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SEX DIFFERENCES IN PATTERNS OF EEG ASYMMETRY

RICHARD J. DAVIDSON, GARY E. SCHWARTZ *, ERIC PUGASH and
EDWARD BROMFIELD **
Department of Psychology and Social Relations, Harvard University, Cambridge, Massachusetts 02138, U.S.A.

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This paper reports three studies showing sex differences in EEG asymmetry during self-generated cognitive and affective tasks. In the first experiment, bilateral EEG, quantified for alpha on-line, was recorded from right-handed subjects while they either whistled, sang or recited lyrics of familiar songs. The results revealed significant asymmetry between the whistle and talk conditions only for subjects with no familial left-handedness and, within this group, only for females and not for males. In the second experiment, bilateral EEG was recorded while right-handed subjects (with no familial left-handedness) self-induced covert affective and non-affective states. Results revealed significantly greater relative right-hemisphere activation during emotion versus non-emotion trials only in females; males showed no significant task-dependent shifts in asymmetry between conditions. The third experiment was designed to test the hypothesis that females show greater percent time asymmetry than males during biofeedback training for symmetrical and asymmetrical EEG patterns. Results confirmed this prediction as well as indicating that females show better control of such asymmetrical cortical patterning. These findings provide new neuropsychological support for the hypothesis of greater bilateral flexibility in females during self-generation tasks.

1. Introduction

Recent research has suggested that the brains of male and female humans are differentially lateralized with respect to cognitive function (e.g. Buffrey and Gray, 1972; Levy, 1972; Marshall, 1973). A variety of evidence has been generated which indicates that cerebral lateralization develops sooner in females than in males (e.g. Taylor, 1969; Kimura, 1967). Whether this greater early hemispheric specialization among females persists into adulthood or whether males catch up and then surpass

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* Now at the Department of Psychology, Yale University, New Haven, Connecticut 06520, U.S.A.
** Address for correspondence: Richard J. Davidson, Department of Psychology and Social Relations, Harvard University, Cambridge, Massachusetts, 02138, U.S.A.

females in cerebral lateralization is 'an issue yet to be resolved' (Maccoby and Jacklin, 1974, p. 126).

Buffrey and Gray (1972) have suggested that lateralization of language function occurs earlier and progresses more quickly in the female brain than in the male brain, and that these differences probably persist into adulthood. Consequently, the non-dominant hemisphere of the female will be freer to subserve non-verbal functions. These investigators suggest that most forms of spatial function benefit from a more bilateral representation which they argue is characteristic of male brains.

Levy and Sperry have proposed a somewhat contradictory hypothesis (Levy-Agresti and Sperry, 1968) on the basis of the seemingly similar performance of left-handers and females on spatial tasks. Evidence exists which suggests that although dextrals and sinistrals have nearly identical verbal IQs, performance IQ for the former group is higher than for the latter group (Levy, 1969). Levy suggests that such a performance decrement is a function of bilateral representation of linguistic functions in left-handers which produces specific interference with Gestalt perception. Levy (1972, p. 174) reasons that since females also show spatial deficits relative to males (e.g. Porteus, 1965; Smith, 1967), 'it might be that female brains are similar to those of left-handers in having less hemispheric specialization than male right-handers' brains'. A number of conceptual and methodological difficulties with the above formulation have recently been pointed out by Marshall (1973).

Surprisingly, no systematic studies employing bilateral EEG as a dependent measure of hemispheric activation have been performed to explore sex differences in cerebral asymmetry. Bilateral EEG has been fruitfully employed in the study of lateralization of cognitive mode in normal intact humans (e.g. Galin and Ornstein, 1972; Morgan, McDonald and MacDonald, 1971; McKee, Humphrey and McAdam, 1973; Schwartz, Davidson, Maer and Bromfield, 1974; Davidson and Schwartz, (1976a); Schwartz and Davidson and Pugash, 1976; Doyle, Ornstein and Galin, 1974; Robbins and McAdam, 1974). Such a measure would appear to be uniquely suited to assess differences in cerebral asymmetry between the sexes during the performance of a variety of cognitive tasks.

This paper reports on three studies employing bilateral EEG as the main dependent measure. The first two studies were concerned with EEG asymmetry during cognitive and affective tasks designed to activate one or the other hemisphere and were not explicitly designed to investigate sex differences. However, a *post hoc* analysis of the data, from these studies revealed significant sex differences in cerebral asymmetry. Based on these findings, a third study was performed with three aims: (1) to replicate the sex difference obtained in experiment I; (2) to explore specifically the degree to which the hemispheres are integrated (cerebral symmetry) versus differentiated (cerebral asymmetry) in males and females using a new pattern procedure of quantifying EEG; and (3) to examine the possible differential ability of males and females to control and accentuate the amount of symmetry and asymmetry in their EEGs using a pattern biofeedback approach (Schwartz, 1974; 1975; Schwartz, Davidson and Pugash, 1976).

2. Experiment I

2.1. Subjects

The sample consisted of 14 subjects, nine male and five female undergraduate students who were recruited for an experiment on 'patterns of physiological activity during singing, whistling, and talking'. All subjects were right-handed. Five of the 14 subjects had at least one left-handed immediate family relative. Among the males and females there was an approximately equal distribution of musical training. Sixty percent of the females and 67% of the males indicated they could play at least one instrument well.

2.2. Apparatus and recording procedure

Bilateral EEG was recorded from the left and right occipital regions (01 and 02; Jasper, 1958) referenced to a common vertex (CZ) with Beckman miniature electrodes, and all electrode resistances were below 5000 Ω. All measures were recorded on a Grass model 7 polygraph and each EEG channel was filtered for 8–13 Hz activity and displayed on two additional channels individually calibrated to yield a pen deflection of 1.5 cm for an average peak alpha burst. Grason–Stadler logic modules were employed to detect and automatically count bursts of criterion alpha on-line. An arbitrary criterion of 0.5 cm was utilized so that alpha activity had to be at least 33.3% of the average peak amplitude to be counted. Bursts of four alpha waves within a maximum of 0.5 sec were required to activate the counter and constituted one alpha unit; this effectively removed any movement artifact from being counted as alpha, and provided a reliable, conservative measure of alpha activity.

2.3. Procedure

Upon entering the laboratory, prior to commencement of experimental trials, the subjects completed a questionnaire requesting them to list three familiar songs, whose words and melody were well known. The subjects were then exposed to three blocks consisting of three 1 min trials where they were required to either whistle the melody of a song, talk the lyrics to a song in a monotone, or sing a song. Each block of three trials was preceded by a 1 min rest period, with order of song and condition counterbalanced within and across the subjects. All trials were performed with eyes closed. The subjects were instructed to sustain all tasks until being told to stop at the end of 1 min, repeating each task as many times as necessary to fill the trial period.

2.4. Data analysis

EEG was evaluated by computing the ratio of the difference in alpha units between 02 minus 01 over the sum of alpha at 01 and 02 $[(R - L)/(R + L)]$. This ratio score serves to 'correct' the obtained values for individual differences in absolute amount of alpha activity. Higher ratios are indicative of greater relative left-hemisphere activation. Analyses of variance with condition as a repeated factor and sex as a between-groups factor were computed. Two-tailed t tests were employed to assess the significance of individual comparisons.

2.5. Results and discussion

The grand means of the EEG ratio score for whistle, sing and talk conditions across subjects ($N = 14$) and trials (three per condition) are presented in table 1. An analysis of variance revealed a significant main effect for condition [$F(2,24) = 4.43$, $p < 0.03$]. This is primarily accounted for by the significant whistle versus talk effect [$t(13) = 3.24, p < 0.01$], thus indicating greater relative left-hemisphere activation during the latter versus the former tasks. When right- and left-hemisphere alpha scores were separately examined, the data suggested that the whistle versus talk effect is primarily a function of less left-hemisphere alpha during the latter versus the former task [mean 01 alpha for talk = 69.93, for whistle = 75.62; $t(13) = 1.96, p < 0.10$]. There were no significant differences in right-hemisphere alpha between conditions (mean 02 alpha for talk = 73.95, for whistle = 76.55). Although singing fell in between whistling and talking, neither of the remaining two comparisons with this condition were significant on the ratio score measure (sing versus talk is $p < 0.10$). A further breakdown of the data revealed that the difference in EEG ratio between whistling versus talking was significantly greater for subjects with no familial left-handedness (pure subjects, $N = 9$) than those with one or more left-handed family relatives (impure subjects, $N = 5$) [$F(1,12) = 5.85, p < 0.04$]. This interaction is illustrated in fig. 1. This finding is consistent with and extends previous research on the influence of familial handedness on tasks subserved by one or the other hemisphere (e.g. McKeever, Van Deventer and Suberi, 1973).

Sex differences in hemispheric asymmetry during whistling versus talking were next examined. Analysis of variance within the total female sample revealed a significant whistle versus talk effect [$F(1,4) = 7.37, p < 0.05$]. An identical analysis on the total male sample was marginally significant [$F(1,8) = 4.11, p < 0.08$]. Importantly, when sex differences were examined within the pure subjects only

Table 1
Experiment I: mean $(R-L)/(R+L)$ score for each condition across all subjects ($N = 14$) and trials (W = whistle, S = sing and T = talk).

W	S	T
0.011	0.022	0.049

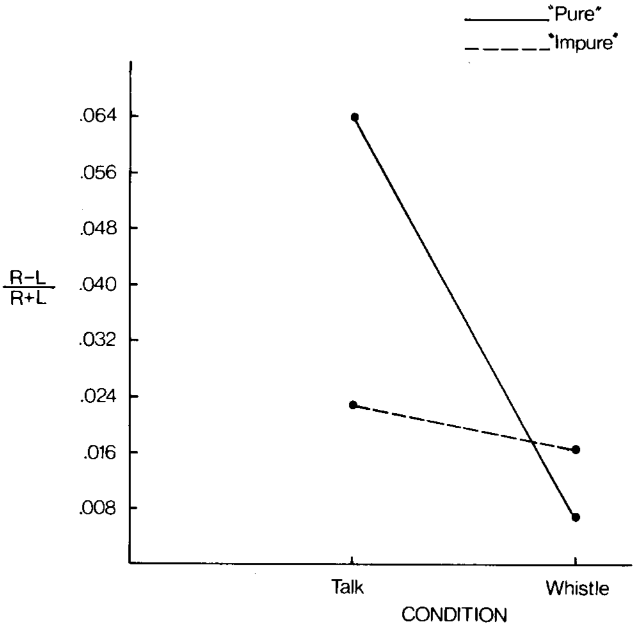

Fig. 1. Experiment I: mean EEG ratio score for talk and whistle conditions for 'pure' subjects (no familial left-handedness, $N = 9$), and for 'impure' subjects (with familial left-handedness, $N = 5$).

(for females $N = 4$, for males, $N = 5$), females show a highly significant condition effect [$F(1,3) = 36.43, p < 0.01$] while males show no significant effect [$F(1,4) = 3.97$, $p > 0.10$]. These data are illustrated in fig. 2. It thus appeared from this initial study than when male and female right-handed subjects with no familial left-handedness whistled the tune to a song versus recited the lyrics, only the females showed significant task-dependent changes in EEG asymmetry. Based on these findings only subjects with no familial left-handedness were employed in subsequent studies.

3. Experiment II

3.1. Subjects

Twelve male and eight female dextrals with no reported familial left-handedness were employed as subjects. All subjects were paid volunteers of college age and were in good health.

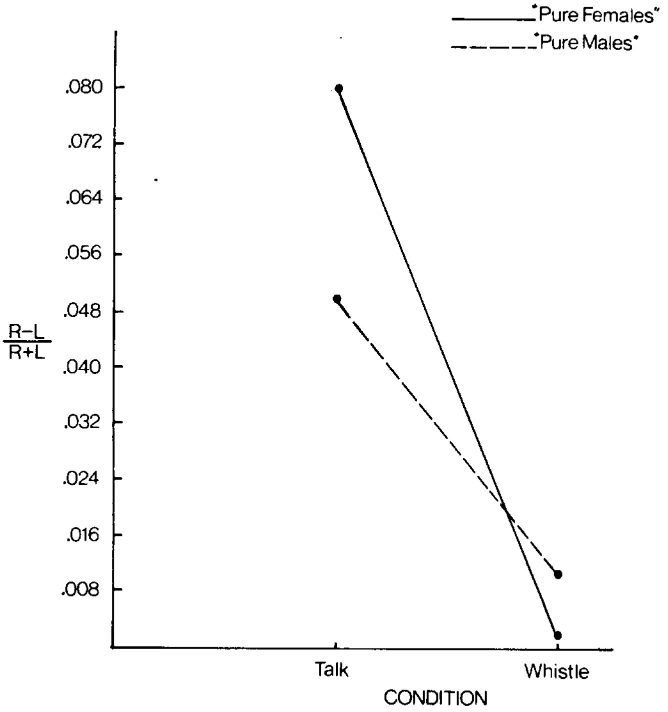

Fig. 2. Experiment I: mean EEG ratio score for talk and whistle conditions of 'pure female' ($N = 4$) and 'pure male' ($N = 5$) subjects.

3.2. Apparatus and recording procedure

Bilateral EEG was recorded from the left and right parietal areas (P3 and P4) referenced to a common vertex (CZ) (Jasper, 1958) with Beckman miniature electrodes *. The EEG recording and quantification procedure for this study was identical to experiment 1.

3.3. Procedure

The experiment was divided into two discrete phases, counterbalanced across subjects. During one phase, subjects were employed in a heart rate biofeedback task; data from this phase have been reported elsewhere (Davidson and Schwartz,

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* Parietal sites were chosen for this and the following experiment because they are association regions and are more likely, on the basis of current neuropsychological knowledge, to subserve complex information processing (e.g. Luria, 1973).

1976a). The remaining phase consisted of a 2 X 2 complete factorial within-subjects design. The subjects were requested to self-induce covert affective and non-affective states using either verbal or imagery strategies in 2 min trials. Four affective and four non-affective trials were presented in counterbalanced order with two 2 min rest periods interspersed between them. During the emotional trials, subjects were asked, in separate trials, to actively 'relive the feelings' from angry and relaxing–contenting scenes from their past which, in a pre-experimental questionnaire, they had rated as being 'very intense' (ratings of 4 or 5 on a five-point scale). Half the trials required reliving anger and the remaining trials required the re-experiencing of relaxation–contentment. During half of the trials (counterbalanced across emotions) subjects were asked to utilize verbal imagery (i.e. 'write a letter to a friend covertly about the events surrounding your experience') while the remaining trials required the utilization of visual imagery ('picture the events surrounding your experience'). During half of the non-affective trials, the subjects were required to simply 'think' about a typical day using either verbal or visual strategies (in separate trials). For the remaining two trials subjects were requested to perform a covert verbal task ('think of as many words as you can beginning with the letter "h" ') and a covert visual task ('picture as many different buildings from the Boston area as you can'). All trials were performed with eyes closed.

3.4. Data analysis

The ratio score $[(R - L)/(R + L)]$, employed in experiment 1, also served as the main dependent variable in the present study. Higher ratios are indicative of greater relative left-hemisphere (P3) activation. Analyses of variance with emotion (emotion versus non-emotion) and mode (verbal versus visual) as repeated factors and sex as a between-groups factor were performed. Two-tailed t tests were employed to assess the significance of individual comparisons.

3.5. Results and discussion

Analysis of variance was performed on the mean emotion (across verbal and visual and across anger and relaxation) and non-emotion (across verbal and visual and across tasks) ratio score as well as on the mean mode (verbal versus visual) score. A significant main effect for emotion was obtained $[F(1,18) = 8.31, p < 0.01]$. This indicates that when subjects are self-generating covert affective states they show significantly more relative right-hemisphere activation than when generating comparable covert non-affective states. Interestingly, the mean ratio scores for the anger and relaxation condition were identical (both means = 0.069) and both were significantly less than the mean ratio score for the non-affective conditions ($p < 0.05$). Although the means for the verbal and visual main effects are in the predicted direction (verbal eliciting greater relative left-hemisphere activation than visual, $\bar{X}$ verbal = 0.101; $\bar{X}$ visual = 0.087) the main effect for mode failed to reach significance.

The independent contributions of the right and left hemispheres to the tasks in question were next examined. Analyses of variance on separate right- and left-hemisphere alpha scores revealed a significant mode effect for right-hemisphere alpha [$F(1,18) = 13.73$, $p < 0.002$], indicating less mean P4 alpha during visual (mean = 84.92) versus verbal (mean = 89.65) tasks. The main effect for emotion was also significant, albeit in the opposite direction of the hypothesis [$F(1,18) = 7.38$, $p < 0.02$]. The mean P4 alpha for the affective tasks was 89.87; for the non-affective tasks the mean was 84.70. The analysis of the left-hemisphere alpha scores revealed no significant main effect for mode and a highly significant main effect, in the predicted direction, for emotion [$F(1,18) = 29.98$, $p < 0.001$]. The mean P3 alpha for the non-affective tasks was 69.23 while for affective tasks it was 78.48. When the right- and left-hemisphere scores are examined together, it can be seen that there is a large increase in left-hemisphere alpha (mean increase = 9.25) from non-affective to affective tasks relative to the smaller increase in right-hemisphere alpha (mean increase = 5.16). An analysis of variance with site (P3 and P4) as a factor revealed a significant emotion X site interaction [$F(1,18) = 6.94$, $p < 0.02$], thus indicating that from non-affective to affective tasks, the left hemisphere shows

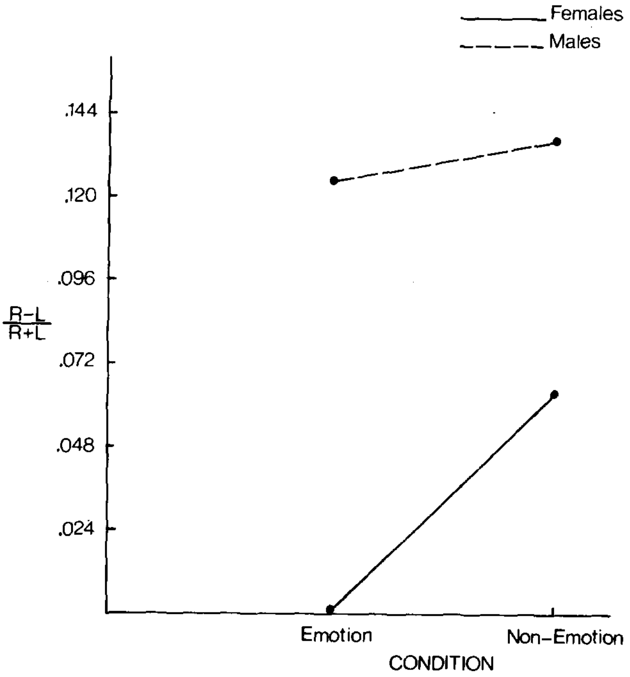

Fig. 3. Experiment II: mean EEG ratio score for emotion (covert affective self-generation) and non-emotion (covert non-affective self-generation) conditions for males ($N = 12$) and females ($N = 8$).

a large increase in alpha activity (indicative of decrements in activation) while the right hemisphere shows a significantly smaller task-dependent shift. These findings parallel those obtained in experiment I, where it was found that the left hemisphere was more labile and showed greater task-dependent changes than the right. The fact that both hemispheres showed increments in alpha activity from the non-affective to the affective tasks may indicate that the latter tasks were less difficult than the former.

When sex differences are examined, a marginally significant sex X emotion interaction was obtained [$F(1,18) = 3.23$, $p < 0.09$]. The emotion data split by sex are presented in fig. 3. This interaction indicates that females show greater cerebral asymmetry between emotion versus non-emotion tasks than males. The main effect for emotion was then examined separately within each sex. The results revealed that males show no significant differences in EEG asymmetry between emotion versus non-emotion trials [$F(1,11) = 0.787, p > 0.35$]. Importantly, this same analysis for females revealed a significant emotion effect [$F(1,7) = 8.27, p < 0.03$], thus indicating that when females are requested to self-generate emotional states they show significant relative right-hemisphere activation compared to non-emotional trials. Males, on the other hand, show no significant shifts in asymmetry between conditions.

The lack of any main effect for mode (verbal versus visual) on the ratio score can probably be accounted for by the ineffectiveness of the manipulation. 70% of the subjects spontaneously reported that it was extremely difficult to perform the verbal emotional trials and the verbal typical day trial in the absence of visual imagery. Since other investigators have reported that covert visual imagery elicits relative right-hemisphere activation (Robbins and McAdam, 1974), it is not surprising that we did not find significant differences in asymmetry between conditions.

It should be noted that the main effect for emotion obtained in this study is the first demonstration of such an effect in the EEG. It is consistent with a growing body of literature suggesting that the right hemisphere plays a special role in emotion (e.g. Schwartz, Davidson and Maer, 1975; Galin, 1974; Gainotti, 1972; Carmon and Nachson, 1973; Wechsler, 1973). However, the data from this study suggest that during the self-generation of affect designed to activate the right hemisphere, females show significant asymmetry between affective and non-affective conditions whereas males do not.

4. Experiment III

4.1. Subjects

The sample consisted of 20 students, 10 males and 10 females whose mean age was 20.5 yr. All subjects were right-handed and had no immediate non-right-handed relatives. Subjects were paid volunteers and in good health. Upon completion of the experiment, it was discovered that the distribution of musical training in males and females was not comparable. This is discussed in section 4.5.

4.2. Apparatus and recording procedure

Bilateral EEG was recorded from the left and right parietal areas (P3 and P4) (Jasper, 1958), referenced to the left ear lobe; the right ear lobe served as ground. The EEG was recorded with Beckman miniature electrodes and all electrode resistances were below $5000\ \Omega$. All measures were recorded on a Grass model 7 polygraph with each of the two EEG channels recorded through an a.c. preamplifier. Each EEG channel was filtered for 8–13 Hz, full wave rectified and displayed on two additional channels individually calibrated to yield a pen deflection of 3 cm for an average peak alpha burst. Level detectors were set to trigger in response to a signal set at or exceeding 1 cm, so that alpha activity had to be at least 33.3% of the average peak amplitude to be counted. Grason–Stadler logic modules were employed to detect instances of criterion alpha on-line and to sample at 0.1 sec intervals to determine which of the following four conditions was present: (a) $L\alpha_{on}R\alpha_{on}$, (b) $L\alpha_{on}R\alpha^{off}$, (c) $L\alpha^{off}R\alpha_{on}$ and (d) $L\alpha^{off}R\alpha^{off}$. After Schwartz (1974), $L\alpha_{on}R\alpha_{on}$ and $L\alpha^{off}R\alpha^{off}$ are considered integration states, while the remaining two patterns are considered differentiation states.

It should be noted that despite full wave rectification and the 33% criterion of the level detectors, this procedure tended to overestimate the percentage of time in the $L\alpha^{off}R\alpha^{off}$ state since the sample pulse was not phase-locked to the occurrence of alpha, and epochs between peaks of the waves were often seen as non-alpha. This procedure is therefore a conservative one, particularly with regard to the two differentiation patterns.

4.3. Procedure

The first phase of this experiment was a replication of experiment I with the different method of quantifying the EEG and with the utilization of different recording sites. Prior to the experiment, each subject listed three familiar songs. The subjects were then exposed to three blocks of three 1 min trials where they were required to either whistle the melody of a song, talk the lyrics to a song in a monotone or sing a song. Order of song and condition was counterbalanced within and across subjects. All trials were performed with eyes closed and the subjects were instructed to sustain all tasks until told to stop at the end of 1 min, repeating each task as many times as necessary to fill the trial period.

The second phase consisted of three blocks of pattern biofeedback training, each consisting of twelve 1 min trials – nine feedback trials with one rest period interspersed between every three trials. Each block began with a 3 min 'free-play' period, during which time the subject was instructed to experiment with different strategies and try to discover what makes the tone go on and off. Each biofeedback block represented training on a different EEG pattern. Subjects were simply told that the tone represented a particular EEG pattern and that each block represented a different pattern. This entire phase was performed with eyes closed.

The first block consisted of $L\alpha^{off}R\alpha^{off}$ training (I). Logic modules were programmed to provide a tone each time the subject produced any pattern other than $L\alpha^{off}R\alpha^{off}$. The subjects were instructed to keep the tone off for as long as possible, thereby producing $L\alpha^{off}R\alpha^{off}$. The pitch of the tone employed for this block was alternated from subject to subject. A suppression paradigm (i.e. turn the tone off) was employed for this block because the $L\alpha^{off}R\alpha^{off}$ pattern typically accounted for the greatest amount of EEG activity during a 1 min trial and it was reasoned that if feedback was provided for the occurrence of this pattern, the subjects would find it difficult to discriminate between a 'good' versus 'poor' trial due to the nearly continuous stream of tones. Additionally, to keep the subjects interested and motivated, they were always exposed to this block first because it was believed to be easier than the subsequent asymmetry training.

Blocks two and three consisted of the differentiation training. Order of training on each of the two differentiation patterns ($L\alpha^{off}R\alpha_{on}$ = differentiation 1; $L\alpha_{on}R\alpha^{off}$ = differentiation 2) was counterbalanced across subjects as was the pitch of the tone (low or high) representing the $L\alpha^{off}R\alpha_{on}$ and $L\alpha_{on}R\alpha^{off}$ states. Tones were presented each time the subject produced the criterion pattern, and the subjects were instructed to keep the tone on for as long as possible. During rest trials they were simply instructed to rest with their eyes closed and to let their thoughts wander.

Following each biofeedback block, the subjects filled out a questionnaire designed to assess their cognitive strategy during the preceding task trials. These data, as well as the across-group biofeedback results are given elsewhere (Schwartz, Davidson, and Pugash, 1976).

4.4. Data analysis

Four scores representing each of the four EEG patterns was obtained for each task and rest trial. Each number represents a 0.1 sec occurrence of a particular pattern. Each of the four pattern scores obtained for each trial were converted to a percentage of the total number of samples for that trial. This eliminated effects of slight variations in trial length. All data analyses were performed on these transformed percentage scores to assess the significance of the task effects in phase I. Analysis of variance was performed with condition as a repeated factor and sex as a between-groups factor. To assess the effects of biofeedback training and sex differences in phase II, analyses of variance with condition (D1, D2, I, and rest) and pattern (the four EEG patterns) as repeated factors and sex as a between-groups factor were performed. Two-tailed t tests were employed to assess the significance of individual comparisons.

4.5. Results and discussion

The pattern scores for each condition (whistle, sing and talk) in phase I were converted to $[(R - L)/(R + L)]$ scores. The means across subjects and trials, by condition are present in table 2 *. Analysis of variance revealed a significant main effect for condition $[F(2,36) = 4.66, p < 0.02]$. The whistle versus talk comparison was marginally significant $[t(19) = 1.80, p < 0.10]$, while the sing versus talk effect was significant in the present study $[t(19) = 3.15, p < 0.01]$. As in experiment I, there were no significant differences between whistle and sing.

Table 2
Experiment III: mean $(R - L)/(R + L)$ scores for each condition across all subjects (N = 20) and trials (W = whistle, S = sing and T = talk).

W	S	T
0.108	0.077	0.328

However, unlike experiment I there was no main effect for sex, nor was there any sex X condition interaction. The lack of any sex difference can probably be attributed to the differential musical training which existed between males and females in this experiment. It is important to note that musical training was comparable in males and females in experiment I. Table 3 presents the 2 X 2 breakdown of musically trained (proficient on at least one instrument) versus untrained subjects for each sex. A chi-square reveals a significant difference between the sexes ($X^2 = 3.52$, df = 1, $p < 0.06$, corrected for continuity). Other investigators (Bever and Chiarello, 1974; Gordon, 1975) as well as the present authors (Davidson and Schwartz, 1976b) have found that hemispheric asymmetry (in the direction of relative right-hemisphere activation for music) during musical tasks is attenuated or even reversed in subjects who are musically trained versus those untrained. In future studies specifically examining sex differences in cerebral asymmetry during musical tasks, care should be taken to match the groups on initial musical training. The lack of such equivalence in the present sample unfortunately precludes any meaningful sex comparison for phase I of the experiment.

In addition, it should also be noted that differences in electrode placement and EEG quantification between this experiment and experiment I may also account for some of the differences in results.

The first question which may be asked concerning phase II of the present study

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* It should be noted that the values provided for the ratio scores throughout this paper are meaningful only relative to other ratio scores *within* the same experiment. A comparison of the absolute value of the ratio scores across experiments is unjustified because of differences in recording technique and lead placement.

Table 3
Experiment III: musical training (proficient on at least one musical instrument) by sex.

	Male	Female
Musically trained	4	9
Musically untrained	6	1

is whether there are any sex differences in the percent–time differentiation (across $L\alpha_{on}R\alpha^{off}$ and $L\alpha^{off}R\alpha_{on}$) across and within conditions. Percent–time total differentiation for each biofeedback condition and for rest, by sex, are presented in fig. 4. Analysis of variance revealed a significant main effect for sex [$F(1,18) = 5.58$, $p < 0.03$] thus indicating that across experimental tasks, females show significantly more total differentiation (asymmetry) in their EEG than males. In addition, a significant sex X condition interaction was obtained [$F(3,54) = 8.80$,

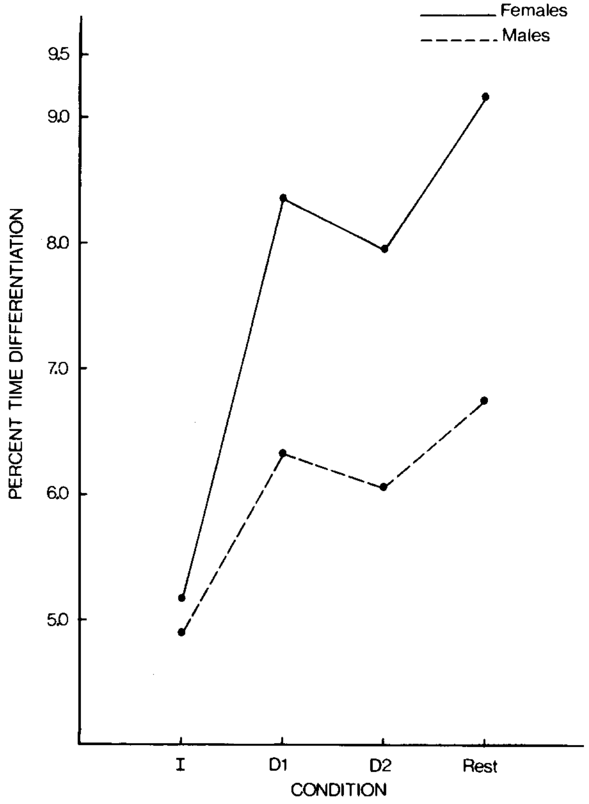

Fig. 4. Experiment III: mean percent–time differentiation (across the two differentiation patterns – $L\alpha_{on}R\alpha^{off}$ and $L\alpha^{off}R\alpha_{on}$) for each condition by sex ($N = 10$ for females, $N = 10$ for males). I = $L\alpha^{off}R\alpha^{off}$ (integration) training, DI = $L\alpha^{off}R\alpha_{on}$ training; D2 = $L\alpha_{on}R\alpha^{off}$ training.

$p < 0.05$]. Separate t tests revealed significant sex differences during D1 and rest [for D1 $t(18) = 2.17, p < 0.05$; for rest $t(18) = 2.25, p < 0.02$] and a marginally significant difference during D2 [$t(18) = 2.00, p < 0.10$], but no sex differences were found during integration. These findings indicate that when feedback is provided for EEG differentiation or during simple rest periods, females show significantly more percent–time asymmetry than males. However, when the contingencies are changed so that feedback is provided for hemispheric integration, males and females show comparable amounts of asymmetry.

A marginally significant sex X pattern ($L\alpha^{\text{off}}R\alpha_{\text{on}}$ versus $L\alpha_{\text{on}}R\alpha^{\text{off}}$) X condition (D1 versus D2) interaction was obtained [$F(1,18) = 2.89, p = 0.10$] and is illustrated in fig. 5. Separate t tests revealed that during D1 ($L\alpha^{\text{off}}R\alpha_{\text{on}}$) versus D2

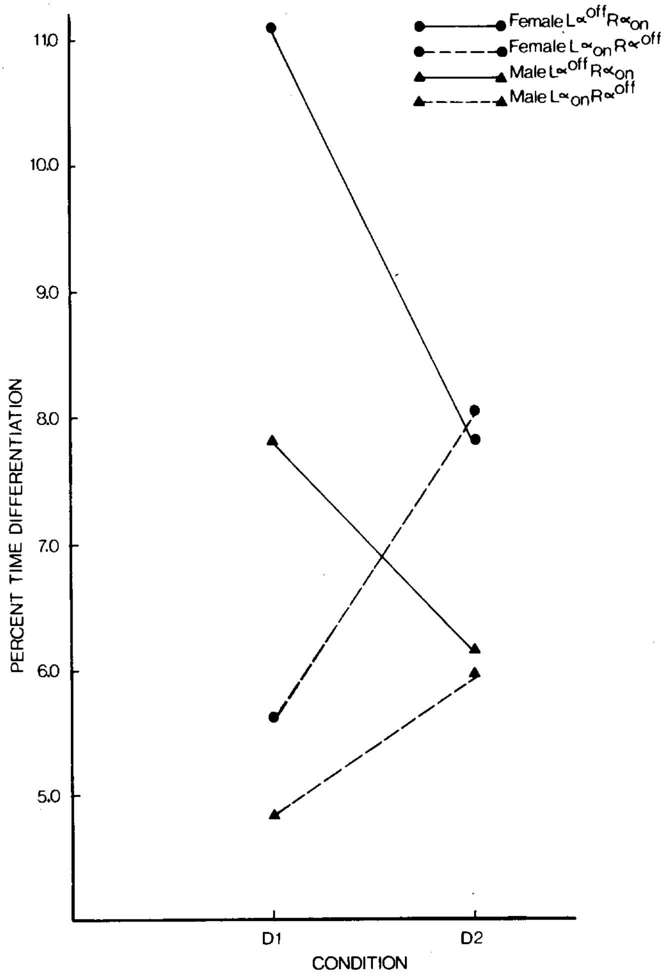

Fig. 5. Experiment III: mean percent–time differentiation separately for each differentiation pattern and condition, by sex.

($L\alpha_{on}R\alpha^{off}$) training, males show no significant training effect on the $L\alpha_{on}R\alpha^{off}$ pattern while females show significantly more of this pattern during D2 versus D1 [$t(9) = 3.23, p < 0.05$]. Similarly, on the $L\alpha^{off}R\alpha_{on}$ pattern, females show a significant condition effect (D1 versus D2) [$t(9) = 4.32, p < 0.01$] while the same comparison for males is marginally significant [$t(9) = 2.15, p < 0.10$]. It thus appears that females show greater specificity of EEG asymmetry pattern control than males.

An alternative way of viewing the present data is by considering percent–time integration (symmetry) across and within conditions. Analysis of variance revealed a significant main effect for sex [$F(1,18) = 5.87, p < 0.03$] indicating that across conditions and the two integration patterns ($L\alpha_{on}R\alpha_{on}$ and $L\alpha^{off}R\alpha^{off}$) females show significantly *less* hemispheric symmetry than males. A significant sex X condition interaction was also obtained [$F(3,54) = 8.80, p < 0.05$] and is illustrated in fig. 6. Separate *t* tests revealed significant sex differences during D1 [$t(18) = 2.17$, $p < 0.05$] and rest [$t(18) = 2.55, p < 0.02$] and a marginally significant difference

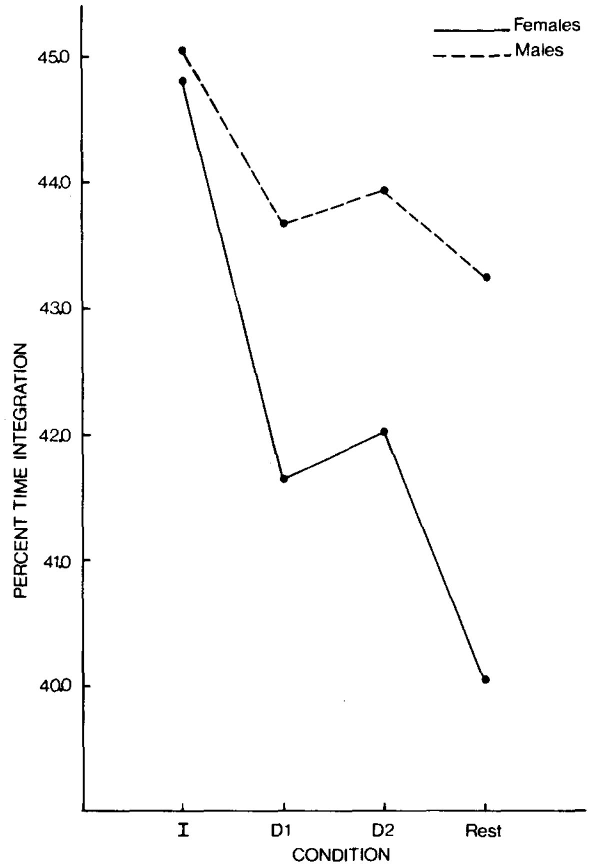

Fig. 6. Experiment III: mean percent–time integration (across the two integration patterns – $L\alpha^{off}R\alpha^{off}$ and $L\alpha_{on}R\alpha_{on}$) for each condition by sex.

during D2 [$t(18) = 2.00, p < 0.10$]. No significant sex difference was found during integration. These findings directly follow from the differentiation data and indicate that during those periods when either the production of differentiation was required or during rest, females show less integration than males. However, when integration becomes the criterion pattern, males and females show comparable amounts of EEG symmetry. Unlike the differentiation scores, no significant sex × pattern interactions were found for the integration patterns ($L\alpha_{on}R\alpha_{on}$ and $L\alpha^{off}$-$R\alpha^{off}$). This suggests that sex differences in specificity of pattern control apply only to the self-regulation of cortical asymmetry (differentiation).

The fact that no sex differences were found during phase I of this experiment (presumably due to the differential musical training which was found to exist between the sexes) while significant sex differences were obtained during the biofeedback phase suggests that the effects of musical training on task-dependent cerebral asymmetry is specific to musical tasks and does not generalize to other cognitive tasks. Whether the effects of all types of such specialized training remain confined to asymmetry changes elicited by the tasks themselves may be further explored in the future by studying additional populations, i.e. artists (who draw), and comparing EEG asymmetry during drawing or visualizing with asymmetry elicited by, for example, whistling. If the specificity hypothesis is correct, the artists should show attenuated asymmetry during the drawing task with normal amounts of lateralization during the musical tasks. Musicians, however, should show the reverse. It stands to reason that a general sex difference factor is but one determinant of cerebral asymmetry. Other factors, including handedness, training experiences and type of task evaluated will likely all interact, producing a more complex configuration of hemispheric patterning (see also Schwartz et al., 1975).

5. General discussion

The present set of three studies all provide support for the conclusion that when right-handed subjects with no familial left-handedness are required to engage in self-generation tasks designed to activate one or the other hemisphere, females show greater task-dependent asymmetry than males. In experiment I, it was found that 'pure' female subjects show significant differences in occipital EEG asymmetry between whistling and talking while 'pure' males do not. In experiment II, females showed greater asymmetry between self-generated covert emotional versus non-emotional tasks than did males. Experiment III was specifically designed to assess sex differences in cortical asymmetry, utilizing a pattern analysis technique. Using these procedures, striking sex differences in cortical symmetry and asymmetry were uncovered. Across the two biofeedback differentiation conditions and the resting conditions, females showed significantly more percent–time differentiation and significantly less percent–time integration than males. Moreover, suggestive evidence was obtained which indicates that females show greater specificity of EEG asymmetry control than males.

The robust sex differences obtained in experiment III indicate that the pattern procedure employed is particularly promising because it separately analyzes the percent–time that one hemisphere is relatively activated while the other is simultaneously less activated (e.g. $L\alpha^{off}R\alpha_{on}$). This finding is consistent with recent advances in biofeedback research which clearly illustrate the importance of considering patterns of biological processes in the study of brain-behavior relationships (Schwartz, 1972; 1974; 1975).

EEG procedures may well be more sensitive than gross performance measures or subjective ratings. For example, to evaluate whether the emotion–non-emotion sex difference in experiment II was simply a function of females showing more intense reactions, the subjects were asked to rate after each emotional trial the intensity of their feelings during that trial on a scale from 1 through 5. Interestingly, there were no significant sex differences on this measure. However, such a finding has bearing only on perceived affective intensity, and it may be that females were generating the affect more intensely but not reporting it as such. Future studies on this topic might fruitfully employ additional psychophysiological measures (e.g. facial EMG; see Schwartz, Fair, Greenberg, Foran and Klerman, 1975) to get an additional index related to affective intensity. In any case, the present data suggest that the electrocortical measures employed were more sensitive than the post-trial questionnaire in uncovering individual differences in task performance. Such a finding beckons future investigators to carefully design behavioral indices which are more sensitive to the type of underlying neural differences obtained in the present studies.

Altogether, these findings support the general hypothesis of greater bilateral flexibility in the brains of right-handed females compared to males during tasks requiring the self-generation of behavior designed to unilaterally engage the hemispheres.

The fact that females, in experiment III, show significantly more percent–time differentiation during resting trials than males may initially appear difficult to reconcile with the present emphasis on sex differences during self-generation (production) tasks. However, a consideration of what subjects do during rest and relaxation reveals that these states are produced and self-generated in a manner similar to more active states (see Davidson and Schwartz, in press). Thus, the self-generation of rest during the resting trials lies more on the production than on the perception side of the organism.

It is important to recognize that a number of investigators who have found the opposite trend in lateralization between the sexes with cognitive measures have employed perceptual tasks (e.g. Kimura, 1969; Knox and Kimura, 1970; McGlone and Davidson, 1973). It may be that on certain perceptual tasks females are less lateralized while on production (self-generated) tasks they are more lateralized. Such an hypothesis can be systematically explored in the future using EEG recorded from perception and production sites on the left (e.g. Wernicke's and Broca's area) and right hemispheres simultaneously while subjects are engaged in both perception and production tasks designed to activate one or the other hemisphere.

Finally, this series of experiments highlights the utility of recording patterns of cerebral psychophysiological measures in uncovering the neural substrates of individual differences in behavior (cf. Schwartz, 1975) and indicates that with such methods females show greater cortical asymmetry than males during self-generation tasks designed to unilaterally activate the cerebral hemispheres.

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References

Bever, T.G. and Chiarello, R.J. (1975). Cerebral dominance in musicians and non-musicians. Science, 185, 537–539.

Buffrey, A.W.H. and Gray, J.A. (1972). Sex differences in the development of spatial and linguistic skills. In: Ounsted, C. and Taylor, D.C. (Eds.) Gender Differences: Their Ontogeny and Significance. Churchill: London.

Carmon, A. and Nachson, I. (1973). Ear asymmetry in perception of emotional non-verbal stimuli. Acta Psychologia, 37, 351–357.

Davidson, R.J. and Schwartz, G.E. (1976a). Patterns of cerebral lateralization during cardiac biofeedback versus the self regulation of emotion: sex differences. Psychophysiology.

Davidson, R.J. and Schwartz, G.E. (1976b). The influence of musical training on patterns of EEG asymmetry during musical and non-musical generation tasks. Submitted for publication.

Davidson, R.J. and Schwartz, G.E. [in press]. The psychobiology of relaxation and related states: a multi-process theory. In: Mostofsky, D.I. (Ed.) Behavior Control and the Modification of Physiological Activity. Prentice-Hall: New York.

Davidson, R.J. and Schwartz, G.E. (1975). Musical sophistication influences patterns of EEG asymmetry during musical and non-musical self generation tasks. Submitted for publication.

Doyle, J.C., Ornstein, R. and Galin, D. (1974). Lateral specialization of cognitive mode: II. EEG frequency analysis. Psychophysiology, 11, 567–578.

Gainotti, G. (1972). Emotional behavior and hemispheric side of the lesion. Cortex, 8, 41–55.

Galin, D. (1974). Implications for psychiatry of left and right cerebral specialization a neurophysiological context for inconscious processes. Archives of General Psychiatry, 31, 572–582.

Galin, D. and Ornstein, R. (1972). Lateral specialization of cognitive mode: an EEG study. Psychophysiology, 9, 412–418.

Gordon, H.W. (1975). Hemispheric asymmetry and musical performance. Science, 189, 68–69.

Jasper, H.H. (1958). The ten twenty electrode system of the International Federation. Electroencephalography and Clinical Neurophysiology, 10, 371–375.

Kimura, D. (1967). Functional asymmetry of the brain in dichotic listening. Cortex, 3, 163–178.

Kimura, D. (1969). Spatial localization in left and right visual fields. Canadian Journal of Psychology, 23, 445–458.

Knox, C. and Kimura, D. (1970). Cerebral processing of nonverbal sounds in boys and girls. Neuropsychologia, 8, 227–237.

Levy, J. (1969). Possible basis for the evolution of lateral specialization of the human brain. Nature, 224, 614–615.

Levy, J. (1972. Lateral specialization of the human brain: behavioral manifestations and possible evolutionary basis. In: Kiger, J.A., Jr. (Ed.) The Biology of Behavior. Oregon State University Press: Corvallis, Oregon.

Levy-Agresti, J. and Sperry, R.W. (1968). Differential perceptual capacities in major and minor hemispheres. Proceedings of the National Academy of Sciences, 61, 1151 (abstract).

Luria, A.R. (1973). The Working Brain, Basic Books: New York.

Maccoby, E.E. and Jacklin, C.N. (1974). The Psychology of Sex Differences. Stanford University Press: Stanford.

Marshall, J.C. (1973). Some problems and paradoxes associated with recent accounts of hemispheric specialization. Neuropsychologia, 11, 463–470.

McGlone, J. and Davidson, W. (1973). The relation between cerebral speech laterality and spatial ability with special reference to sex and hand preference. Neuropsychologia, 11, 105–113.

McKee, G., Humphrey, B. and McAdam, D.W. (1973). Scaled lateralization of alpha activity during linguistic and musical tasks. Psychophysiology, 10, 441–443.

McKeever, W.F., Van Deventer, A.D. and Suberi, M. (1973). Avowed, assessed and familial handedness and differential hemispheric processing of brief sequential and non-sequential visual stimuli. Neuropsychologia, 11, 235–238.

Morgan, A.H., McDonald, P.J. and MacDonald, H. (1971). Differences in bilateral alpha activity as a function of experimental task, with a note on lateral eye movements and hypnotizability. Neuropsychologia, 9, 459–469.

Porteus, S.D. (1965). Porteus Maze Test, Fifty Years' Application. Pacific Books: Palo Alto, California.

Robbins, K.I. and McAdam, D.W. (1974). Interhemispheric alpha asymmetry and imagery mode. Brain and Language, 1, 189–193.

Schwartz, G.E. (1972). Voluntary control of human cardiovascular integration and differentiation through feedback and reward. Science, 175, 90–93.

Schwartz, G.E. (1974). Toward a theory of voluntary control of response patterns in the cardiovascular system. In: Obrist, P.A., Black, A.H., Brener, J. and DiCara, L.V. (Eds.) Cardiovascular Psychophysiology. Aldine: Chicago.

Schwartz, G.E. (1975). Biofeedback, self-regulation and the patterning of physiological processes. American Scientist, 63, 314–324.

Schwartz, G.E., Davidson, R.J. and Maer, F. (1975). Right hemisphere lateralization for emotion in the human brain: interactions with cognition. Science, 190, 286–288.

Schwartz, G.E., Davidson, R.J., Maer, F. and Bromfield, E. (1974). Patterns of hemispheric dominance in musical, emotional, verbal, and spatial tasks. Psychophysiology, 11, 227 (abstract).

Schwartz, G.E., Davidson, R.J. and Pugash, E. (1976). Voluntary control of patterns of EEG parietal asymmetry: Cognitive concomitants. Submitted for publication.

Schwartz, G.E., Fair, P.L., Greenberg, P.S., Foran, J.M. and Klerman, G.L. (1975). Self-generated affective imagery elicits discrete patterns of facial muscle activity. Psychophysiology, 12, 234 (abstract).

Smith, I.M. (1967). Spatial ability. Knapp: San Diego, California.

Taylor, D.C. (1969). Differential rates of cerebral maturation between sexes and between hemispheres. Lancet, ii, 140–142.

Wechsler, A.F. (1973). The effect of organic brain disease on recall of emotionally charged versus neutral narrative texts. Neurology, 23, 130–135.