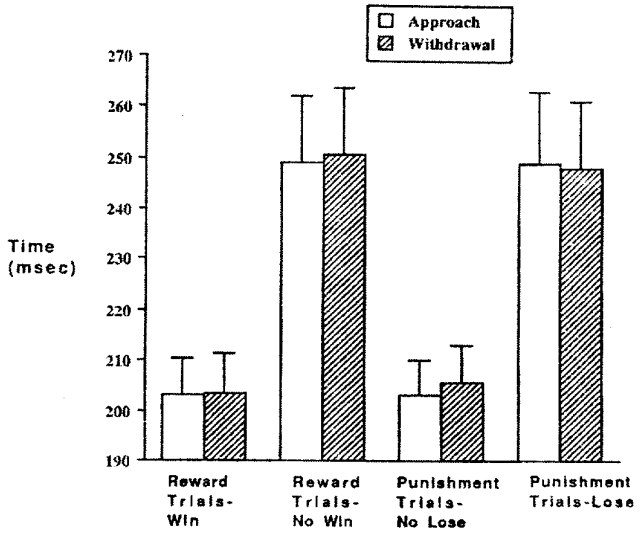

Fig. 2. Mean reaction time, by trial type. Error bars represent standard errors of the mean. Approach and withdrawal refer to movement type – approach movements were finger presses and withdrawal movements were finger lifts.

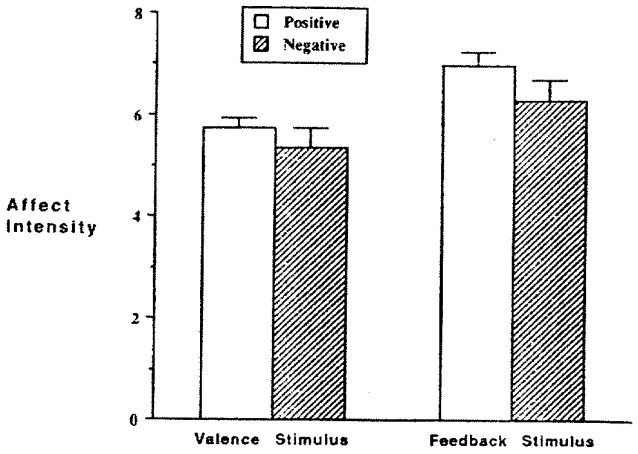

Fig. 3. Mean ratings of self-reported positive and negative affect in response to the valence stimulus (arrow up or down) and the feedback stimulus. Error bars represent standard errors of the mean.

EEG data

An example of the grand mean (across subjects) power spectrum in one experimental condition is presented in Fig. 4. As can be seen, for most electrode sites, the majority of the power was in the alpha band.

The basic structure of these analyses consisted of ANOVAs with movement type (approach/withdrawal), valence (arrow up/arrow down), outcome (win/lose), and hemisphere (left/right) as factors. Sex was not included as a factor since preliminary analyses revealed no main effects or interactions with this factor. Separate ANOVAs with these factors were performed on the EEG data from each of the 6 regions (F3-F4, F7-F8, C3-C4, T3-T4, TP3-TP4 and O1-O2).

Alpha power data

The statistically significant results from the ANOVAs on alpha power are presented in Table I. Of most relevance for the principal hypotheses of this study were the valence × hemisphere interactions. We predicted significant valence × hemisphere interactions for the frontal leads. As can be seen from Table I, this interaction was significant for both F3/4 and F7/8,

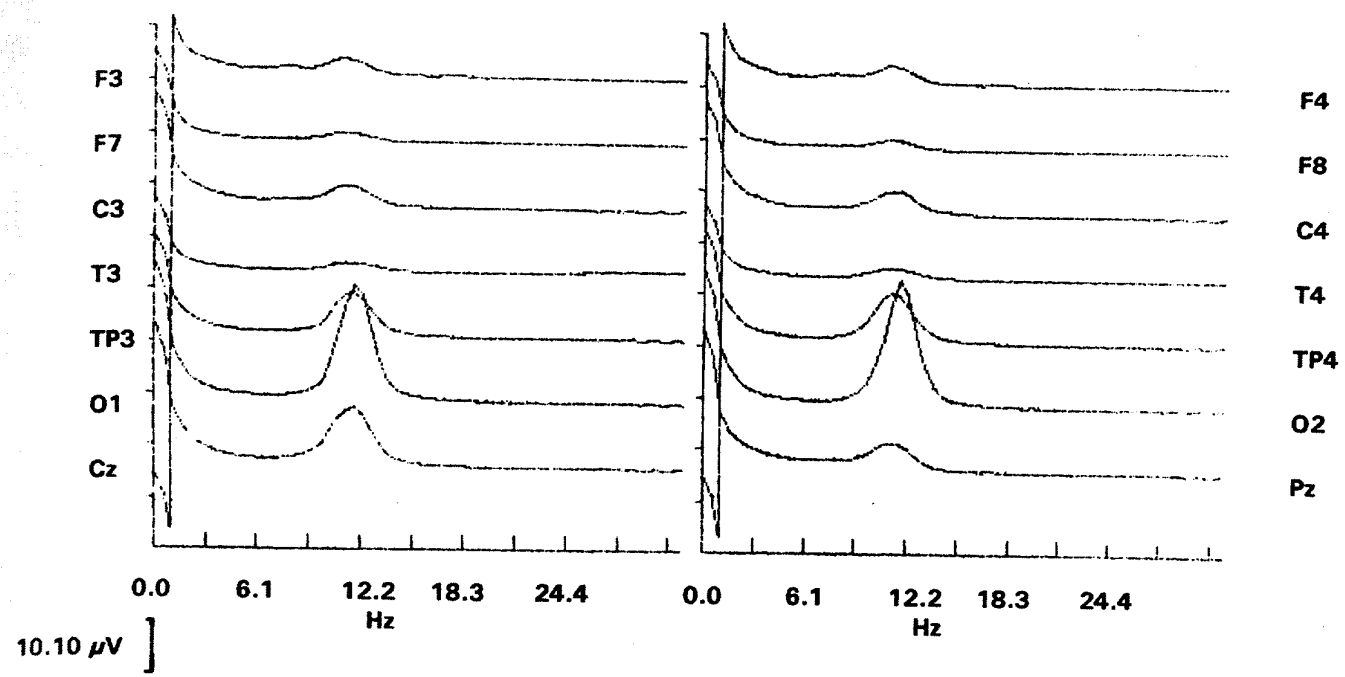

Fig. 4. Average spectra (across subjects), by channel, from one condition of the experiment. The condition displayed here is positive (arrow up) during trials on which subjects won when they used a button press (approach response). The basic form of the spectra for other conditions was very similar. The abscissa is calibrated in units of 3.05 Hz per division. The ordinate is calibrated in units of 10.10 μV^2 per division.

but was not significant for any of the other regions. These interactions are depicted in Figs. 5 and 6. As can be seen from these figures, the arrow up condition is associated with more left-sided frontal activation (i.e., less alpha power) compared with the arrow down condition, while the latter condition is associated with more right-sided frontal activation compared with the former condition. Importantly, the valence × hemisphere interaction is not significant elsewhere on the scalp, indicating considerable specificity for the difference in asymmetry between positive and negative valence conditions. The topographic difference in alpha power between the positive and negative valence conditions is illustrated in Fig. 7.

As Table I also indicates, there was a main effect for hemisphere for the mid-frontal leads, with the left hemisphere showing less alpha power compared with the right. A similar main effect was obtained for the central and temporo-parietal leads.

Table I reveals several additional noteworthy effects. We predicted that, across all other conditions, approach movements would be associated with greater left-sided anterior activation compared with withdrawal movements. While this prediction was not con-

TABLE I

ANOVA F and P values for analyses of alpha power, by region.

	df	F3-F4	F7-F8	C3-C4	T3-T4	TP3-TP4	O1-O2
Hemisphere	1, 14	7.92 0.001	2.52	9.52 0.001	4.21	23.3 0.001	2.12
Valence × Hemisphere	1, 14	5.48 0.03	4.95 0.04	2.02	0.34	1.10	0.07
Movement × Hemisphere	1, 14	2.21	4.44	0.52	0.15	5.75 0.03	0.18
Outcome	1, 14	0.55	0.39	1.21	1.58	4.35	5.48 0.03

Note: the ANOVAs reported include Movement, Valence, Outcome and Hemisphere as repeated measures factors. Table includes all effects that reached significance. P values are included below all significant F values. If an effect was significant for one region, the F values for all regions are presented.

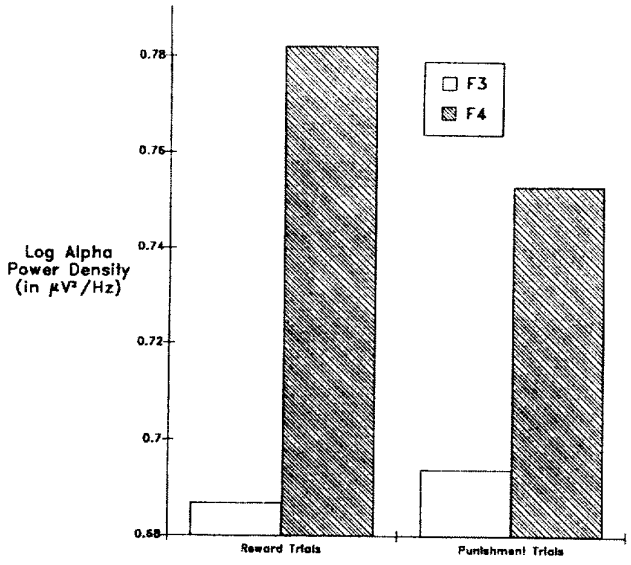

Fig. 5. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the left and right mid-frontal regions (F3 and F4) in response to reward and punishment trials.

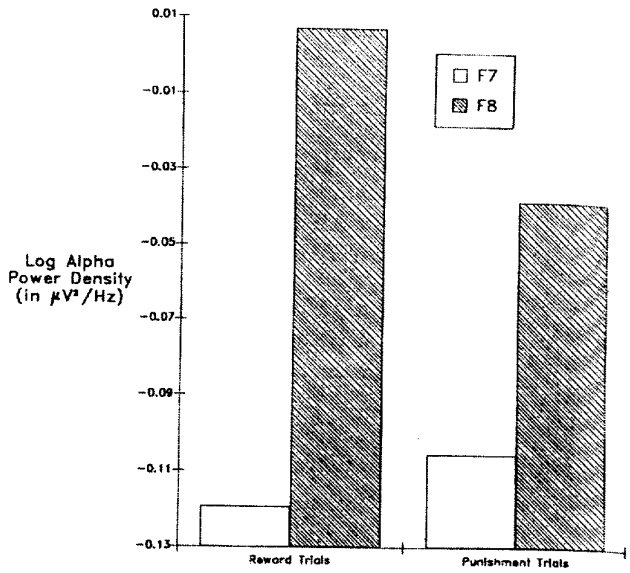

Fig. 6. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the left and right lateral frontal regions (F7 and F8) in response to reward and punishment trials.

firmed for the frontal regions, we did find a significant movement × hemisphere interaction in the temporo-parietal region. As Fig. 8 reveals, approach movements were associated with more left-sided activation (i.e., less alpha power) compared with withdrawal movements, while the opposite pattern was obtained for the right hemisphere.

One final effect presented in Table I is the main effect for outcome in the occipital leads. Outcome refers to win vs. lose which is by definition associated with fast vs. slow trials respectively. As predicted, fast trials are associated with less alpha power compared with slow trials. While this effect was present throughout the posterior scalp region, it was significant only for the occipital leads (see Fig. 9).

Correlations between alpha power asymmetry and self-report of emotion

We hypothesized that anterior activation asymmetry during the task would predict the reports subjects offered about their emotional experiences to the feedback stimuli. Specifically, we predicted that the greater the left frontal activation during the task, the more intense would be the positive affect subjects reported in response to the feedback stimulus which denoted winning and, conversely, the greater the right frontal activation during the task, the more intense would be the negative affect reported in response to the feedback stimulus which denoted losing. For these analyses, we used only data from the positive valence trials during which subjects won, and the negative valence trials during which subjects lost. The EEG measure was a metric of asymmetry which we have used extensively in our previous research (log right-log left alpha power) (Davidson 1988). Higher numbers on this metric denote greater relative left-sided activation. One aspect of these predictions was confirmed. The greater the left-sided frontal activation during the task, the more intense was the positive affect reported in response to the feedback stimulus which denoted winning (midfronal: $r = 0.68$, $P < 0.006$; lateral frontal: $r = 0.36$, $P =$ n.s.). Contrary to prediction, we found no significant relation between frontal asymmetry and negative affect for the lose trials.

TABLE II

ANOVA F and P values for theta and beta power, by region (see note for Table I).

	df	F3-F4	F7-F8	C3-C4	T3-T4	TP3-TP4	O1-O2
Theta power							
Hemisphere	1, 14	11.34 0.005	2.17	2.04	0.17	5.78 0.03	1.03
Beta power							
Hemisphere	1, 14	7.93 0.02	0.74	15.73 0.001	0.94	0.99	0.59

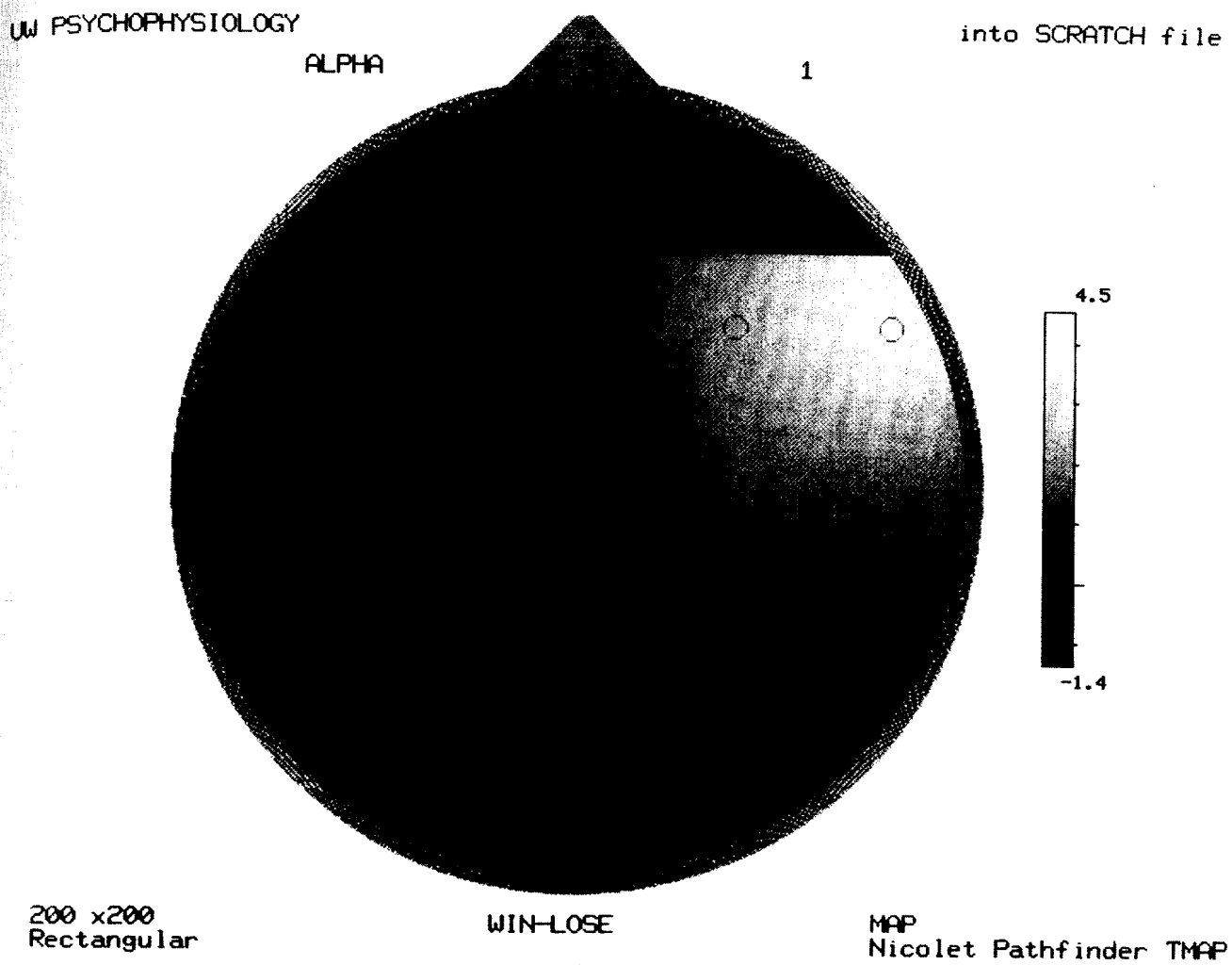

Fig. 7. Topographic map of the mean difference in alpha power between the reward and punishment trials (reward-punishment). The frontal pole region is blocked out since we did not have electrodes in this region. The white-yellow end of the scale indicates greater alpha power during the reward than punishment condition. No difference between conditions is represented at the point in the color scale where the red turns into blue (see calibration bar). As can be seen from this map, the primary difference between conditions is in the right frontal region, with the punishment trials associated with more activation (i.e., less alpha power) compared with the reward trials.

Analyses of power in the theta and beta bands

We conducted ANOVAs on power in the theta and beta bands for exploratory purposes. We were specifically interested in determining whether there were any significant valence × hemisphere or movement × hemisphere interactions in any region for theta and beta power. In light of our considerable previous evidence which indicated robust valence × hemisphere interactions in the alpha band *only*, we did not expect significant interactions for these bands in the current study. In neither band was the valence × hemisphere or movement × hemisphere interaction significant for any region. However, there were several significant main effects for hemisphere which paralleled the hemisphere main effects in the alpha band. As Table II indicates, in the theta band there were significant main effects for hemisphere in the mid-frontal and temporo-parietal regions. As we found for alpha power, the right hemisphere was associated with greater power compared with the left. In the beta band, hemisphere main effects were obtained for the mid-frontal and central leads. Again, the direction of the difference was the same as we found for alpha power: less power in the left than the right hemisphere. The fact that the direction of the hemisphere main effect was the same across band is consistent with our previous findings (Davidson et al. 1990a).

CNV data

Fig. 10 presents the average wave forms for one condition across all subjects for each electrode site. The CNV can be readily seen, particularly in the central leads. The structure of the analyses of CNV amplitude was identical to those performed for the

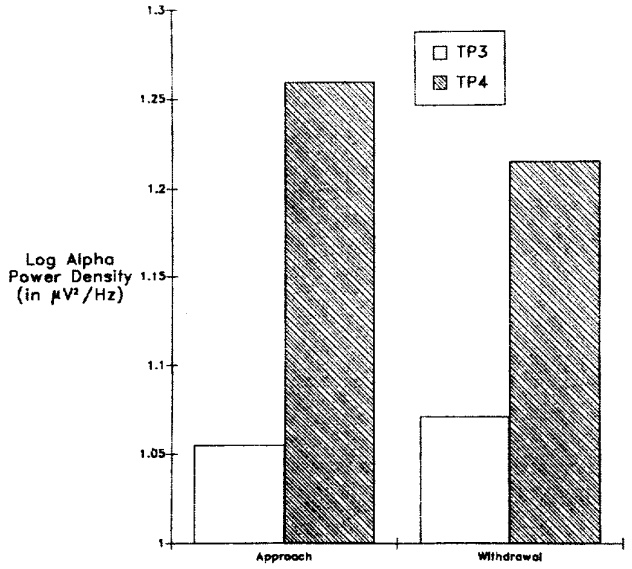

Fig. 8. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the left and right temporo-parietal regions (TP3 and TP4) during trials accompanied by approach and withdrawal responses.

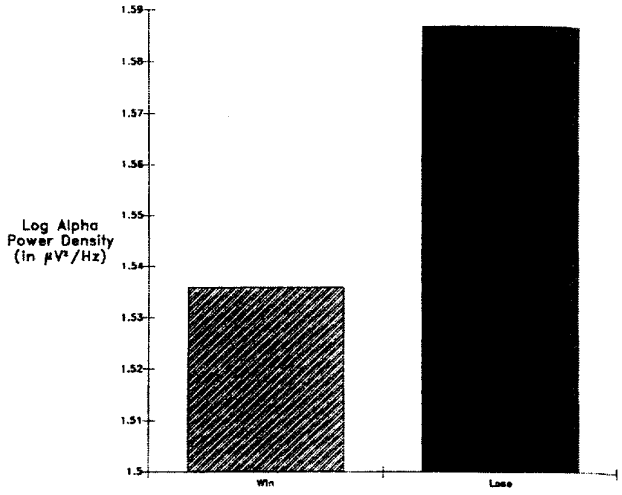

Fig. 9. Mean log-transformed alpha power (in $\mu V^2/Hz$) for the occipital region (average of O1 and O2) during trials on which the subjects' reaction time was fast and they won (during reward trials) or avoided loss (during punishment trials) and during trials on which the subjects' reaction time was slow and they did not win (during reward trials) or lost (during punishment trials).

EEG. Unlike our findings for EEG power, there were no significant valence × hemisphere interactions for any region. The only consistent effects were main effects for hemisphere and outcome. In all regions except the occipital, significant main effects for hemisphere were obtained (mid-frontal: F (1, 14) = 22.76, $P < 0.001$; lateral frontal: F (1, 14) = 19.37, $P < 0.001$; central: F (1, 14) = 8.34, $P = 0.01$; temporal: F (1, 14) = 22.08, $P < 0.001$; temporo-parietal: F (1, 14) = 5.72, $P = 0.03$). The direction of this main effect was such that the CNV amplitude was higher in the left compared with the right hemisphere (see Fig. 11).

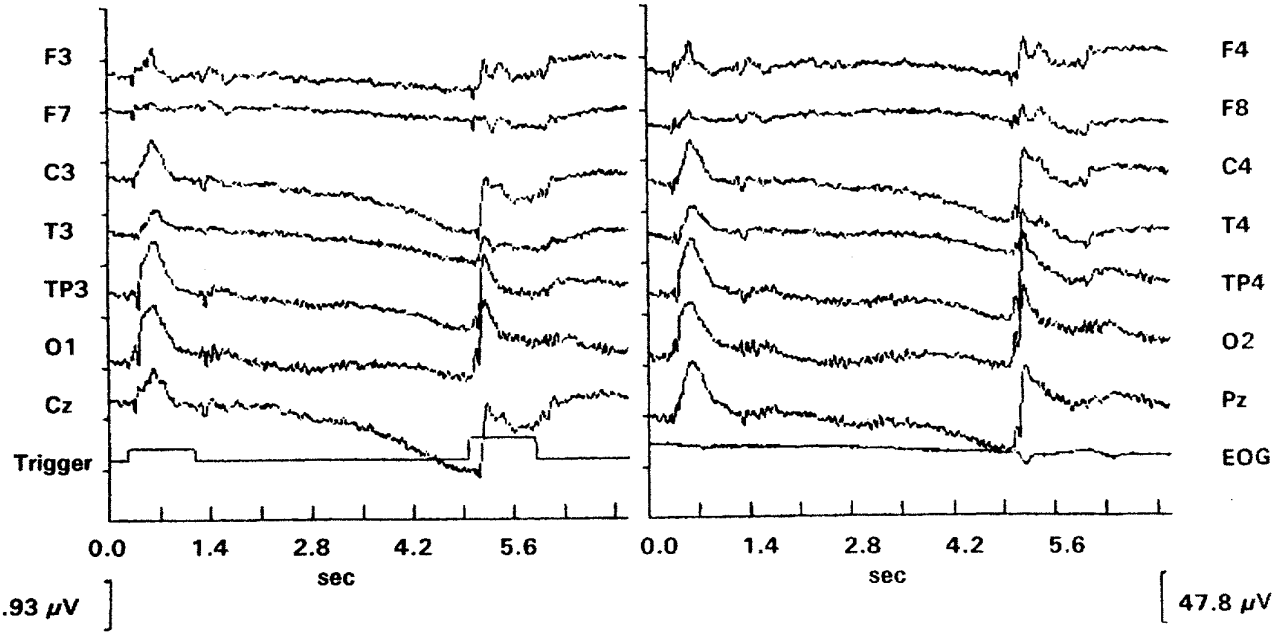

Fig. 10. Average wave forms (across subjects), by channel, from one condition of the experiment. The condition displayed here is the same condition represented in Fig. 4 (arrow up-button press-win trials). The abscissa is calibrated in units of 0.7 sec per division and the ordinate is calibrated in units of 11.93 μV per division for brain potentials and 47.75 μV per division for the EOG lead.

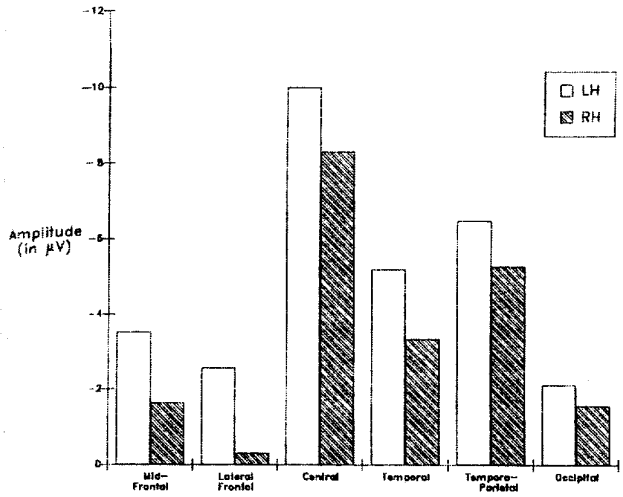

Fig. 11. Mean CNV amplitude for left and right hemisphere electrode sites, separately by region. Data are averaged across all other conditions.

The main effect for outcome was a function of win trials (during which RT was fast) showing greater CNV amplitude compared with lose trials (during which RT was slow) (all $Fs > 4.92$). This effect occurred at every scalp position (see Fig. 12).

Correlations between CNV and EEG measures

We examined correlations between measures of alpha power and CNV amplitude, for each electrode site as well as for measures of asymmetry. These correlations were computed both across condition as well as separately by condition. No significant relation at any electrode location was detected between CNV amplitude and power in the alpha band.

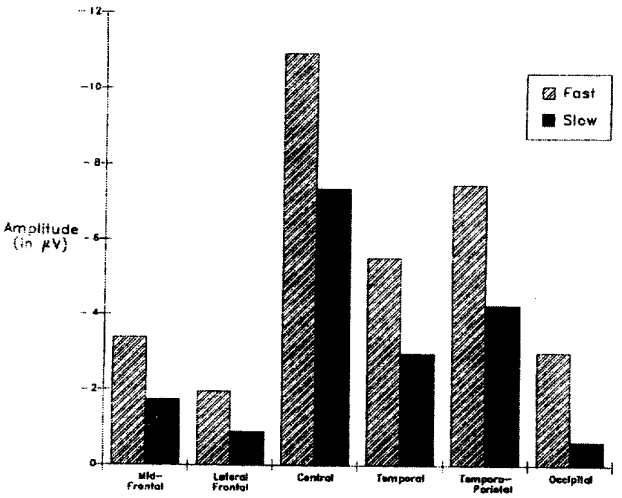

Fig. 12. Mean CNV amplitude for fast (win) and slow (lose) trials, separately by region averaged across hemisphere.

Discussion

In this experiment, we directly manipulated reward and punishment contingencies to observe their effects on the topographic patterning of alpha power. Consistent with our predictions, we found that punishment trials were associated with less alpha power in the right mid and lateral frontal regions (F4 and F8) compared with reward trials. Reward trials, on the other hand, were associated with less alpha power in the left mid and lateral frontal regions (F3 and F7) compared with punishment trials. Based upon the view of alpha power inversely reflecting activation, the data support our hypothesis of greater relative right-sided frontal activation during punishment trials compared with reward trials. These effects were highly regionally specific, since the valence × hemisphere interaction was not close to being significant elsewhere on the scalp. Our findings lend additional support to the notion that left and right frontal regions in particular are differentially specialized for approach and withdrawal behavior, respectively (for other evidence, see Davidson et al. 1990b; see Davidson and Tomarken 1989 and Davidson 1992, for reviews). This is the first study in which frank manipulations of reward and punishment contingencies were found to shift frontal asymmetry within subjects.

Localization of this asymmetry to anterior cortical zones is consistent with a large body of data using a diverse array of methods which suggest that the left frontal region is specifically implicated in certain forms of positive affect, while the right frontal region is implicated in certain forms of negative affect. Such effects have been found in unilateral brain damaged patients (e.g., Robinson et al. 1984). Depressed patients have been found to show specific decreases in left frontal glucose metabolic activity (e.g., Baxter et al. 1989) and to show accentuated alpha power specifically in the left frontal region (Henriques and Davidson 1991). This pattern of decreased activation in the left frontal region has been interpreted to reflect a pervasive deficit in depressives in the experience of positive affect.

Our self-report data suggest that our reward and punishment conditions produced comparable intensities of positive and negative affect respectively. This is important for it suggests that we successfully produced equivalent levels of positive and negative affect by our reward and punishment contingencies. The reaction time data are also consistent in revealing no differences between reward and punishment trials in overall speed of responding. Taken together, these findings indicate that the differences in brain activity we observed during the reward and punishment conditions were not produced by unintended intensity differences between these conditions.

In addition to the inclusion of the reward/punish-

ment manipulation, we also included a manipulation of movement type (i.e., approach and withdrawal motor responses). We found that approach responses are associated with a pattern of greater left-sided temporo-parietal activation compared with withdrawal responses. While we expected a more anterior distribution for this effect, the direction of the difference in asymmetry between these two forms of response is consistent with prediction. This is the first evidence of which we are aware which demonstrates that the simple manipulation of response form (i.e., approach versus withdrawal) is predicted by differences in alpha power asymmetry in the period immediately prior to the response. We did not find that response form interacted with valence in affecting asymmetry. It may be that our valence manipulation was so strong that it overrode any moderating effects of movement type. In light of the large differences in self-reported emotion between the reward and punishment trials, we suspect that this may have been the case.

Another important finding consistent with prediction was that frontal asymmetry during the 4 sec period between the warning and imperative stimuli predicted subjects' reports of positive affect in response to the imperative stimulus when they won. Frontal asymmetry (F3-F4) during this period accounted for more than 45% of the variance in subjects' reports of positive affect in response to the subsequent presentation of the imperative stimulus in this condition. We did not find any significant association between frontal asymmetry and reports of negative affect in response to the subsequent presentation of the imperative stimulus when subjects lost. It may be that our questions did not tap the negative emotions most relevant to this manipulation. In addition to including other emotions, it would also be useful in future research to include a multi-item measure of emotion or mood to improve its reliability.

As we expected from our previous findings (e.g., Davidson et al. 1990b), asymmetries in the theta and beta bands failed to differentiate between conditions. We did, however, find main effects for hemisphere in several regions across several different bands. The direction of this main effect was always less power in the left than right hemisphere. This is consistent with other findings from our laboratory which have used right-handed subjects.

Our findings on the CNV indicated that overall, left-sided amplitude was greater than right-sided amplitude and that fast responses were associated with greater CNV amplitude compared with slow responses. The fact that the CNV was larger in amplitude over the left hemisphere in most regions was likely a function of the fact that subjects were required to respond with their right hands. We did not find any valence × hemisphere interactions, nor did we find that our measures of EEG alpha power from the identical point in time were correlated with the CNV measure. This pattern of data suggests that the CNV is reflecting a different set of neural processes than is indexed by alpha power. It is also clear that in the context of the task presented in this study, measures of alpha power showed considerably more regional specificity than simultaneously obtained measures of CNV amplitude.

In conclusion, the findings from this study add further support to the hypothesis that approach-related processes are associated with greater left-sided and less right-sided anterior activation compared with withdrawal-related processes. The data also underscore both the regional and spectral selectively of this finding by establishing that the reward and punishment-related effects occur only in the frontal region and only in the alpha band.

References

Andino, F.L.G., Marqui, R.D.P., Sosa, P.A.V., Lirio, M.B., Machado, C., Diaz, G., Rodriguez, P.F. and Torrez, C.C. Brain electrical field measurements unaffected by linked earlobes reference. Electroenceph. clin. Neurophysiol., 1990, 75: 155–160.

Baxter, L.R., Schwartz, J.M., Phelps, M.E., Mazziotta, J.C., Guze, B.H., Selin, C.E., Gerner, R.H. and Sumida, R.M. Reduction of prefrontal cortex glucose metabolism common to three types of depression. Arch. Gen. Psychiat., 1989, 46: 243–250.

Davidson, R.J. EEG measures of cerebral asymmetry: conceptual and methodological issues. Int. J. Neurosci., 1988, 39: 71–89.

Davidson, R.J. Anterior cerebral asymmetry and the nature of emotion. Brain Cogn., 1992, in press.

Davidson, R.J. and Tomarken, A.J. Laterality and emotion: an electrophysiological approach. In: F. Boller and J. Grafman (Eds.), Handbook of Neuropsychology, Vol. 3. Elsevier, Amsterdam, 1989: 419–441.

Davidson, R.J., Chapman, J.P., Chapman, L.P. and Henriques, J.B. Asymmetrical brain electrical activity discriminates between psychometrically-matched verbal and spatial cognitive tasks. Psychophysiology, 1990a, 27: 528–543.

Davidson, R.J., Ekman, P., Saron, C.D., Senulis, J.A. and Friesen, W.V. Approach/withdrawal and cerebral asymmetry: emotional expression and brain physiology I. J. Pers. Soc. Psychol., 1990b, 58: 330–341.

Henriques, J.B. and Davidson, R.J. Regional brain electrical asymmetries discriminate between previously depressed and healthy control subjects. J. Abnorm. Psychol., 1990, 99: 22–31.

Henriques, J.B. and Davidson, R.J. Left frontal hypoactivation in depression. J. Abnorm. Psychol., 1991, 100: 535–545.

Leventhal, H. and Tomarken, A.J. Emotion: today's problems. In: M.R. Rosenzweig and L.Y. Porter (Eds.), Annual Review of Psychology, Vol. 37. Annual Reviews, Palo Alto, CA, 1986: 565–610.

Miller, G.A., Lutzenberger, W. and Elbert, T. The linked-reference issue in EEG and ERP recording. J. Psychophysiol., 1991, 5: 273–276.

Nunez, P.L. Electrical Fields of the Brain: The Neurophysics of EEG. Oxford University Press, New York, 1981.

Oldfield, R.C. The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia, 1971, 9: 97–113.

Robinson, R.G., Kubos, K.L., Starr, L.B., Rao, K. and Price, T.R. Mood disorders in stroke patients. Brain, 1984, 107: 81–93.

Schneider, W. Micro experimental laboratory: an integrated system for IBM PC compatibles. Behav. Res. Meth. Instrum. Comput., 1988, 20: 206–217.

Schneirla, T.C. An evolutionary and developmental theory of biphasic processes underlying approach and withdrawal. In: M.R. Jones (Ed.), Nebraska Symposium on Motivation. University of Nebraska Press, Lincoln, 1959.

Senulis, J.A. and Davidson, R.J. The effects of linking the ears on the hemispheric asymmetry of EEG. Psychophysiology, 1989, 26: S54.

Shagass, C. Electrical activity of the brain. In: N.S. Greenfield and R.A. Sternbach (Eds.), Handbook of Psychophysiology. Holt, Rinehart and Winston, New York, 1972: 263–328.

Silberman, E.K. and Weingartner, H. Hemispheric lateralization of functions related to emotion. Brain Cogn., 1986, 5: 322–353.

Tucker, D.M., Stenslie, C.E., Roth, R.S. and Shearer, S.L. Right frontal lobe activation and right hemisphere performance decrement during a depressed mood. Arch. Gen. Psychiat., 1981, 38: 169–174.