

# Covariations in ERP and PET Measures of Spatial Selective Attention in Human Extrastriate Visual Cortex

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**Abstract:** In a previous study using positron emission tomography (PET), we demonstrated that focused attention to a location in the visual field produced increased regional cerebral blood flow in the fusiform gyrus contralateral to the attended hemifield (Heinze et al. [1994]: *Nature* 372:543). We related these effects to modulations in the amplitude of the P1 component (80–130 msec latency) of the visual event-related brain potentials (ERPs) recorded from the same subjects, under the identical stimulus and task conditions. Here, we replicate and extend these findings by showing that attention effects in the fusiform gyrus and the P1 component were similarly modulated by the perceptual load of the task. When subjects performed a perceptually demanding symbol-matching task within the focus of spatial attention, the fusiform activity and P1 component of the ERP were of greater magnitude than when the subjects performed a less perceptually demanding task that required only luminance detection at the attended location. In the latter condition, both the PET and ERP attention effects were reduced. In addition, in the present data significant activations were also obtained in the middle occipital gyrus contralateral to the attended hemifield, thereby demonstrating that multiple regions of extrastriate visual cortex are modulated by spatial attention. The findings of covariations between the P1 attention effect and activity in the posterior fusiform gyrus reinforce our hypothesis that common neural sources exist for these complementary, but very different measures of human brain activity. *Hum. Brain Mapping* 5:273–279, 1997. © 1997 Wiley-Liss, Inc.

**Key words:** functional neuroimaging; attention; event-related potentials; vision; human; perceptual load; PET

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## INTRODUCTION

Contract grant sponsor: Human Frontiers Science Program Organization; Contract grant sponsor: NIMH; Contract grant sponsor: NINDS; Contract grant sponsor: NSF; Contract grant sponsor: Deutsche Forschungsgemeinschaft.

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Studies of human visual-spatial attention have shown that when attention is covertly focused on a visual field location, target detection and discrimination performance is significantly improved [e.g., Downing, 1988; Hawkins et al., 1990; Posner et al., 1980]. Physiological studies in humans have also demonstrated

attentional influences on neuronal activity recorded from the intact scalp in the form of event-related brain potentials (ERPs). During spatial selective attention, the occipital P1 component (onset 70–80 msec latency) is the earliest sensory-evoked response to be reliably modulated by attention [e.g., Eason, 1981; Luck et al., 1994; Mangun and Hillyard, 1991; Van Voorhis and Hillyard, 1977; see Mangun, 1995 for a review].

In a recent study that combined ERP recordings with positron emission tomography (PET), we investigated the functional anatomy of sustained visual-spatial selective attention [Heinze et al., 1994]. In this study, we found that focal attention to a lateral field location resulted in increased regional cerebral blood flow (rCBF) in the fusiform gyrus of the hemisphere contralateral to the attended hemifield. We proposed that this effect in the fusiform gyrus was the probable generator of the P1 attention effect observed in the ERPs. This is because both attention effects were obtained in the same stimulus and task conditions in the same volunteers, and because dipole modeling of the ERPs showed that a generator placed in the posterior fusiform could account for most of the scalp P1 pattern we recorded. Thus, we argued that spatial attention first modulated information processing in the extrastriate visual cortex of humans at a post-stimulus latency of 80–130 msec, thereby providing evidence for an early visual cortical modulation of perceptual processing during spatial attention.

In the present report, we replicate and extend our previous finding using combined PET and ERP methods. The logic here is that ERP and PET activities that are generated as the result of the same attentional processes should covary across conditions in which spatial attention is varied. We know from previous studies that the P1 attention effect is modulated by several factors including voluntary attentional allocation between competing locations [Mangun and Hillyard, 1990] and variations in perceptual load [Handy and Mangun, submitted]. Here we manipulated perceptual load in order to vary the allocation of spatial attention [see Lavie and Tsal, 1994; Lavie, 1995]. Spatial attention effects were compared for the symbol-matching task we [Heinze et al., 1994] used previously (replication), and a lower perceptual load condition where subjects performed a luminance detection task. If the fusiform activations and the P1 attention effects are not closely related, then it might be possible to dissociate the PET and ERP effects by manipulating perceptual load within the “spotlight” of attention.

## METHODS

Stimuli consisted of bilateral arrays of symbols ( $2.0 \times 1.2$  deg. of visual angle each) flashed in rapid sequence (ISI = 250–550 msec, rectangular distribution) on a video monitor (see top Fig. 1). The symbols were in the upper visual field (0.8 deg. to bottom edge) and were located at eccentricities of 4.5 and 7.0 deg. (to center of symbol) in the left and right visual half fields. Stimulus durations were 50 msec, and the symbols were presented in white on a black background. There was a central fixation cross and two outline boxes present continuously on the screen throughout the sequence—the boxes demarcated the to-be-attended and to-be-ignored locations. In addition to the bilateral stimuli, a unilateral white square stimulus ( $2.0 \times 2.0$  deg., 50 msec duration) appeared on a random 25% of the trials within the box outlines, but was task irrelevant—these were designated as “probe” stimuli, but will not be considered in this report.

Subjects<sup>1</sup> (N = 12, one female, eleven male) were run separately in three recording sessions (one PET and two ERP). They were instructed to fixate the central cross on the screen and maintain fixation, which was monitored by an infrared video zoom lens system (PET and ERP sessions), and monitoring of their electrooculograms (ERP session only).

In order to manipulate perceptual load, two main *task* conditions were presented in separate counterbalanced blocks (Symbol vs. Dot conditions), and within each task condition, two spatial attention conditions were included (attend left vs. attend right). In the *symbol condition*, a random 20% of the arrays contained targets consisting of identical symbols in one half field at a time; these required a manual right-hand button press by the subjects only when at the attended location. In the *dot condition*, a random 20% of the arrays contained a small “dot” stimulus (one-to-four video pixels illuminated anywhere within the area traversed by the symbols) that had to be detected and responded to instead of the symbol matches (at the attended location only). The dot appeared simultaneously with the symbols and remained on for the same duration. For each task condition, subjects attended the right half of the array in some runs, and the left half of the arrays in other runs. Attention was sustained on the to-be-attended location for the duration of each run. In addition to these task and attention conditions, a passive viewing condition was included

<sup>1</sup>One male subject could not be recorded in the ERP session, hence 11 subjects participated in the electrophysiological recordings and 12 in the PET session.

in the ERP session, and both passive viewing and fixation-only conditions were included in the PET session—here we will only consider the data from the active attention conditions in order to compare effects from conditions that are matched for general behavioral arousal.

In the PET session, a total of 12 bolus intravenous injections of  $^{15}\text{O}$ -water (15 mCurie each) were administered, two in each of six different conditions: (1) Symbol condition: attend left; (2) Symbol condition: attend right; (3) Dot condition: attend left; (4) Dot condition: attend right; (5) Passive viewing; and (6) Fixation only. Subjects were rigidly fixed in the scanner in a head holder, and viewed a suspended video monitor (NEC 4FG color) located above their chest as they lay in the scanner gantry. The scanner was a SIEMENS ECAT 921 EXACT running in 3D mode (septa retracted).

One minute prior to bolus injection of the  $^{15}\text{O}$ -water, the stimuli were started and the subject was instructed to fixate the fixation cross. Thirty seconds prior to injection the subject was given the task instructions for that run and told to begin performing the task. Following the injection, the data was acquired for a 40 sec period that began when radiation counts in the head reached a threshold value. The onset of this acquisition period varied somewhat between subjects; however, the time to begin acquisition was consistent within subjects—overall the data were acquired from about 20–60 sec after injection. The subjects continued task performance until about 1 min after injection. The order of attention conditions was counterbalanced across subjects but always began and ended with fixation-only runs (scans 1 and 12) and passive viewing runs (scans 2 and 11).

Analyses were performed using the SPM95 package [Friston et al., 1995]. The multiple scan images from each subject were first realigned within-subject using the least-squares approach of SPM95 with six-parameter rigid body spatial transformations. Images were then stereotactically normalized (using a 12-parameter affine transformation and a six-parameter, 3D quadratic deformation) to a standardized space corresponding to the Talairach and Tournoux [1988] brain atlas, and then convolved with an isotropic Gaussian kernel of 18 mm. Only those voxels showing activity greater than 80% of the whole brain mean (grey matter threshold) and having a significant F-ratio ( $P < 0.05$  uncorrected) were used in further analyses. In order to account for changes in global activity between scans and between subjects, all scans were proportionally scaled to have a mean global blood flow of 50 ml/min/dl. Analyses were then performed using a multiple

subjects with replications design, using the six scan conditions described above.

In the ERP session, EEG was recorded from 92 channels (.1–100 Hz bandpass), digitized at 256 Hz, and stored for off-line analysis. The tin electrodes were mounted in an elastic electrode cap (Electrocap Int., Inc.) and electrode impedances were maintained below 5 KOhm. The electrodes were approximately equally spaced across the scalp, and the precise locations were digitized in 3D for each subject. The scalp electrodes were referenced to the right mastoid process. Following artifact rejection for eye movements, blinks, blocking, and movement artifacts, ERPs were separately calculated for the non-target bilateral arrays, the target bilateral arrays, and the left and right unilateral probes as a function of the differing task conditions. Scalp topographic mapping was performed using the spherical spline method of Perrin et al. [1989].

## RESULTS

The direction of attention led to significant activations in regions of the extrastriate visual cortex. These main effects of spatial attention were assessed by comparing rCBF for the attend-left vs. attend-right conditions. Independent of task, focused attention to the left half of the arrays produced an activation in the right posterior fusiform gyrus, while attention to the right produced activation in the left posterior fusiform gyrus (Fig. 1a and Table I). In addition, significant activations were observed in the middle occipital gyrus of the contralateral hemisphere. No activations were obtained in either the thalamus or striate cortex in these comparisons. In order to assess the extent to which differences in perceptual load across the different task conditions influenced the pattern of spatial attention effects, the statistical interaction of the direction of spatial attention (attend left vs. attend right) and task (symbol matching vs. dot detection) was evaluated and plotted as SPM maps in Figure 1b. The only region of extrastriate cortex to show statistically significant interactions of task and attention was in the posterior fusiform gyrus, where greater activity was found in the symbol condition than in the dot detection condition. Task-related differences in the attention effects in the middle occipital gyrus were in the same direction, but of reduced amplitude and not statistically reliable.

Significant amplitude enhancements of the P1 component (110–140 msec) were obtained over lateral occipital scalp regions contralateral to the attended hemifield (Fig. 1c and Table I). That is, attention to the

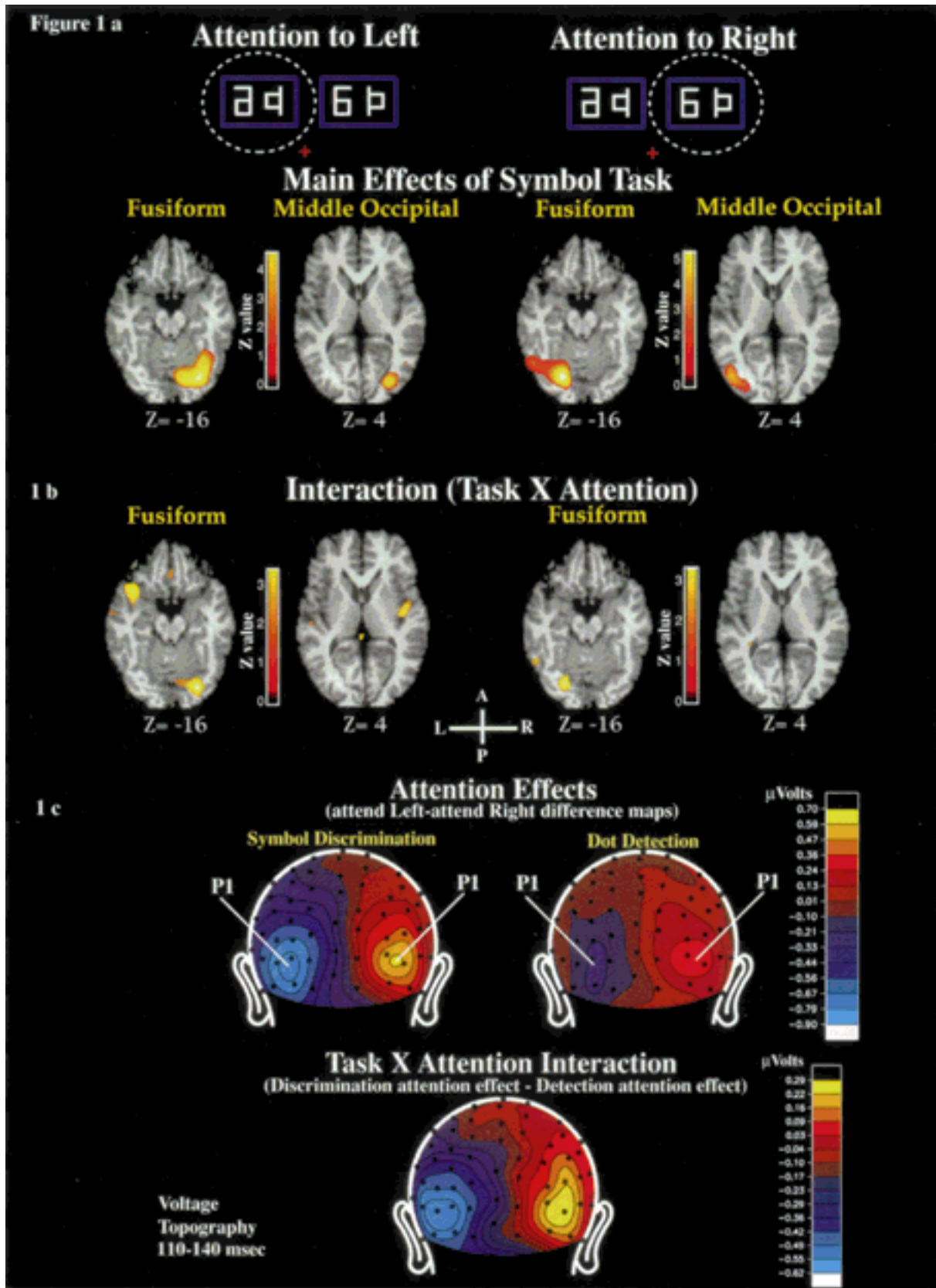


Figure 1.

left field led to an increase in the amplitude of the P1 component over the right occipital scalp, while attention to the right produced a similar increase in amplitude during the P1 latency range over the left occipital scalp. As the scalp topographic voltage maps of Figure 1c indicate, the attention effect in the latency range of the P1 component was sharply localized to scalp regions that overlie lateral extrastriate cortex, in line with previous studies [e.g., Mangun et al., 1993, Heinze et al., 1994]. There was a statistical interaction between spatial attention and task conditions, as the P1 attention effect during symbol discrimination was significantly larger than the effect produced during dot-detection.

**Figure 1.**

**a.** Top: Example of the stimulus display with dashed circles indicating the direction of the subjects' attention during attend-left and attend-right conditions (circles not actually present on display). Bottom: Main effects for the symbol (form discrimination) condition of attending left (left two images) or attending right (right two images) mapped onto MRI images from SPM95. Horizontal sections are shown for low brain sections ( $z = -16$ ) and slightly more dorsal sections ( $z = +4$ ). Attention to the left half of the stimulus arrays produced activations in the right fusiform and middle occipital gyri, whereas attention to the right produced activations in these regions of the left hemisphere. Note that the left of the image is the left of the brain, and anterior is at the top. **b:** Interactions between attention and task showing significant effects in the fusiform gyrus contralateral to the attended field. Note that in addition to the fusiform activity in the left hemisphere, there is another region of activity in the posterior region of the  $z = -16$  slice. This small region corresponds to a more lateral portion of the fusiform, bordering on the inferior temporal gyrus. This region did not correspond to any a priori regions of interest and did not attain significance in corrected-tests. Other more anterior regions are also seen in the interaction effects—these regions correspond to the left uncus (or between superior and medial temporal gyri, at  $-32, 8, -28$ ) and the right insula (at  $40, -14, 0$ )—these regions lie outside of the visual areas of interest, and will not be discussed here. **c:** Scalp topographic voltage maps in rear view of the head. The projection of the 3D maps to the 2D plane of the figure are using a radial projection. The maps are for the peak of the P1 attention effect in the 110–140 msec latency range for attend-left minus attend-right maps. As a result of the direction of subtraction, the values are positive over the right hemisphere but negative over the left hemisphere for the P1 attention effect. Significant attention effects for the P1 were obtained for both symbol (left) and dot (right) conditions, but the amplitude of the attention effects was larger for the symbol condition. The topographic map at the bottom of the figure displays the subtraction of dot from symbol condition (i.e. labelled "Discrimination attention effect–Detection attention effect" in figure), thereby illustrating the interaction effect.

Behavioral measures of target detection accuracy ( $d'$ ) for dot detection were better than symbol discrimination (2.70 vs. 2.06;  $P < .001$ ), supporting the view that the dot-detection task was an easier and less demanding task than was the symbol matching task.

## DISCUSSION

The present findings replicate our previous results of modulations of rCBF in the contralateral posterior fusiform gyrus during lateralized, focused spatial attention. They also extend this finding by showing attentional modulations in an additional extrastriate region—the middle occipital gyrus. The spatial attention effects in the fusiform gyrus interacted with perceptual load of the task: During dot detection the fusiform gyrus showed less activation than during symbol matching. Importantly, this pattern was paralleled in the findings for the P1 component of the ERP. The P1 attention effect was larger for symbol than for dot conditions. Thus, the P1 attention effects and the fusiform gyrus PET effects covaried. This strongly suggests that the P1 attention effect and the PET activations in the fusiform gyrus are closely associated, and can be interpreted as additional evidence supporting the idea from our previous dipole modeling [Heinze et al., 1994] that the P1 effect is actually generated in the fusiform gyrus. Furthermore, a more recent dipole modeling study [Clark and Hillyard, 1996] localized the P1 attention effect to an occipital area corresponding very well with the average coordinates of the visual activations found in the present study. Although we cannot exclude the idea that the P1 effect and fusiform attention effect reflect activities in separate neural structures which are nonetheless both modulated similarly with spatial attention, our previous modeling data suggest that the most parsimonious interpretation is that they are both reflections of the same underlying neural activity.

The localization of the P1 attention effect in the fusiform gyrus must be interpreted in light of the retinotopic mapping of the visual field on to the human visual cortex [Serenio et al., 1995; Engel et al., 1994; Schneider et al., 1993]. If the P1 effect is generated in the fusiform gyrus, changing the location of the visual stimulus should result in shifts of the P1 component and PET activations to other regions of the retinotopic map within the fusiform gyrus. A recent study by Woldorff and colleagues provides evidence that this is indeed the case, because in their study using lower field stimuli (upper field stimuli were used here and in our prior work) the localization of the P1 component and related PET activations shifted in a

TABLE I. Locations and statistical significance of attention and task effects

PET rCBF				
Contrast	Talairach x, y, z	Structure	Z	
Symbol matching condition				
Attend left–attend right	26, –80, –12	Right fusiform	4.68	$P < .001$
	48, –62, –4	Right middle occipital	3.45	$P < .001$
Attend right–attend left	–20, –78, –16	Left fusiform	5.33	$P < .001$
	–44, –74, 0	Left middle occipital	3.65	$P < .001$
Attention × task interaction				
Attend left–attend right	24, –84, –12	Right fusiform	3.46	$P < .001$
Attend right–attend left	–20, –80, –20	Left fusiform	3.32	$P < .001$
P1 component of ERP (110–140 msec)				
			Scalp recording sites	F
Effect of attention and interaction with task*				
Attention × hemisphere**		OL OR T5 T6	23.08	$P < .001$
Attention × hemisphere × task		OL OR T5 T6	18.00	$P < .005$

\* ANOVA factors: task (symbol vs. dot), attention (left vs. right), hemisphere (left vs. right), electrode (OL & OR vs. T5 & T6), subjects.

\*\* Effect of attention is revealed by interaction of attention with hemisphere of recording given the ANOVA factors above (see text for details).

predictable fashion within the brain (Woldorff et al., 1997—this issue).

What does the modulation of both the fusiform and P1 attention effects between dot and symbol condition tell us about the nature of the processing taking place in the posterior fusiform gyrus during spatial attention? Because the fusiform gyrus was active in both conditions, it does not appear that the posterior fusiform activity is only involved in higher-order pattern matching processes within the attentional spotlight. Rather, as with the P1 attention effect [see Mangun, 1995 for a review], the fusiform activity is modulated by spatial attention in a manner that facilitates the processing of all stimuli that fall within the attended region. Hence, this pattern of results fits well with the conceptualization that at relatively early stages of visual processing (extrastriate but not striate cortex in these data) one effect of spatial attention is to facilitate the processing of any stimulus at the attended location, rather like an attentional spotlight [e.g., Posner et al., 1980]. Thus, an early filter or gain control process is acting to alter the signal-to-noise ratio for attended vs. unattended regions of visual space. Thereupon, higher-order processing stages receiving inputs from the attended region perform specific analyses under the requirements of the task at hand (e.g., feature, form, or object analyses). The present data provide further evidence that this early attentional gain control process acts within extrastriate visual cortex beginning about

70–80 msec after stimulus onset, thus demonstrating the anatomical locus and functional time course of the effects of spatial attention on human visual information processing.

#### ACKNOWLEDGMENTS

We thank T. Handy, A. Jones, K. Kiehl, Dr. C.M. Wessinger, Dr. H. Hinrichs, Dr. M. Scholz, Dr. P. Valk, Dr. M. Woldorff, Dr. J.C. Hansen, Dr. S. Hillyard, Dr. M. Gazzaniga, Dr. M.E. Raichle and Dr. S.E. Petersen for their comments and assistance. We also thank Dan Kern, Marty Martinez, Ruth Tesar, Letty Villaneuva, Judi Semple, Diane Tribbey, Rene Tsang, Nancy Mortimer, and the rest of the staff at the Northern California PET Imaging Center for their invaluable assistance. Supported by grants from the Human Frontiers Science Program Organization, the NIMH, the NINDS, the NSF, and the Deutsche Forschungsgemeinschaft.

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