tyrosine seems to depend in part on pH—being negative below pH 6.0, positive above 6.3, and somewhat variable in the pH range 6.0 to 6.3. Response to γ-aminobutyric acid appears to be concentration dependent, being positive at low (10^{-6} to $10^{-5}M$) and negative at high (10^{-4} to $10^{-2}M$) concentrations. However, both chemicals gave somewhat variable results from one experiment to the other; this subject requires further study. Phenylalanine ($6 \times 10^{-3}M$) and 5-hydroxytryptophan ($5 \times 10^{-4}M$) gave negative responses only at the highest concentration tested. Response to the choline analog carbachol (carbamyl choline) was positive in the range 5×10^{-6} to $5 \times 10^{-4}M$.

When the epinephrine threshold is compared to Avogadro's number, it appears that this species is responding to concentrations below 10^6 molecules per milliliter (10^3 molecules per cubic millimeter). We were initially skeptical of these results but repeated trials have consistently borne them out. Possibly the swimming cell explores a sufficiently extensive surface of agar to be influenced by very small concentrations. This hypothesis in turn invites further speculation. It seems likely that stimulation by some minimum threshold number of molecules is needed to evoke the behavioral response but at these concentrations, if the molecules are randomly distributed in the gel, the organism is unlikely to encounter more than one at a time. Perhaps there is a functional "memory" that keeps track of stimulation by molecules encountered during a given time. A plausible mechanism would be a graded series of subthreshold increases in a membrane generator potential, as with nerve cells and some known protozoan responses (*8*).

Most pharmacological studies with protozoa have assayed growth or metabolic responses to much higher concentrations (*9*). Some studies of behavioral responses to chemicals may be related to those reported here; in particular, Sleigh noted stimulation of the motion of ciliate protozoa by epinephrine (*10*).

The specificity of responses is seen in the difference in effects of choline and its analog carbachol. Elsewhere (*2*) we reported a positive response to L-fucose, found in seaweeds, but the synthetic D-fucose is inert. Similarly, responses to β-dimethyl-propiothetin and betaine were positive, whereas the analog dimethyl-β-acetothetin was inert.

These observations indicate the presence of relatively specific chemoreceptors in this species, comparable to those in bacteria (*11*) and both cellular (*12*) and true slime molds (*13*). The great sensitivity to certain neurochemicals seems puzzling from an ecological point of view, but it suggests that *C. cohnii* may prove to be a useful pharmacological tool.

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7. In a random, or Poisson, distribution the expected values of variance and mean of the samples are equal. A number of indices of aggregation or "clumpedness" based partly on this fact are described in E. C. Pielou, *An Introduction to Mathematical Ecology* (Wiley, New York, 1969). For instance, F. N. David and P. G. Moore [*Ann. Bot. Lond.* **18**, 47 (1954)] studied the "index of clumping" I = (variance/mean) − 1. By their test and others, our data all have very clumped distributions, so that standard (parametric) methods are inappropriate.
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Right Hemisphere Lateralization for Emotion in the Human Brain: Interactions with Cognition

Abstract. *Right-handed subjects tend to look to the left when answering affective questions. The relative shift in gaze from right to left is accentuated when the questions also involve spatial manipulation and attenuated when the questions require verbal manipulation. The data support the hypothesis that the right hemisphere has a special role in emotion in the intact brain, and that predictable patterning of hemispheric activity can occur when specific combinations of cognitive and affective processes interact.*

When a person is asked to picture and describe a happy experience he had, a complex pattern of both cognitive and affective processes is evoked. In the past, such intricate behavioral epochs were studied merely descriptively, since sensitive methods to test relevant process-oriented theories were lacking. However, recent research assessing hemispheric asymmetry in the intact brain has provided a new means of revealing some of the component neuropsychological mechanisms underlying complex, multiprocess tasks. This can be accomplished by comparing the relative activation of the electroencephalogram (EEG) between the two hemispheres (*1*), by assessing performance on a variety of behavioral tasks which reflect hemispheric involvement (*2*), or more simply by observing the direction in which a person shifts his gaze while answering a reflective question (for example, looking to the right is indicative of relative left hemispheric involvement) (*3–8*). When these measures are used with right-handed subjects, verbal and sequential processes and behaviors such as writing a letter or reflecting on a verbal question have typically been associated with a predominance of left hemispheric function, while processes found to be more associated with relative right hemispheric activation include (i) spatial tasks such as a block design test or reflecting on a spatial-pictorial question, and (ii) musical tasks such as identifying instances of a particular theme in an unfamiliar musical selection.

Recently, the right hemisphere has been indirectly implicated as having a special role in the regulation of affective tone (*9, 10*) although few data in the intact human have been collected to date (*11*). Clinically, patients with unilateral left hemispheric lesions typically respond quite severely to their illness, evidencing more instances of "catastrophic reaction" than do comparable patients with unilateral right hemispheric lesions. Interestingly, the latter patients often show a characteristic "indifference reaction" to their condition. After discussing the brain damage literature on asymmetry of affective tone, Galin (*10*) concluded that "at present, the evidence for these differences pertains only to reactions to injury; we do not know whether or to what extent the two hemispheres in the intact brain may each subserve characteristic defensive styles or affective tone."

Using lateral eye movements as an indicator of asymmetric hemispheric engagement (activation of each cerebral hemisphere tends to produce orientation to the contralateral side of the body) (*12*), we report that in intact right-handed subjects, emotional questions elicit greater right hemispheric activation than comparable nonemotional questions. Moreover, the affective quality can be distinguished from the more cognitive (verbal or spatial) demands of the questions, and their interaction can be uncovered. We find that questions requiring both spatial and emotional processing result in accentuated right hemispheric activation, whereas questions demanding both verbal and nonemotional processes result in the greatest left hemispheric activation. The remaining two types of questions (verbal-emotional and spatial-nonemotional) fall predictably in between.

Table 1. Mean and standard deviations (S.D.'s) of left and right LEM's and difference scores for the main effects and interactions. Separate means are presented for each experiment (exp. 1, $N = 10$; exp. 2, $N = 14$); S.D.'s are based on the total sample ($N = 24$). Each mean is based on ten questions.

Question type	Left LEM's			Right LEM's		
	Means		Total S.D.	Means		Total S.D.
	Exp. 1	Exp. 2		Exp. 1	Exp. 2	
V	3.90	4.73	2.86	5.35	3.29	2.88
S	4.20	5.18	2.33	3.40	2.05	1.76
NE	3.60	4.43	2.46	5.05	2.98	2.46
E	4.50	5.48	2.68	3.70	2.36	2.16
VNE	3.40	4.04	3.00	6.10	3.79	3.25
SNE	3.80	4.82	2.41	4.00	2.18	2.29
VE	4.40	5.43	3.05	4.60	2.79	2.86
SE	4.60	5.54	2.53	2.80	1.93	1.81
			Differences			
V–S	–0.30	–0.45	1.56	1.95	1.24	1.91
NE–E	–0.90	–1.05	1.35	1.35	0.62	1.52
VNE–SE	–1.20	–1.50	2.23	3.30	1.86	2.35
VNE–SNE	–0.40	–0.78	2.29	2.10	1.61	2.74
VNE–VE	–1.00	–1.39	1.98	1.50	1.00	2.11
SNE–SE	–0.80	–0.72	1.68	1.20	0.25	2.16
VE–SE	–0.20	–0.11	1.66	1.80	0.86	2.07
VE–SNE	0.60	0.61	1.85	0.60	0.61	2.52

Two experiments were performed involving 10 and 14 right-handed undergraduate subjects, respectively, recruited for an experiment on "cognitive processes in response to different kinds of questions." They were instructed that their answers would be recorded on audio tape for subsequent content analysis, thereby minimizing attention to the eyes or face.

The basic procedure in each experiment was the same. Subjects were seated behind a desk with a microphone in the center directly facing the experimenter, who was approximately 1.5 m away with a homogeneous visual field serving as the background. Subjects were told that the experimenter was interested in their verbal answers to mask the true dependent variable.

Lateral eye movements subtending an arc of 5° or more were unobtrusively scored visually by the experimenter and served as the main dependent measure. Blinks and stares were scored as no response. In the second experiment, to assess reliability and potential bias of the observer, eye movements were scored by two independent experimenters; high reliability was obtained, and disagreements about judgments of left versus right occurred in only 2 percent of the trials. Care was taken to ensure that the experimenter asking the questions was directly in front of the subject; the position of a second experimenter was also randomly alternated to the right and to the left of the active experimenter across subjects.

Most studies concerned with asymmetry of eye movements in response to differential cognitive demands of reflective questions have not employed a situation with the experimenter facing the subject because, as Gur and co-workers (*5*) have shown, subjects may move their eyes predominantly in one direction regardless of question type. This is particularly true if attention is directed to the subject's face and if the situation is anxiety producing. Furthermore, situations without the experimenter facing the subject, which nevertheless require subjects to fixate centrally, also attenuate or abolish question-specific lateral eye movement shifts (*6*). However, if care is taken to provide subjects with a cover story to distract them from noticing that their eye movements are being recorded, lateral eye movements can be a useful index of cerebral lateralization of cognitive function (*7*), including situations involving face-to-face interaction (*8*).

Forty questions were created to make a two-by-two design involving the following four classes of stimuli: verbal-nonemotional (VNE), verbal-emotional (VE), spatial-nonemotional (SNE), and spatial-emotional (SE). Examples of each type of question are: VNE, "What is the primary difference between the meanings of the words 'recognize' and 'remember'?" or "What is meant by the proverb 'One today is worth two tomorrows'?"; VE, "What is the primary difference between the meanings of the words 'mischief' and 'malice'?" or "For you, is anger or hate a stronger emotion?"; SNE, "On the face of a quarter, does the face of George Washington look to the right or to the left?" or "Imagine a rectangle. Draw a line from the upper left-hand corner to the lower right-hand corner. What two figures do you now see?"; and SE, "When you visualize your father's face, what emotion first strikes you?" or "Picture and describe the last situation in which you cried." To minimize any differences on the verbal-spatial continuum from confounding the interpretation of the emotional-nonemotional comparison, the significant words in these latter questions were matched as closely as possible on Paivio *et al.*'s scale of imagery value for nouns (*13*). An attempt was made to equate the affective quality of the VE and SE questions; ratings of the items by the subjects after the experiments yielded comparable emotion ratings for the two sets of questions. Questions were presented in blocks of four trials containing each of the four types of questions, randomized in order over the ten blocks.

The 40 questions were read to each subject in the counterbalanced order, and the direction of the first lateral eye movement following each question was recorded (*14*). The mean and standard deviations of left and right lateral eye movements (LEM's) per question type, as well as difference scores for the main effect and interactions, are presented in Table 1. Since the pattern of findings within each experiment yielded similar results, the data from both studies were averaged together and are displayed in Fig. 1. An overall three-way analysis of variance was performed with verbal-spatial, nonemotional-emotional, and left-right eye movement as repeated factors, followed by two-tailed t-tests on the significant interactions. There was a highly significant interaction of verbal versus spatial question type and left versus right LEM's ($P < .001$). This is primarily due to a greater number of right LEM's elicited on verbal questions than on spatial ones ($t = 3.933$, $P < .001$). Thus, we confirm that verbal questions on the average elicit greater relative left hemispheric activation than comparable spatial questions.

The overall effect for emotional versus nonemotional questions by left versus right LEM is also highly significant ($P < .005$). This difference is attributed to not only significantly fewer right LEM's on the emotional questions than on the nonemotional questions ($t = 2.99$, $P < .01$), but also to significantly more left LEM's on the emotional versus nonemotional questions ($t = 3.929$, $P < .001$). We thus confirm that emotional questions, on the average, elicit more right hemispheric activation and less left hemispheric activation than comparable nonemotional questions (*15*).

The final result deserves particular emphasis: when each of the four classes of questions is separately examined, Fig. 1 indicates that SE questions, predicted to enhance right hemispheric activation and decrease left hemispheric activation, elicited the fewest right LEM's and the most left LEM's, while VNE questions, predicted to accentuate left hemispheric activation, elicited the most right movements and the fewest left movements. The results for the other two classes of questions fell in between (*16*).

Separate t-tests for the left and right LEM's comparing each pair of the four question types clarifies this interaction. Simply stated, the two extreme question types (SE and VNE) differ significantly from each other on both left ($P < .01$) and right ($P < .001$) LEM's, and, furthermore, each differs from the other two intermediate question types (SNE and VE) on at least one of the LEM measures. The intermediate question types do not differ significantly from one another on either LEM measure. The pattern of t-tests also provides further support for the overall analyses, indicating that for left LEM's the emotional-nonemotional effect holds separately for both verbal ($P < .01$) and spatial ($P < .05$) questions, whereas a verbal-spatial effect is not observed for either emotional or nonemotional questions. On the other hand, for right eye movements a significant verbal-spatial effect is separately observed for both emotional ($P < .01$) and nonemotional ($P < .01$) questions, whereas a significant emotional-nonemotional effect is obtained only for the verbal questions ($P < .02$). These data support the hypothesis that patterning of hemispheric processes can occur in complex tasks, and that affective processes can be differentiated from cognitive processes in terms of hemispheric functioning.

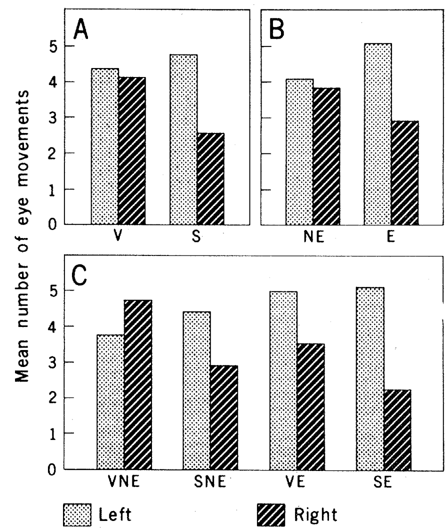

Fig. 1. Mean number of left and right LEM's averaged across experiments 1 and 2 for the following conditions: (A) verbal and spatial; (B) nonemotional and emotional; and (C) verbal-nonemotional, spatial-nonemotional, verbal-emotional, and spatial-emotional. Each mean is based on ten questions.

Additional research distinguishing between different classes of emotions (*17*) and types of affective tasks, as well as utilizing other measures of hemispheric involvement (such as the EEG), should more precisely localize the source of this phenomenon and the variables affecting it (*18*). In the meantime, the results of this experiment provide new support for the hypothesis of a special role for the right hemisphere in regulation of emotional processes in the intact human and its relationship to cognitive tasks involving differential hemispheric patterning (*19*).

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14. In instances of disagreement between experimenters 1 and 2, the average of their scoring was utilized.
15. Spatial questions elicited significantly more no responses than verbal questions (mean = 2.62 and 1.47, respectively; $P < .001$), while there were no significant differences between emotional versus nonemotional questions (mean = 2.01 and 2.07, respectively). In addition, spatial questions elicited significantly more no responses than both nonemotional ($P < .02$) and emotional ($P < .001$) questions. Moreover, when the four interactive conditions were examined, every comparison involving verbal versus spatial including the two intermediate conditions (that is, SNE versus VE, SNE versus VNE, SE versus VNE, and SE versus VE) was significant at $P < .01$, while the remaining two comparisons (VE versus VNE and SE versus SNE) were nonsignificant. Since the no response scores included both blinks and stares, it is difficult to unambiguously interpret data from this category. However, one possible interpretation of this finding is that if no response (composed primarily of stares) is indicative of bilateral involvement, as suggested by Galin and Ornstein (*3*), then spatial questions elicit greater bilateral activation than any other question type. This further supports our notion of differential hemispheric patterning subserving verbal versus spatial and nonemotional versus emotional processes, and is consistent with recent data suggesting that at least some spatial tasks may benefit by bilateral engagement [A. W. H. Buffery and J. A. Gray, in *Gender Differences: Their Ontogeny and Significance*, C. Ounsted and D. C. Taylor, Eds. (Churchill, London, 1972), p. 123].
16. The difference between left and right eye movements was higher during SE questions (indicative of greater relative right hemispheric activation) than VNE questions for 87.5 percent of the sample. Of these subjects, 71.4 percent also showed the predicted ordering for VE and SNE questions, with the average L minus R values falling in between or equal to SE and VNE scores. The number of left LEM's exceeds the number of right LEM's for each of the four main question types. It is possible that our sample contained a larger number of individuals who consistently looked left following the questions than those who consistently looked right. If we adopt the convention employed by other investigators (*5*) of classifying an individual as a "left mover" or "right mover" if on at least 70 percent of all questions he moved his eyes in a consistent direction, 25 percent of the present sample are left movers while none are right movers. Thus, the greater proportion of left movers in the present sample could account for the greater number of overall left LEM's obtained. The majority of subjects, however, did not show consistent unidirectional LEM's.
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