counted without knowledge of the age group. For each case, the number of cells labeled in ZI was obtained by summing the results of the three rostral to caudal levels. For each age, results were expressed as means and standard deviations. Means were compared with the use of one-way analysis of variance. This analysis showed that the young animals (2 and 3 weeks old) contained significantly more retrogradely labeled cells in the ZI than normal adults ($P < 0.01$).

19. S. J. Shammah-Lagnado *et al.*, *Neuroscience* **15**, 109 (1985); M. E. Bickford and W. C. Hall, *Soc. Neurosci. Abstr.* **13**, 173 (1987); M. Peschanski, *Neuroscience* **12**, 465 (1984); K. J. Berkley, *J. Comp. Neurol.* **193**, 283 (1980); M. Rogerand and J. Cadusseau, *J. Comp. Neurol.* **241**, 480 (1985).
20. M. Steriade, A. Parent, N. Ropert, A. Kitsikis, *Brain Res.* **238**, 13 (1982).
21. U. Kim, E. Gregory, W. C. Hall, *Soc. Neurosci. Abstr.* **15**, 239 (1989).
22. The GAD antibodies were provided by D. Schmechel. The authors thank A. Kosobud for reading the manuscript. Supported by grants from the National Institute of Neurological and Communicative Disorders and Stroke (NS 26722), the National Institute on Alcohol Abuse and Alcoholism (AA 06965 and KO2-AA 00089), and the Air Force Office of Scientific Research (90-0266) to J.K.C. and by a fellowship from the University of São Paulo to M.A.L.N. (FAPESP 88/4044-9).

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Attentional Modulation of Neural Processing of Shape, Color, and Velocity in Humans

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Positron emission tomography (PET) was used to measure changes in regional cerebral blood flow of normal subjects, while they were discriminating different attributes (shape, color, and velocity) of the same set of visual stimuli. Psychophysical evidence indicated that the sensitivity for discriminating subtle stimulus changes was higher when subjects focused attention on one attribute than when they divided attention among several attributes. Correspondingly, attention enhanced the activity of different regions of extrastriate visual cortex that appear to be specialized for processing information related to the selected attribute.

PEOPLE CAN RESPOND TO ONLY A small amount of the sensory information present at any moment. Selection of information is necessary to ease the computational problems introduced by the enormous number of signals present at the sensory surfaces and to ensure that people respond to stimuli that are relevant to their goals.

Although many studies have investigated visual attention to spatial location (*1*), attention can be focused along several other dimensions (or attributes). People can attend to, or "look for," a specific kind of visual information (for example, a red hat worn by a friend in a crowd). Attending to an attribute improves accuracy on visual detection or discrimination tasks, particularly under conditions of near-threshold discriminability (*2*).

Attending to a visual attribute, such as its color, might be expected to modulate neuronal activity in brain areas that are specialized for processing that attribute. Such feature-specific changes have been reported for color and orientation in monkey V4 (*3*), an area in the occipitotemporal system that is critical for object recognition (*4*). Both behavioral and electrophysiological analyses also indicate that these modulations are stronger during difficult discriminations (*5*).

Selective changes in neural activity may occur in areas of the visual cortex other than V4 and apply to attributes other than color and orientation (for example, velocity) (*6*). Cueing subjects to different dimensions (color, shape, or velocity) might therefore modulate different regions of extrastriate visual cortex, each specialized for processing a particular dimension. We tested this hypothesis in normal subjects with PET by measuring changes in local blood flow (BF), which correlate with changes in neuronal activity (*7*). PET enabled us to monitor activity simultaneously from several brain regions, and therefore determine the effect of attending to different stimulus dimensions on multiple extrastriate visual regions.

We developed a psychophysical task to study the influence of visual attention on the discrimination of subtle stimulus changes in the shape, color, or velocity of a visual stimulus. We then measured BF changes while subjects were performing the task. A same-different paradigm was used. On each trial, subjects fixated a small spot and were presented with two 400-ms stimulus frames, separated by a 200-ms blank display interval (Fig. 1). The stimulus frame was a spatially random distribution of small bars identical in color and shape, moving horizontally as a coherent sheet either to the left or to the right. The direction of motion was constant within a trial but was randomly shifted across trials. The shape, color, and velocity of all elements might independently change between the first and the second frame. The subject's task was to compare the first stimulus frame with the second, and report (by a key-press) if the two frames were same or different for a particular dimension, specified at the beginning of each experimental block. Stimulus changes were close to threshold as assessed for each subject in a separate psychophysical session (*8*).

In three blocks of trials subjects discriminated a stimulus change of either shape, color, or velocity (selective attention) (*9*). Half the trials were "different" and contained a change in the specified dimension, and half the trials were the "same." Same and different trials also contained (in equal proportions) stimulus changes in zero, one, or two of the unspecified or irrelevant dimensions. For instance, during same or different trials in a color block, velocity and shape might stay constant in both frames, velocity might change, shape might change, or both velocity and shape might change. In a fourth block, subjects detected changes in any attribute, dividing attention across dimensions (divided attention). In this case none of the stimulus dimensions varied in half of the trials (same trials) and changes in only one dimension (that is in color, shape,

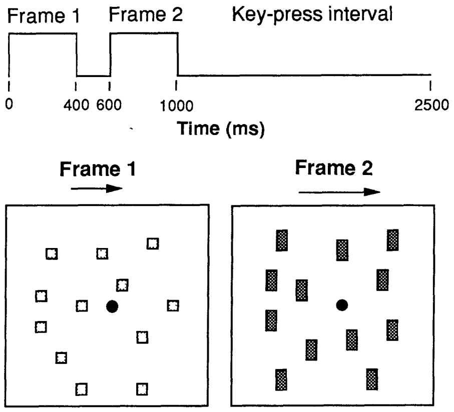

Fig. 1. The size of each element was either 0.8° × 0.8° of visual angle or the just noticeable difference obtained by modifying the length and width. Colors were either red or green, or the respective just noticeable difference in hue obtained by, respectively, adding a small amount of green or red. Velocity was either 18 degrees per second or the just noticeable difference obtained by increasing the velocity. Background luminance was 0.18 foot lamberts (ft-L). The luminance for a single element was about 3.4 ft-L in the red range, and 10.2 ft-L in the green range.

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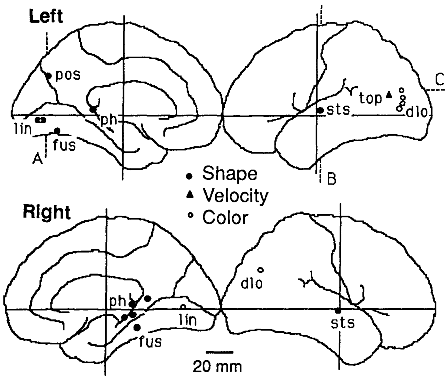

Fig. 2. A plot of visual areas showing enhanced BF response in each of the selective attention conditions, in comparison to the divided attention task. See legend to Table 1 for abbreviations of anatomical regions, and Table 1 for corresponding stereotactic coordinates. A and B are coronal planes corresponding to Figs. 3 and 4A, respectively. C is a horizontal plane corresponding to Fig. 4C.

or velocity) occurred in the other half (different trials).

The effects of attention were evaluated in a group of 11 normal subjects (aged 23 to 41 years) by comparing the accuracy of discriminating a single dimensional change in the selective and divided attention condition (*10*). Selective attention improved discriminative sensitivity ($F(1,10) = 13.25$; $P < 0.001$], and the advantage (on average 0.9 d' units) was similar for all three tested dimensions (*11*).

The effects of selective attention on feature discrimination might be explained by "early" modulations in extrastriate regions specialized for processing those features (*12*) or by the operation of a "late" decision and response selection stage (*13*). Furthermore, in the visual cortex the mechanism of selection might be represented by a neural enhancement in the attended visual channel or by a relative inhibition in the unattended visual channels (*14*).

In order to address these questions, a group of nine subjects (aged 22 to 34 years) (*15*) performed the same tasks during a series of PET BF scans (*16*). The scans included one scan for each selective-attention condition (shape, velocity, or color), two scans during the divided-attention condition, and three scans in which the same set of stimuli was displayed but subjects were not required to make a discrimination (no task). The order of scan conditions was counterbalanced across individuals. Psychophysical performance, calculated from the same trials used for the PET analysis, paralleled the results of the first experiment (*18*).

Here we report only BF activations detected in extrastriate visual cortex after subtracting a divided-attention scan from each of the selective-attention scans (*19*). In this subtraction, factors such as sensory stimulation, arousal, task-related anxiety, and motor output were matched, so that differences in the attentional set are the most likely factor in explaining the obtained activations. However, all the reported activations were also found when subtracting the no-task from the selective-attention scans.

The main result was that different regions of extrastriate visual cortex were activated when attending to different attributes of a visual display (*20*) (Table 1 and Fig. 2). In the ventromedial occipital cortex, a focus of activation in the lingual gyrus (Fig. 3) was found for both attention to color and shape. The response was bilateral for color (with a larger response on the left side) and unilateral on the left for shape. No activation was found in this region for attention to velocity.

Attending to shape activated several other ventromedial occipital regions along the fusiform and the parahippocampal gyri. More dorsally, another focus was localized in the occipitoparietal sulcus. On the lateral surface, bilateral activations were localized midway along the superior temporal sulcus (*sts*), between areas 21 and 22. The magnitude of this response was stronger on the right side (Fig. 4A). None of these regions were activated by attention to color or velocity. Attending to a color change activated a bilateral strip of cortical tissue on the lateral occipital gyri (dorsolateral area 19) (Fig. 4C), in addition to the focus on the lingual gyrus that was also activated by shape. Finally, the selection of velocity information activated a region of the inferior parietal lobule in area 39 (Fig. 4B) on the left side (*21*).

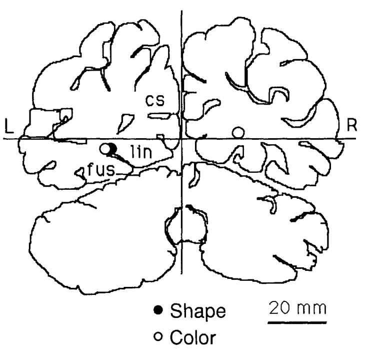

Fig. 3. A coronal slice taken 60 mm behind the C point of the stereotactic space, corresponding to plane A in Fig. 2. cs, Calcarine sulcus; lin, lingual gyrus; fus, fusiform gyrus. Note activations for attention to color and shape, and not for velocity.

The activation of distinct visual cortical regions as a function of the attended visual attribute cannot be explained by sensory factors or changes in general arousal. The divided task was more difficult, as measured by lower d' values, suggesting that arousal was probably higher in the divided than in

Table 1. Foci of activation in extrastriate visual cortex: lin, lingual gyrus; fus, fusiform gyrus; ph, parahippocampal; pos, parieto-occipital sulcus; sts, superior temporal sulcus; top, inferior parietal lobule; and dlo, dorsolateral occipital. S/I, supero-inferior; M/L, medio-lateral; and A/P, antero-posterior. The coordinates are in millimeters from a 0,0,0 point, situated at the level of the anterior and posterior commissures (S/I = 0), at the mid-line of the brain (M/L = 0), and antero-posteriorly halfway between the commissures (A/P = 0). The magnitude is in normalized PET counts, which are linearly correlated with BF (*16*). All foci of change in the visual association cortex with a z-score of >1.96 are reported: unmarked, z-score of >1.96 ($P < 0.05$), *z-score of >2.17 ($P < 0.03$), and †z-score of >2.58 ($P < 0.01$).

Area name		Coordinates			Magnitude
		S/I	M/L	A/P	
			Shape-divided		
lin	L	−4	25	−63	28*
lin	L	−4	29	−67	29*
fus	L	−12	45	−51	32†
fus	R	−14	−27	−25	25
ph	L	4	18	−23	31†
ph	R	−6	−33	−15	27
ph	R	−4	−21	−21	33
ph	R	4	−17	−19	29*
pos	L	30	19	−59	33†
sts	L	4	53	−3	26*
sts	R	−2	−55	−1	39†
			Velocity-divided		
top	L	16	43	−56	32*
			Color-divided		
lin	L	−4	27	−65	39*
lin	R	2	−21	−61	30
dlo	L	20	23	−66	31
dlo	L	14	25	−67	33
dlo	L	10	27	−67	34*
dlo	L	6	29	−65	35*
dlo	R	30	−25	−62	30

the selective attention condition. These activations are best explained by attribute-dependent attentional (top-down) modulations of visual cortex activity. The modulations took the form of a positive change in BF. We believe this BF enhancement occurred in areas of the visual system that were processing the relevant attended stimulus attribute. This notion is supported by comparing the location of the several foci of activation of this study with previous PET activation and lesion studies in humans, and available physiological data in primates. Lesions of lingual and fusiform gyri impair color and object discrimination in humans (*22*). PET activation of the lingual gyrus occurs during the passive presentation of colored stimuli (Mondrian) (*23*) at a location near that found for attending to shape and color.

In macaques, regions of inferotemporal cortex are critical for learning and performance of object recognition and discrimination tasks (*24*). In humans, attending to shape produces activation in temporal cortex midway along *sts*. In a previous PET study, we also found activation in the middle temporal gyrus (area 21) during several object recognition tasks using static colored and oriented bars (*25*). The magnitude of the BF response in both sets of PET experiments is stronger in the right than in the left temporal cortex. This result suggests that neural substrates for object recognition are asymmetrically organized in humans, in agreement with neuropsychological studies (*26*).

Finally, the location of the velocity-modulated focus in the inferior parietal lobule overlapped the location of a region activated by a smooth pursuit visual-tracking task (*27*). This region is adjacent to one activated by the presentation of coherently moving low-contrast dots and high temporal frequency (above 30 Hz) flashes (*28*). These two areas have been proposed as human homologs of the middle superior temporal (MST) and middle temporal (MT) areas in monkeys (*27, 28*). The finding that attentional modulation was present in an MST-like area, but not in an MT-like area, agrees with single-unit studies in macaques showing that only MST neurons appear to be affected by "extraretinal" attention signals (*6*).

In conclusion, attention to basic visual attributes, such as shape, color, or velocity, appears to influence behavioral and physiological measures of visual processing. Behaviorally, sensitivity for making subtle discriminations is increased by attention. Physiologically, neural activity is increased in extrastriate regions specialized for processing information related to the selected visual attribute. These enhancements reflect cognitive (top-down) control of visual processing and offer a promising tool for studying visual areas of the human brain.

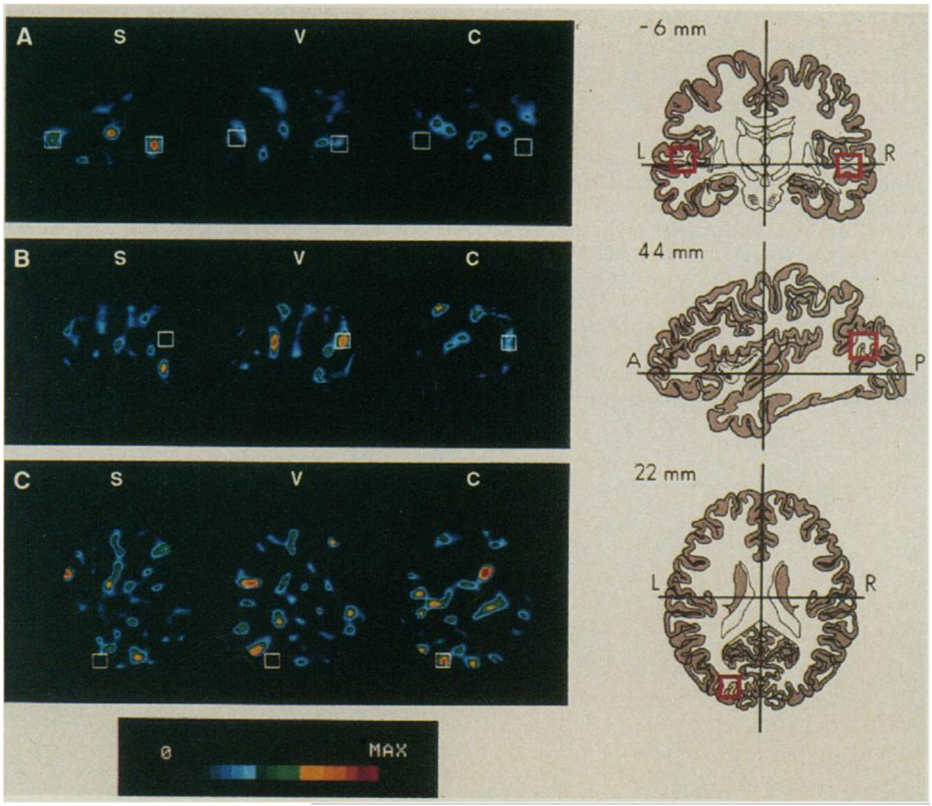

Fig. 4. PET BF image and corresponding anatomical sections. (**Left**) PET sections under S are averaged subtraction BF images for selective attention to shape-divided attention, under V for velocity-divided, and under C for color-divided. (**Right**) The nearby anatomical sections with the response locale plotted from the corresponding row of PET sections. The boxes were centered at the S/I, M/L, and A/P coordinates from Table 1 for each response as determined by computer search (*17*). (**A**) A coronal slice taken 3 mm behind the 0 point of the stereotactic space (section A, Fig. 2). Temporal cortex (sts) activation for attention to shape. (**B**) A sagittal slice 43 mm left of midline. Left inferior parietal lobule (top) activation for attention to velocity. (**C**) A horizontal slice taken 20 mm above the AC-PC plane (section C, Fig. 2). Left dorsolateral occipital (dlo) cortex activation for attention to color. The response on the right side is displaced about 10 mm superiorly.

REFERENCES AND NOTES

1. C. W. Eriksen and J. E. Hoffman, *Percept. Psychophys.* **12**, 201 (1972); M. I. Posner, *Q. J. Exp. Psychol.* **32**, 3 (1980); M. C. Bushnell *et al.*, *J. Neurophysiol.* **46**, 755 (1981); S. E. Petersen, D. L. Robinson, W. Keys, *ibid.* **54**, 867 (1985).
2. K. Ball and R. Sekuler, *Psychol. Rev.* **87**, 435 (1980); R. Vogel, H. Eeckhout, G. A. Orban, *Perception (London)* **17**, 565 (1988).
3. P. E. Haenny and P. H. Schiller, *Exp. Brain Res.* **69**, 225 (1988).
4. L. G. Ungerleider and M. Mishkin, *Two Cortical Visual Systems* D. J. Ingle, M. A. Goodale, R. J. W. Mansfield, Eds. (MIT Press, Cambridge, MA, 1982).
5. H. Spitzer, R. Desimone, J. Moran, *Science* **240**, 338 (1988).
6. W. T. Newsome, R. H. Wurtz, H. Komatsu, *J. Neurophysiol.* **5**, 825 (1988).
7. M. E. Raichle, *Handbook of Physiology*, section 1, *Nervous System*, vol. 5, *Higher Functions of the Brain*, F. Plum, Ed. (Oxford Univ. Press, New York, 1987), part 1, pp. 643–669.
8. Eye fixation was monitored by electrooculogram (EOG) throughout all the experiments. The day before the experiment, thresholds were measured with the method of constant stimuli [J. G. Snodgrass, G. Levy-Berger, M. Haydon, *Human Experimental Psychology* (Oxford Univ. Press, New York, 1985)], comparing for each attribute a reference value with a pool of five test values in a random order of presentation. The selected threshold value was about 1.6 *d'* units, where *d'* is a criterion-free index of discriminability [D. McNicol, *A Primer of Signal Detection Theory* (Allen & Unwin, London, 1972)] that measures the separation between the internal representation of the stimuli measured in units of the standard deviation of the noise of the stimulus representation. Values for *d'* were calculated from the hit and false alarm rates in each condition. The hit rate was the percentage of trials in which subjects correctly reported that two "different" frames were different, the false alarm rate the percentage in which subjects incorrectly reported that two "same" frames were different.
9. Since the set of stimuli for color discrimination was not equiluminant, subjects were also tested with red or green reference hue stimuli and test stimuli of the same hue with comparable or larger luminance differences. All subjects performed at a level expected for chance, indicating that brightness cues were not used in the color judgments.
10. For the selective conditions, only those trials containing a stimulus change in the relevant dimension (for example, color in a color block) without variations in the other dimensions (that is, shape or velocity) were selected for the analysis. These trials (25% of the total number) were visually identical to those collected in the divided attention condition.
11. The increase in sensitivity related to attention was (means ± SEM) 0.86 ± 0.29 for shape discrimination, 0.69 ± 0.20 for color discrimination, and 1.01 ± 0.21 for velocity discrimination. No interaction was found between stimulus dimension (shape,

color, or velocity) and attentional condition (selective versus divided) [$F(2,20) = 0.39$ not significant].

12. D. E. Broadbent, *Acta Psychol.* **50**, 253 (1982).
13. J. Duncan, *Psychol. Rev.* **87**, 272 (1980); J. Deutsch and D. Deutsch, *ibid.* **70**, 80 (1963).
14. B. J. Richmond and T. Sato, *J. Neurophysiol.* **58**, 1292 (1987); J. Moran and R. Desimone, *Science* **229**, 782 (1985).
15. Informed consent was obtained from each subject with forms and procedures approved for this study by the Human Studies and Radioactive Drug Research Committees of Washington University.
16. The PET methods used the PET VI scanning system [M. Yamamoto, D. C. Ficke, M. M. Ter-Pergossian, *IEEE Trans. Nucl. Sci.* **29**, 529 (1982)] and the standard O15 (half-life 123 s) labeled water bolus injection technique that have been extensively described [(*17*); M. A. Mintun, P. T. Fox, M. E. Raichle, *ibid.* **9**, 96 (1989); P. Herscovitch, J. Markham, M. E. Raichle, *J. Nucl. Med.* **24**, 782 (1983); M. E. Raichle *et al.*, *ibid.*, p. 790; P. T. Fox and M. A. Mintun, *ibid.* **30**, 141 (1989)]. Scans were 40 s long, which allowed eight scans to be acquired during a single recording session. Images were obtained from each subject for each experimental condition and were normalized to a common value. For each subject, change images corresponding to specific conditions (see text) were created by subtracting one image from another. All change images were transformed to a standard stereotactic space [P. T. Fox, J. Perlmutter, M. E. Raichle, *J. Comput. Assist. Tomography* **9**, 141 (1985)] and then averaged together across subjects improving the signal-to-noise level of the image (*17*). The averaged subtraction image was then searched by an automatic maximum-value detection algorithm to identify the magnitude and location in stereotactic coordinates of all positive and negative local maxima. The statistical analysis was two-tiered. First, an omnibus test (gamma-two statistics) was used to determine whether an image had any significant responses (distribution outliers). Second, as a post-hoc analysis (if significance was achieved), the magnitude of a response was described relative to the noise level by z-score (response magnitude per standard deviation of the distribution).
17. P. T. Fox, M. A. Mintun, E. M. Reiman, M. E. Raichle, *J. Cereb. Blood Flow Metab.* **8**, 642 (1988).
18. The use of a d' analysis was precluded in this case by the small number of trials ($n = 24$) that could be collected from each individual during the 40-s duration of a PET scan. A lower percentage of false alarms, 18% versus 33% (mean difference = 15 ± 4% SE) [$F(1,8) = 8.94$ $P < 0.02$], was recorded when subjects focused attention on one stimulus dimension than when they divided attention across several stimulus dimensions. Although the mean hit rate was also higher in the selective condition (77% versus 67%, mean difference = 10 ± 8% SE) this difference was not significant [$F(1,8) = 2.27$] presumably because of the small sample size.
19. For each selective-attention scan either one or the other divided-attention scan was subtracted. Usually the closest divided-attention scan in the sequence was selected to minimize image artifacts produced by subject's movement. However, the psychophysical performance in the first or the second divided-attention scan did not differ in the group.
20. Areas outside of visual cortex were also activated in the different conditions, but are not reported here. In a region corresponding to areas 17 and 18 positive BF responses were recorded for attention to shape and velocity, and nearly significant responses occurred for attention to color.
21. There was some lateralization of response in many of the areas, which might not be expected given the bilateral presentation of the stimuli. It is unclear if these laterality effects reflect true anatomical asymmetry, or are due to functional interactions between the hemispheres.
22. A. R. Damasio, in *Principles of Behavioral Neurology*, M. Mesulam, Ed. (Davis, Philadelphia, PA, 1985), pp. 259–288.
23. C. J. Lueck *et al.*, *Nature* **340**, 386 (1989).
24. C. G. Gross, in *Handbook of Sensory Physiology*, R. Jung, Ed. (Springer-Verlag, New York, 1973), pp. 77–123.
25. S. E. Petersen, S. Dobmeyer, M. Corbetta, P. T. Fox, F. M. Miezin, unpublished data.
26. B. Milner, *Neuropsychologia* **6**, 191 (1968).
27. F. M. Miezin, C. Applegate, S. E. Petersen, P. T. Fox, *Soc. Neurosci. Abstr.* **14**, 795 (1988).
28. F. M. Miezin, P. T. Fox, M. E. Raichle, J. M. Allman, *ibid.* **13**, 625 (1987); *Assoc. Res. Vis. Ophthalmol. Abstr.* **29**, 326 (1988).

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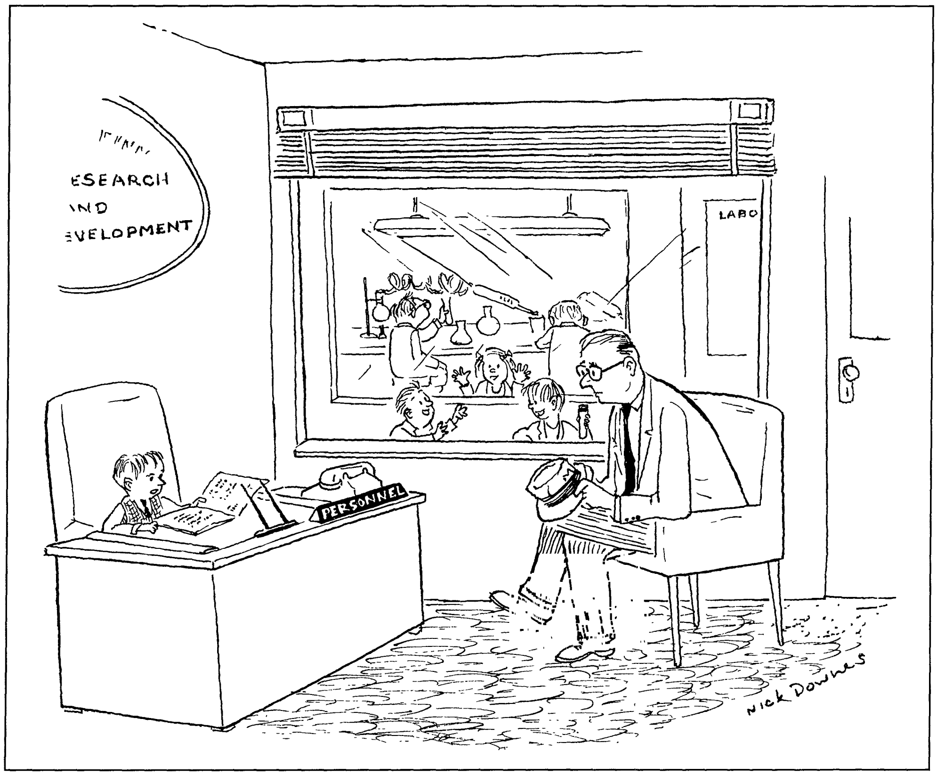

" It's our assumption, Mr. Rollins, that if one is going to make a significant contribution in Physics, one tends to do so at a fairly young age."