21. Testing began 48 hours after surgery and was completed within 2 weeks, before recovery of function could be expected to occur (*1*). Deafferentated rats were tested regularly for recovery of facial responsiveness to a blunt or sharp probe.
22. For presentation, data are reported as follows: lateral tongue protrusion, gaping, bouts of face washing, forelimb flailing, and headshaking as the number of occurrences; rhythmic tongue protrusion as (number of occurrences)/15; and mouth movement and passive drooling as (integrated number of seconds spent performing)/4. Data were analyzed by the Wilcoxon paired test for the high concentrations and by the Mann-Whitney *U* test for the low concentrations (four deafferentated rats had not been tested intact on the low concentrations; therefore, data from four separate intact rats were used to complete the Mann-Whitney *U* test).
23. Headshaking, an aversive action, was actually increased in deafferentated rats in response to 3×10^{-4} quinine HCl. This was not seen in response to any other stimulus, however. When ingestive actions were combined across all tastes, producing a single ingestive score for each rat, deafferentated rats again showed significantly fewer ingestive responses than did intact rats ($P < 0.01$). When aversive actions were similarly combined, there was no difference between the two conditions.
24. The fact that mouth movements also increased in response to quinine further suggests that such increases do not occur simply in default of tongue protrusions, but rather signify a reduction in the perceived palatability even of aversive solutions.
25. The temporal structure of actions following deafferentation was as follows ($n = 5$ rats; 20 observations per rat; resolution, 1/30 second): duration of lateral tongue protrusion, 164 msec; duration of tongue protrusion, 56 msec; and cycle length, 161 msec. These values are not significantly different from those for intact rats.
26. The fact that deafferentation produces at least as large an effect at high concentrations as at low ones suggests that trigeminal input does not add a constant increment to palatability (Weber's law); rather it may multiply or raise palatability logarithmically.
27. The conclusion that a positive assessment of palatability is asymmetrically affected by deafferentation requires that the positive and negative evaluations of palatability be processed separately [K. C. Berridge and H. J. Grill, *Behav. Neurosci.* **97**, 563 (1983); *Appetite* **5**, 221 (1984)].
28. J. Louis-Sylvestre and J. Le Magnen, *Neurosci. Biobehav. Rev.* **4** (Suppl. 1), 43 (1980); T. L. Powley, *Psychol. Rev.* **84**, 89 (1977).
29. N. Rowland, M.-J. Meile, S. Nicolaidis, *C. R. Acad. Sci.* **277**, 1783 (1973).
30. Supported by grants from the Canadian Medical Research Council and Natural Sciences and Engineering Research Council to J.C.F. K.C.B. was supported by fellowships from NATO and the Killam Foundation. We thank C. R. Gallistel, H. J. Grill, and B. Rusak for their helpful comments; W. G. Danilchuk and H. Parr for assistance with the analysis and programming; and M. F. Jacquin for demonstrating the deafferentation procedure.

12 October 1984; accepted 28 January 1985

EEG Alpha Activity Reflects Attentional Demands, and Beta Activity Reflects Emotional and Cognitive Processes

Abstract. *Two experiments were designed to examine the effects of attentional demands on the electroencephalogram during cognitive and emotional tasks. We found an interaction of task with hemisphere as well as more overall parietal alpha for tasks not requiring attention to the environment, such as mental arithmetic, than for those requiring such attention. Differential hemispheric activation for beta was found most strongly in the temporal areas for emotionally positive or negative tasks and in the parietal areas for cognitive tasks.*

Electroencephalography (EEG) has been used to probe the relation of hemispheric functioning to both emotion and cognition (*1, 2*). Underlying this research is a simple arousal model that dates to the beginnings of EEG research (*3*), under which alpha activity (8 to 12 Hz) is assumed to be inversely related to mental processing. Along with criticism of the unitary arousal model (*4*) and the development of information processing approaches to attentional processes (*5*), ample evidence suggests that the traditional model of EEG alpha interpreted in terms of arousal cannot account for the complexity of human behavior to which it has been applied. One concern we address in this report is the lack of specificity in terms of attentional demands in EEG studies of hemispheric lateralization.

In two studies, one emotional and one cognitive, we sought to determine the role of attentional demands on EEG processes. Following Darrow (*6*) and Lacey (*7*), we distinguished between attentional tasks that required observation of environmental stimuli (intake tasks) and those tasks such as mental arithmetic that require attention be paid to internal processing (rejection tasks). Intake and rejection tasks produce differential responding in the cardiovascular system, both when only simple observation of external stimuli is required (*8*) and when more active processing is demanded (*9*). Until now the intake-rejection dimension has not been incorporated into EEG research although both empirical evidence (*10*) and theoretical formulations (*11*) suggest the importance of such an approach.

In experiment 1, 18 right-handed subjects (nine males and nine females) of college age were given two trials of eight cognitive tasks on each of 3 days. The tasks were of the type used in lateralization studies to reflect left- and right-hemispheric processing and not require overt motor responses (*12*). The verbal-analytic (left-hemispheric) tasks and the spatial-synthetic (right-hemispheric) tasks were crossed with the intake-rejection dimension in a 2 by 2 design. The intake–left-hemispheric tasks were counting verbs in a passage and finding the error in a mathematics problem (*13*). The intake–right-hemispheric tasks (*14*) were a paper-folding task (choose the correct three-dimensional representation of a geometric figure presented as a blueprint) and Mooney facial closure task (pick out the face in a high-contrast presentation that initially looks like meaningless forms and contours). The rejection–left-hemispheric tasks were mental arithmetic and creating sentences that begin with a certain letter. The rejection–right-hemispheric tasks were mental rotation of a geometric figure and the visualization of an imaginary walk. All intake tasks were presented on a screen in front of the subject, and the tasks were matched for visual angle and relative brightness. During the rejection tasks, subjects were instructed to keep their eyes open and to look at the screen. In experiment 1, EEG was recorded from F3, F4, P3, and P4 referenced to linked ears. The EEG was subjected to Fourier analysis, and estimates of spectral power were computed for 4-Hz frequency bands from 0.5 to 28 Hz (*15*). These data were evaluated with analysis of variance, in which sex was the between-subjects variable and day, task (analytic or synthetic), attentional demand (intake or reject), and side (right or

Table 1. Relative mean power estimates ($\times 10^5$) for intake and rejection tasks for frequencies with significant ($P < 0.01$) attention-by-hemisphere interaction. Experiment 1 was conducted only at parietal sites.

Frequency (Hz)	Task			
	Intake		Rejection	
	Left	Right	Left	Right
	Experiment 1			
8 to 12	540.5	649	1244.5	1791.5
12 to 16	196	256	234	327
16 to 20	97	126	118	165.5
	Experiment 2			
8 to 15 (parietal)	272.2	319.6	721.2	892.2
8 to 15 (temporal)	127	188.6	227.1	353.8

left hemisphere) as within-subject variables. Separate analyses were performed for each frequency band by site (frontal or parietal). EEG ratio scores (left minus right divided by left plus right) were also computed in each experiment for each frequency band.

In experiment 2, 40 right-handed males of college age completed two trials of eight separate tasks on each of 2 days. In the 2 by 2 design, intake-rejection demands were crossed with positively and negatively valenced tasks. The rejection tasks were based on those used previously (*16*) and included remembering a happy and sad event from one's past and imagining future pleasant and unpleasant events. The intake tasks consisted of the presentation of slides considered to evoke positive (*17*) and negative (*18*) affect. These included landscapes, happy faces, sad faces, and accident scenes. During all tasks subjects were instructed to keep their eyes open and to focus on the screen. Each trial was 30 seconds long. EEG activity from F3, F4, T3, T4, P3, and P4 (referenced to linked ears) was subjected to Fourier analysis, and power estimates for a low band including theta (2 to 7 Hz), a middle range band including alpha (8 to 15 Hz), and a higher band composed of beta (16 to 24 Hz) were computed (*19*). These data were analyzed by analysis of variance (day × attentional focus × emotional valence × hemisphere) and by a factor analytic technique (PARAFAC) (*20*). Mean heart rate during the tasks was also computed.

From these two experiments we can report that attentional, cognitive, and emotional factors are differentially represented in terms of EEG frequency and site. In both studies, the intake-rejection dimension was reflected in parietal areas for the middle frequencies including alpha. This finding is supported by a statistically significant interaction of attention (intake or rejection) with hemisphere in both experiments (Table 1). The ratio data also showed the same pattern. In both studies, more alpha activity occurred during the rejection than during the intake tasks in both hemispheres; an interaction also showed differentially greater right-hemispheric alpha activity during rejection tasks. Specifically, this interaction was found in experiment 1 for parietal mid-frequencies [8 to 12 Hz, $F(1, 16) = 11.657$, $P < 0.004$; 12 to 16 Hz, $F(1, 16) = 11.894$; $P < 0.003$; 16 to 20 Hz, $F(1, 16) = 11.026$, $P < 0.004$] and in experiment 2 for the mid-frequencies (8 to 15 Hz) for both the parietal [$F(1, 39) = 10.891$; $P < 0.002$] and temporal [$F(1, 39) = 10.068$; $P < 0.003$] areas (Table 1). This interaction was not found in the frontal areas in either experiment.

Whereas the attentional demands of the experiments were reflected in the middle frequencies including alpha, the task demands (both cognitive and emotional) were reflected in beta. In experiment 1, this finding was supported by a significant task (verbal-analytic versus spatial-synthetic) by hemisphere interaction in the three upper beta bands [16 to 20 Hz, $F(1, 16) = 5.762$, $P < 0.029$; 20 to 24 Hz, $F(1, 16) = 8.968$, $P < 0.009$; 24 to 28 Hz, $F(1, 16) = 6.335$, $P < 0.023$] for the parietal areas. This same pattern was reflected in the ratio scores and was also statistically significant (analysis of variance, $\alpha = 0.05$). The interaction data show greater differences in beta activity between the hemispheres during verbal than during spatial tasks. In experiment 2, there was a significant main effect for emotional valence in the temporal [$F(1, 39) = 7.91$; $P < 0.008$] and parietal [$F(1, 39) = 6.328$; $P < 0.016$] areas, with more beta during positive than during negative tasks. Differential hemispheric emotional involvement is described by the PARAFAC analysis: more beta activity was present in the right temporal area during positive than during negative emotional tasks (Table 2).

Table 2. PARAFAC analysis of beta activity for emotional tasks: factor structure of the first factor extracted. Mode 3 (subjects) is not included. Weights should be interpreted only in terms of their pattern (for example, right temporal activity and positive tasks).

Factor	Relative weight
Mode 1—site	
Frontal	
Left	0.03
Right	0.16
Temporal	
Left	0.60
Right	2.36
Parietal	
Left	0.09
Right	0.20
Mode 2—task	
Positive	
Day 1	
Rejection	
Past	1.76
Future	2.02
Intake	
Landscape	0.92
Face	1.24
Day 2	
Rejection	
Past	1.38
Future	1.06
Intake	
Landscape	0.71
Face	1.14
Negative	
Day 1	
Rejection	
Past	0.60
Future	0.46
Intake	
Accident	0.70
Face	0.20
Day 2	
Rejection	
Past	0.58
Future	0.17
Intake	
Accident	0.38
Face	0.01

In experiment 2, the intake tasks were accompanied by a lower heart rate ($\bar{X} = 72.17$) than rejection tasks ($\bar{X} = 73.79$) [analysis of covariance $F(1, 39) = 39.14$; $P < 0.0001$]; this result is consistent with previous cardiovascular research (*21*). Since intake-rejection differences also appeared in alpha activity in our experiments, we can consider formulations relating cardiovascular activity and hemispheric alpha. For example, Walker and Walker (*22*) reported a relationship between alpha and increased carotid pressure, with the reading from the carotid artery being time-locked to the rhythmic oscillations of the EEG, especially in the alpha band. Lacey and Lacey (*23*) are among those reporting an inhibitory influence of the cardiovascular system on the central nervous system especially during rejection tasks. Thus, increased alpha during our rejection tasks may have been associated with such a mechanism, which reduced unneeded external stimulation and permitted more efficient processing of internal tasks, either cognitive or emotional.

The EEG alpha differences in response to attentional demands and the lack of any alpha differences in response to the cognitive or emotional tasks further raises the possibility that previous hemispheric lateralization research may have inadvertently confounded the external (intake) and internal (rejection) attentional dimension with right- and left-hemispheric processing demands. For example, a verbal-analytic (left hemispheric) task that requires subjects to create sentences that begin with a certain letter and a spatial-synthetic (right hemispheric) task in which subjects were to solve a spatial problem presented on a table in front of them would confound the task dimension (verbal-spatial) with the attentional (intake-reject) demands of the task.

Gevins (*24*) has suggested that EEG differences in different tasks do not reflect cognitive processes and has offered differential motor requirements as an alternative interpretation. Our data also indicate potential problems in studies that have used alpha activity as a measure of cognitive or emotional process-

ing: differential attentional demands may have confounded the results. In the two experiments reported here we controlled both for attentional and for motor requirements; no differences in alpha activity resulted, in terms of cognitive and emotional processes. However, EEG alpha activity is important in its ability to reflect attentional processes. In addition, even with the motor and attentional controls, we report beta differences reflecting both cognitive and emotional dimensions (*25*), suggesting that EEG beta may be a useful measure of appropriate cognitive and emotional processes.

WILLIAM J. RAY
HARRY W. COLE

Department of Psychology,
Pennsylvania State University,
University Park 16802

References and Notes

1. D. Galin and R. Ornstein, *Psychophysiology* **9**, 412 (1972); J. G. Beaumont, A. R. Mayes, M. D. Rugg, *Electroencephalogr. Clin. Neurophysiol.* **45**, 393 (1978); R. Davidson and H. Ehrlichman, *Science* **207**, 1005 (1980); W. Ray, N. Newcombe, J. Semon, P. Cole, *Neuropsychologia* **19**, 719 (1981).
2. D. Harmon and W. Ray, *Neuropsychologia* **15**, 457 (1977; H. Ehrlichman and M. S. Wiener, *Psychophysiology* **17**, 228 (1980).
3. E. D. Adrian and B. H. C. Matthews, *Brain* **57**, 355 (1934).
4. J. Lacey in *Research in Psychotherapy*, E. A. Rubinstein and M. B. Parloff, Eds. (American Psychological Association, Washington, D.C., 1959); D. Kahneman, *Attention and Effort* (Prentice Hall, New York, 1973).
5. D. E. Broadbent, *Decision and Stress* (Academic Press, London, 1971); K. H. Pribram and D. McGuinness, *Psychol. Rev.* **82**, 116 (1975); M. Posner, in *Handbook of Psychobiology*, M. Gazzaniga, Ed. (Academic Press, New York, 1975).
6. C. Darrow, *Psychol. Bull.* **26**, 185 (1929).
7. J. Lacey in *Psychological Stress: Issues in Research*, M. H. Appley and R. Trumbull, Eds. (Appleton-Century-Crofts, New York, 1967).
8. ———, J. Kagan, B. Lacey, H. Moss, in *Expression of the Emotions in Man*, P. H. Knapp, Ed. (International Universities Press, New York, 1963).
9. R. Williams, T. Bittker, M. Buschsbaum, L. Wynne, *Psychophysiology* **12**, 427 (1975).
10. B. Walker and K. Sandman, *J. Comp. Physiol. Psychol.* **93**, 717 (1979).
11. K. Pribram, in *Handbook of Clinical Neuropsychology*, S. K. Filskov and T. J. Boll, Eds. (Wiley-Interscience, New York, 1981); D. M. Tucker and P. A. Williamson, *Psychol. Rev.* **91**, 185 (1984).
12. A. Gevins *et al.* [*Science* **203**, 665 (1979)] have suggested that previous EEG research could be explained in terms of motor requirements of the tasks and not cognitive processes.
13. A paragraph of textbook-like material was shown on a screen to the subject, who was instructed to count the numbers of verbs in the passage. The math task consisted of a long division problem containing an error the subject was to find. The subjects were instructed that there might be more than one error.
14. C. M. Mooney, *Can. J. Psychol.* **11**, 219 (1957).
15. In both studies EEG was recorded by polygraph (Beckman R612). Beckman Ag-AgCl electrodes were held in place by a specially designed elastic cap which ensured location at the sites specified. Impedance for each electrode was below 5000 ohm (Grass EZM1E impedance meter). The fast Fourier transform program was performed with a PDP 11-34 sampling at a rate of approximately 100 per second.
16. These tasks were used by Harman and Ray and Erlichman and Weiner (*2*).
17. R. Hare, K. Wood, S. Britain, J. Shadman, *Psychophysiology* **7**, 408 (1970); P. Ekman and W. Friesen, *Unmasking the Face* (Prentice-Hall, Englewood Cliffs, N.J., 1975).
18. M. Safer, *J. Exp. Psychol. Gen.* **110**, 86 (1981).
19. Differences between frequency bands in experiment 1 suggested that little information would be lost by combining them in the manner of experiment 2.
20. PARAFAC is a three-mode factor-analytic procedure that implements Cattell's concept of proportional profiles. It is designed to identify a unique mathematical factor model which reflects the latent factor structure without the distortions introduced by most rotational techniques. For applications and models see R. Harshman, P. Ladefoged, and L. Goldstein [*J. Acoust. Soc. Am.* **62**, 693 (1977)] and R. A. Harshman and S. A. Berenbaum [in *Present and Past in Middle Life*, D. H. Eichorn *et al.*, Eds. (Academic Press, New York, 1980)].
21. This research has been recently reviewed by M. W. van der Molen, R. J. M. Somsen, J. F. Orlebeke in *Advances in Psychophysiology* (JAI Press, Greenwich, Conn., 1984).
22. B. Walker and J. Walker, *Int. J. Psychophysiol.* **1**, 65 (1983).
23. J. Lacey and B. Lacey, *Am. Psychol.* **33**, 99 (1978).
24. A. Gevins *et al.* (*12*); in *Cerebral Hemispheric Asymmetry*, J. Hellige, Ed. (Praeger, New York, 1983).
25. Whether the EEG beta results reflect differences in processing or differential hemispheric involvement is not yet known. Unlike alpha activity, beta activity has not been the topic of extensive research.
26. Supported in part by BRSG grant RR07082-14 (NIH) and the Faculty Research Fund (Liberal Arts) of Pennsylvania State University.

7 January 1985; accepted 15 January 1985

Widespread Distribution of Brain Dopamine Receptors Evidenced with [^{125}I]Iodosulpride, a Highly Selective Ligand

Abstract. *The new benzamide derivative [^{125}I]iodosulpride is a highly sensitive and selective ligand for D-2 dopamine receptors and displays a very low nonspecific binding to membrane or autoradiographic sections. On autoradiographic images, D-2 receptors are present not only in well-established dopaminergic areas but also, in a discrete manner, in a number of catecholaminergic regions in which the dopaminergic innervation is still unknown, imprecise, or controversial, as in the sensorimotor cerebral cortex or cerebellum. This widespread distribution suggests larger physiological and pathophysiological roles for cerebral dopamine receptors than was previously thought.*

More than 20 radioactive ligands have been used to label dopamine receptors, and these ligands have already provided much information about the pharmacology, biochemistry, and localization of the receptors, as well as information about the mode of action of antipsychotic drugs (*1*). Nevertheless, the ligands available until now either have lacked selectivity or have a relatively high nonspecific binding, so that a detailed autoradiographic mapping of cerebral dopamine receptors, particularly in regions of low density, has not been obtained despite several attempts (*2*). Ligands labeled with ^{125}I, because their specific radioactivity is 50 to 100 times higher than that of corresponding ^{3}H-labeled ligands, have been successfully used in sensitive assays of various receptors (*3*) but so far have not been proposed for dopamine receptors. We have now shown that [^{125}I]iodosulpride—that is, *N*-[(1-cyclopropylmethyl-2-pyrrolidinyl) methyl]-2methoxy-4-iodo-5-ethylsulfonyl-benzamide (specific activity, 2000 Ci/mmol)—is a highly selective dopamine ligand that allows the demonstration of dopamine receptors in cerebral areas in which they were only suspected or were not known to occur.

[^{125}I]Iodosulpride was prepared (*4*), and its properties were first assessed in standard filtration assays. With 0.2 n*M* [^{125}I]iodosulpride, binding was linear with up to 100 μg of tissue protein in striatum and up to at least 150 μg of tissue protein in substantia nigra (Fig. 1A). The sensitivity of the receptor assay is such that 5 μg of striatal or 40 μg of nigral protein per incubation was sufficient to ensure a total binding value twice as high as the nonspecific binding plus the filter blank. Scatchard and computer-assisted (*5*) analyses of the saturation curve at equilibrium (reached after 15 to 20 minutes at 30°C) revealed an apparently homogeneous population of striatal sites (Fig. 1B) with a dissociation constant (*K*d) of 1.6 ± 0.3 n*M*, a Hill coefficient of 0.99 ± 0.12, and a maximum number of binding sites (B_{max}) of 449 ± 25 fmol per milligram of protein, the latter value being closely similar to the B_{max} of [^{3}H]domperidone in the same preparation. The pharmacology of striatal [^{125}I]iodosulpride recognition sites (Fig. 1C) was also similar to that of sites labeled with [^{3}H]domperidone, which is generally recognized (*5, 6*) as the most selective ligand yet available for D-2 receptors—that is non–D-1 receptors, according to the nomenclature of Kebabian and Calne (*7*). More recently, there has been a proposal to distinguish two subclasses of [^{3}H]domperidone sites in striatum (termed D-2 and D-4, respectively, among which only D-2 sites are present in the pituitary) on the basis of discrimination by a few benzamide derivatives like sulpiride (but not metoclopramide) (*5*). Initial studies indicate that