reticular nature could be observed. In the presence of 10 μM Colcemid (Fig. 2D), the fluorescence was scattered throughout the cytoplasm, consistent with the morphology of the Golgi apparatus in fixed, Colcemid-treated cells (*19*).

Finally, we asked whether the distribution of the Golgi apparatus in living cells at different mitotic stages would parallel that of fixed cells in which the Golgi becomes fragmented and almost disappears during metaphase (*6, 20*). Human skin fibroblasts were labeled with C_6-NBD-ceramide and chromosomes were vitally stained with Hoechst 33342 (*21*). During interphase (Fig. 3A) the Golgi had its distinctive, threadlike appearance. As the cell rounded up in prophase (Fig. 3B), the Golgi was visible as scattered punctate regions in the cytoplasm. At metaphase (Fig. 3C), these regions were reduced to infrequent, pinpoint areas of fluorescence. The background fluorescence appeared to have increased because of the rounding of the cell. During anaphase (Fig. 3D), the Golgi apparatus reappeared close to the separating chromosomes. Finally, in late telophase (Fig. 3E), the characteristic perinuclear structure reappeared.

In conclusion, C_6-NBD-ceramide was distributed in the same manner as traditional Golgi stains in various cell types and during mitosis or drug treatment. The advantages of rapidity and ease of labeling permitted immediate visualization of alterations in Golgi morphology in living cells.

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11. Lipid vesicles were formed (*9*) by ethanol injection of C_6-NBD-ceramide and dioleoylphosphatidylcholine (in a molar ratio of 20/80) in 10 mM Hepes-buffered calcium- and magnesium-free Puck's saline and dialysis at 2°C overnight against this buffer. The vesicle preparation was diluted with 18 mM HMEM to a final concentration of 5 to 10 nmol of C_6-NBD-ceramide per milliliter.
12. A solution of defatted BSA (0.68 mg/ml; Sigma) in HMEM was added to a tube containing desiccated C_6-NBD-ceramide for a final concentration of 10 nmol of C_6-NBD-ceramide per milliliter. The tube was immersed in a bath sonicator for 5 to 10 seconds to obtain a clear solution.
13. Although the distribution of fluorescence obtained by both methods was identical, the uptake of C_6-NBD-ceramide may occur by different mechanisms in the two procedures. In liposome-cell incubations at 2°C, uptake of C_6-NBD-ceramide is solely by net transfer (*9*). Therefore, this method may be preferable when the route of uptake must be known. In C_6-NBD-ceramide–BSA incubations, the route of incorporation is unknown and may involve an endocytic pathway, resulting in the uptake of both BSA and ceramide by the cells. However, this method was rapid and convenient for use with cells whose morphology changed during incubations at low temperatures.
14. Fluorescence microscopy was carried out with a Zeiss IM-35 inverted microscope, equipped with filter packs (Zeiss 487717 and 487715) that allowed no crossover between NBD and rhodamine fluorescence. For visualization of Hoechst 33342 fluorescence, Zeiss filter pack 487702 was used.
15. Cells were fixed as described by G. Griffiths, P. Quinn, and G. Warren [*J. Cell Biol.* **96**, 835 (1983)] and stained for thiamine pyrophosphatase (*4*), except that cover slips were inverted (*20*) in the reaction medium for 3 hours at 37°C. No product was formed in the absence of substrate, and the presence of C_6-NBD-ceramide had no effect on the reaction.
16. Fluorescent antibody staining of the Golgi apparatus was carried out as described (*8*) with a monoclonal antibody (53FC3) directed against a Golgi membrane protein found in rodent cells (*6*).
17. BHK-21 and 3T3 cell lines were obtained from American Type Culture Collection (Rockville Md.). Human cell line GM302 was obtained from the Genetic Mutant Cell Repository (Camden, N.J.). Other established cell lines (B104 CHO, LA-23, MDCK, MDBK, NB77, PTK2 and Vero) were supplied by B. Geiger (Weizmann Institute, Israel). Primary cultures of chick sympathetic ganglia and chick myotubes were supplied by M. Tamkun and D. Fambrough (Carnegie Institution, Baltimore, Md.) rat hepatocytes by S. Yedgar (Hebrew University, Israel), and a newt intestinal cell preparation by L. Epstein (Carnegie Institution).
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21. GM302 cells were first incubated with C_6-NBD ceramide–containing vesicles for 1/2 hour at 2°C, then washed and incubated in medium containing Hoechst 33342 (2.5 μg/ml) for 3 minutes at 37°C [M. E. LaLande, V. Ling, R. G Miller, *Proc. Natl. Acad. Sci. U.S.A.* **78**, 36 (1981)].
22. We thank J. Gall and L. Epstein for helpful discussions, A. Novikoff and P. Novikoff (Albert Einstein College of Medicine, New York for the gift of thiamine pyrophosphate and advice on the staining procedure, and B. Burke (Johns Hopkins School of Medicine, Baltimore Md.) for providing the monoclonal antibody Supported by grant GM-22942 from the U.S Public Heath Service and by a postdoctoral fellowship (GM-08848) from the National Institutes of Health (N.G.L.).

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Trigeminal-Taste Interaction in Palatability Processing

Abstract. *Peripheral transection of the sensory branches of the trigeminal nerve in rats unbalanced palatability, selectively reducing the ingestive actions elicited by preferred tastes but leaving unchanged the aversive actions elicited by unpreferred tastes. The reduction in the number of positive ingestive actions occurred even though the capacity to emit these actions remained unimpaired. These findings show that there is an interaction between somatosensation and gustation in the processing of palatability.*

Trigeminal deafferentation, which removes somatosensation selectively from the mouth and face, severely disrupts food intake in rats, cats, and pigeons (*1–6*). The disruption is not attributable solely to a simple incapacity to execute required movements, but also to reduced responsiveness to food, reduced probability of initiating a meal (*1, 2*), and disrupted dietary selection of protein and carbohydrate nutrients (*3*). Deafferentated rats are hypophagic in response to food pellets, and can be maintained best on highly preferred foods (such as moist cereal mash).

The severity and nature of the feeding deficit produced by deafferentation have led to the suggestion that trigeminal oro sensation contributes more to the motivational control of ingestive behavio than does gustatory information (*1*); conversely, it has been suggested that trigeminal deafferentation leaves a rat ab normally sensitive to the perceived palatability of its diet (*1*), possibly becaus remaining gustatory cues are more sa

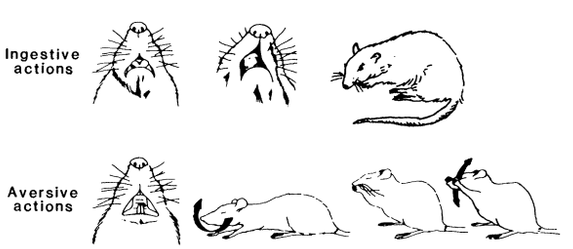


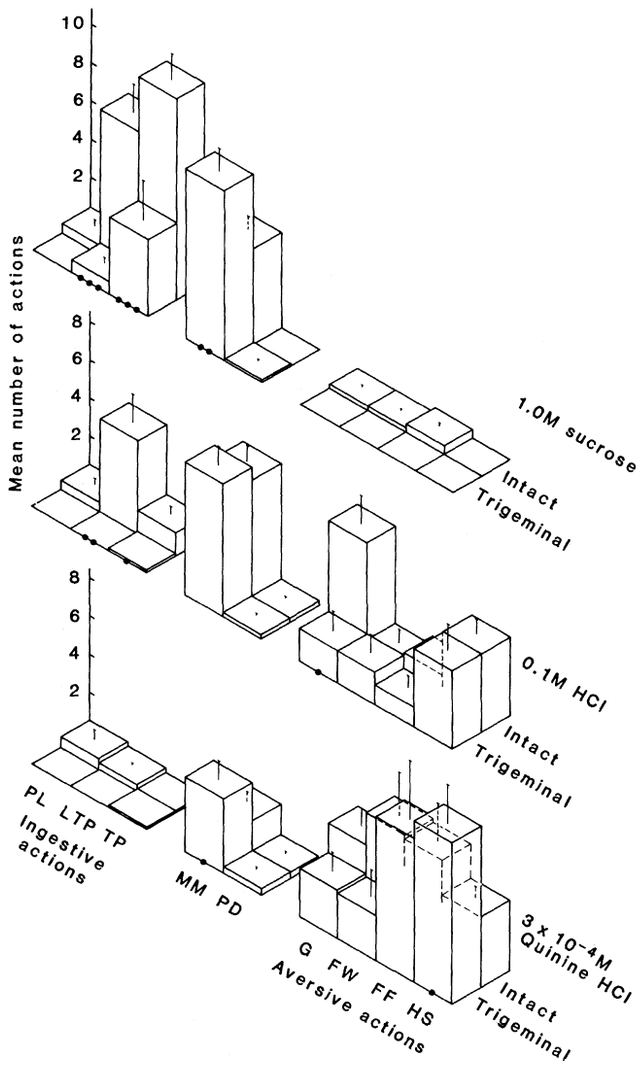
Fig. 1. Taste-elicited actions Ingestive actions are rhythmi tongue protrusion, nonrhyth mic lateral tongue protrusion and paw licking. Aversive ac tions are gaping, headshaking face washing, and forelim flailing.

lient in the absence of trigeminal input (*3*). Others, however, have not found clear support for exaggerated "finickiness" (*3*).

A change in the control of feeding by palatability (*7, 9*) after trigeminal deafferentation can be studied best by measures that evaluate palatability directly, rather than inferentially through measures of food consumption. Such measures are provided by the highly stereotyped action patterns (tongue protrusion, gaping, and so forth) that are elicited in rats by oral infusion of solutions (Fig. 1). These actions are controlled in their most basic form by the caudal brainstem, but are also influenced by descending forebrain controls (*8*, 9). The type and number of these actions are determined chiefly by the composition of the taste solution (*8*). Physiological factors (such as satiety and sodium balance) that alter palatability ratings of certain tastes in humans (*10*) also change taste-elicited actions in rats in ways that parallel the human effects (*11*). Learned associations between tastes and postingestive consequences, such as illness, which change palatability ratings in humans (*12*), also change taste-elicited actions in rats (*13–15*). Finally, associations with consequences that would not be expected to change palatability ratings in humans, such as shock or lactose intolerance (*12*), do not change these actions in rats.

The results reported here, obtained by combining behavioral measures of taste-elicited actions with peripheral trigeminal deafferentation, suggest that the perceived palatability of taste stimuli is altered after deafferentation. Positive reactivity to taste solutions appears to be strongly diminished; negative reactivity is either unaffected or only slightly diminished.

Adult male Sprague-Dawley rats were anesthetized and implanted bilaterally with oral cannulas to allow solutions to be infused into the mouth (*16*). After recovery, the rats were presented with two concentrations of three taste stimuli: sucrose, which elicits primarily ingestive actions; HCl, which elicits both ingestive and aversive actions; and quinine HCl, which elicits primarily aversive actions (*17*). Responses to the six stimuli were videotaped via a mirror positioned beneath the transparent floor of the test chamber. The occurrence and duration of each ingestive and aversive action were analyzed in slow motion by an observer who keyed the responses into a computer (*18*).



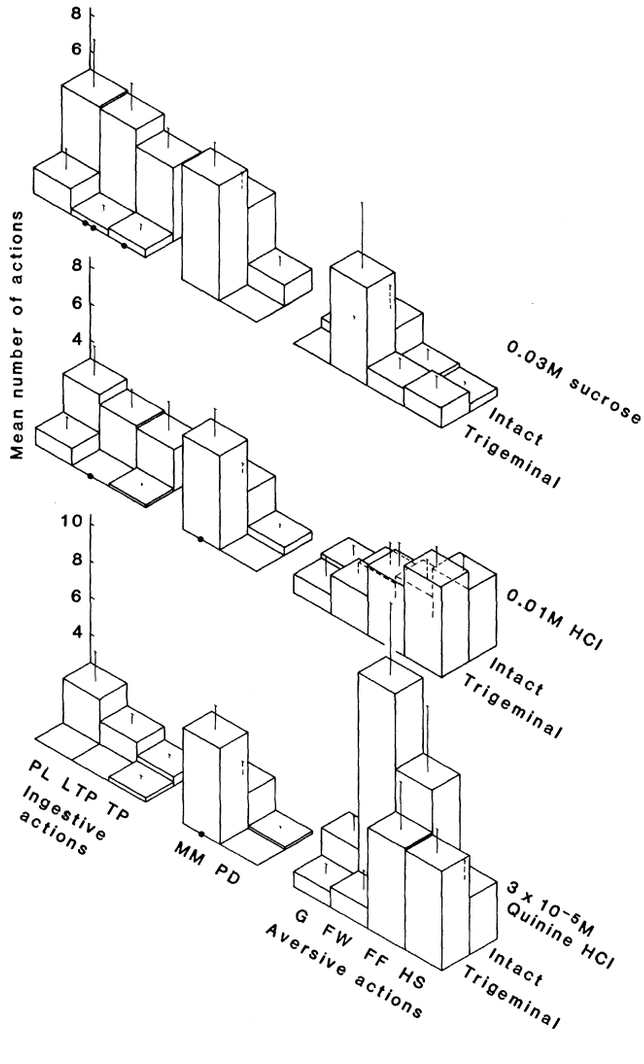


Fig. 2 (left). Actions in response to high concentrations of solutes. Each column gives the number of repetitions of a particular action elicited by the indicated taste (mean ± standard error; $n = 11$ rats). Ingestive actions are paw licking (PL), lateral tongue protrusion (LTP), and tongue protrusion (TP). Neutral or compromise responses are mouth movements (MM) and passive dripping (PD). Aversive actions are gaping (G), face washing (FW), forelimb flailing (FF), and headshaking (HS). Dots denote significance [three dots, $P < 0.01$; two dots, $P < 0.02$; and one dot, $P < 0.05$ (Wilcoxon paired test)]. Fig. 3 (right). Actions in response to low concentrations of solutes. As in Fig. 2, dots denote significance (determined here by Mann-Whitney U test).

Eleven of the rats were reanesthetized and subjected to bilateral trigeminal deafferentation [section of the inferior alveolar, lingual, and auriculotemporal nerves of the mandibular branch and of the anterior superior alveolar and infraorbital nerves of the maxillary branch (*19*)]. This procedure removes pain and somatosensation from the upper and lower lips, gums, and incisors; the chin; the anterior tongue; the oral mucous membrane; the vibrissae; and the facial pads. Gustation and trigeminal motor function are spared (*1, 2, 6*). Four other rats served as surgical controls in which the nerves were exposed but not sectioned. To prevent our measurements from being affected by general debilitation, body weight was not allowed to drop below 85 percent of its predeafferentation value (*20*). Each rat was presented again with the six taste solutions (*21*).

The responses of intact and deafferentated rats to the three high concentrations are shown in Fig. 2 (*22*). Among intact rats, sucrose elicited ingestive nonrhythmic lateral tongue protrusions and rhythmic midline tongue protrusions, together with more neutral rhythmic mouth movements (*18*). Hydrochloric acid elicited ingestive actions plus a number of aversive actions, including gaping and headshaking. Quinine elicited primarily aversive actions: gaping, face washing, forelimb flailing, and headshaking. Deafferentated rats showed significantly fewer ingestive lateral and rhythmic tongue protrusions in response to sucrose and significantly more of the more neutral mouth movements. Similarly, they showed fewer lateral and rhythmic tongue protrusions and fewer aversive gapes in response to HCl. To quinine, deafferentated rats again showed more of the more neutral mouth movements, and aversive responses were not diminished (*23*).

In summary, the deafferentated rats showed reliably fewer overall ingestive actions to most tastes [ingestive scores for intact and deafferentated rats, 59.6 ± 12.0 and 12.4 ± 4.3, respectively (means $\pm$ standard error; $P < 0.01$, Wilcoxon paired test)], but overall aversive actions were not affected to a statistically significant extent. Furthermore, the deafferentated rats showed more neutral mouth movements than did the intact rats, again suggesting that they perceived tastes as being less palatable (*24*). An essentially identical pattern was seen in response to the lower concentrations (Fig. 3). It is important to note that tongue protrusions were not abolished by deafferentation, which might have suggested that the rats were unable to perform them. All the components of ingestive actions were observed after deafferentation, but in significantly smaller number. Furthermore, the actions that did occur in deafferentated rats were not slowed or prolonged—as far as could be determined in a frame-by-frame analysis (*25*)—suggesting again that the capacity to emit the actions was not affected. Most important, a separate analysis of the responses occurring during postprandial grooming, after the infusion had ended, showed deafferentated rats to protrude the tongue more frequently than intact rats [mean scores for intact and deafferentated animals, 8.1 ± 1.5 and 46.5 ± 18.3, respectively ($P < 0.01$, Mann-Whitney U test)]. This eliminates a general motor incapacity to protrude the tongue as an explanation for our observations. The number of ingestive actions by surgical controls was not reduced in response to any taste.

These results suggest that trigeminal input interacts with gustatory information to enhance primarily the positive aspects of palatability. Palatability is therefore not independent of trigeminal input, but neither does trigeminal sensation mask gustation nor add a simple constant value to the positive or negative assessment of palatability. Instead, the positive assessment of the palatability of a solution is markedly amplified by the presence of trigeminal orosensation (*26*). The negative assessment of the palatability of solutions is much less affected (*27*). The apparent "finickiness" of deafferentated rats may result from the need for stronger positive factors to balance stable aversive ones. Ordinary foods may no longer be perceived as being sufficiently palatable to evoke ingestion. This interaction between distinct sensory systems could have consequences that extend beyond behavior. The reflexive, preabsorptive release of insulin that is elicited by the taste of food depends in part on the perceived palatability of the taste (*13, 28*). Our findings suggest that this response, at least, should be much diminished in deafferentated rats. The loss of this neuroendocrine reflex would profoundly affect the subsequent metabolism of ingested foods, especially carbohydrates (*29*). Changes in palatability after trigeminal deafferentation could therefore change the physiological response to foods as well as the behavioral reaction.

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16. Flared polyethylene 100 tubing was implanted anterolateral to the first maxillary molar, brought out at the dorsal skull, attached to 19-gauge steel tubing, and anchored with skull screws and dental cement (*8*).
17. Solution concentrations were 1.0 and 0.03M sucrose; 0.1 and 0.01M HCl; and 3×10^{-4} and $3 \times 10^{-5}M$ quinine HCl. After being habituated to the test chamber, rats received one solution per day in balanced order. Each presentation consisted of 1 ml of solution infused remotely into the mouth over 1 minute.
18. Ingestive actions were paw licking; nonrhythmic lateral tongue protrusion past the lip followed by forward extension, lasting 164 ± 9 msec (mean $\pm$ standard error); and rhythmic tongue protrusions along the midline, with a cycle length of 166 ± 7 msec. Rhythmic mouth movements at the same or lower frequency were classified as weakly ingestive or ambivalent and passive drooling of the solution as a neutral response. Aversive actions were gaping (wide opening of the mandible and retraction of the lips, lasting 124 ± 8 msec); face washing (either a single wipe with the paws or a bout of several wipes); forelimb flailing (shaking of the forelimb in the horizontal plane with a frequency of greater than 60 Hz); and headshaking at greater than 60 Hz. Videotapes were scored blind at one-tenth speed. A microcomputer was calibrated to this speed, and each action corresponded to a key on the computer keyboard. As each action occurred its key was pressed, creating a transcript of the number, timing, and order of each action.
19. Access to the mandibular branch nerves was obtained through the ventral neck approach of C.P. Richter [in *L'Instinct dans le Comportement des Animeaux et de l'Homme*, M. Autori, Ed. (Masson, Paris, 1956), pp. 556–629]. Maxillary branch nerves were approached in the infraorbital canal, medial to the eye. All surgery was conducted under $\times 15$ visual magnification. Identified nerves were hooked and then sectioned with microscissors (*1*).
20. After deafferentation rats were given access to commercial baby cereal mixed with water to form a loose mash. In addition, they were intubated with 10 ml of water twice daily for 3 days after surgery to prevent dehydration. If body weight fell below 85 percent of its original value, intubations of a milk diet (equal parts sweetened condensed milk and water) were substituted until body weight recovered (which occurred within 1 week). Since the reduced caloric intake of deafferentated rats might be expected to enhance the palatability of sweet tastes (*10, 11*), the apparent reduction of palatability after trigeminal deafferentation is especially striking. To prevent incisor overgrowth, rats were briefly anesthetized once weekly for clipping and sanding of the incisors.

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)].
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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