Functional Connectivity of the Macaque Posterior Parahippocampal Cortex

Justin L. Vincent,1,2 Itamar Kahn,1–3 David C. Van Essen,4 and Randy L. Buckner1–3,5

1Department of Psychology and Center for Brain Science, Harvard University, Cambridge, Massachusetts; 2Athinoulia A. Martinsos Center for Biomedical Imaging, Massachusetts General Hospital, Charlestown, Massachusetts; 3Howard Hughes Medical Institute; 4Department of Anatomy and Neurobiology, Washington University School of Medicine, St. Louis, Missouri; and 5Departments of Psychiatry and Radiology, Massachusetts General Hospital, Harvard Medical School, Charlestown, Massachusetts

Submitted 24 June 2009; accepted in final form 25 November 2009

INTRODUCTION

Human posterior parietal cortex and limbic cortex are activated during long-term memory retrieval (Cabeza et al. 2008; Vilberg and Rugg 2008; Wagner et al. 2005). Specifically, greater responses in human lateral parietal regions as well as the posterior cingulate and retrosplenial cortex have been repeatedly observed with functional magnetic resonance imaging (fMRI) when participants correctly recognize previously studied items (hits) versus correctly identified new items (correct rejections). The human lateral parietal retrieval success effect occurs regardless of whether the stimuli are lexical, graphic, or acoustic (Henson et al. 1999; Kahn et al. 2004; Konishi et al. 2000; Leube et al. 2003; McDermott 2000; Shannon and Buckner 2004; Wheeler and Buckner 2003, 2004) and does not depend on response contingency (i.e., whether a motor response is made only to new vs. only to old items) (Shannon and Buckner 2004). Furthermore, activation in the human posterior parietal cortex is implicated in retrieval of episodic details: recollection elicits a greater response than familiarity-based decisions in the absence of recollection (Ca- beza et al. 2008; Vilberg and Rugg 2008; Wagner et al. 2005).

The functional nature of the human parietal old/new effect remains unclear and would benefit greatly from study in the monkey where the anatomy and physiology of the parietal cortex is accessible. However, it is uncertain whether or not the macaque monkey has parietal regions that are homologous to those responsive during human memory-retrieval experiments. One way to compare species using the same technique is to compare patterns in fMRI-based functional connectivity (Biswal et al. 1995; Fox and Raichle 2007; Van Dijk et al. 2009; Vincent et al. 2007). Spontaneous blood oxygenation-level-dependent (BOLD) (Ogawa et al. 1990) fluctuations reflect both direct and indirect anatomic connectivity (Hagmann et al. 2008; Honey et al. 2009; Vincent et al. 2007) and are correlated with fluctuations in neuronal activity as reflected in the gamma band of the local field potential, multifunit activity, and spiking activity (Shmuel and Leopold 2008). While there are caveats and limitations to the technique (reviewed recently in Van Dijk et al. 2009), functional connectivity appears sufficiently constrained by anatomic connectivity to facilitate comparative study of brain systems between species.

Previous studies of intrinsic functional connectivity in the human have demonstrated that BOLD fluctuations in human medial temporal lobe are correlated with the same regions in posterior parietal and limbic cortex that respond during memory retrieval (Vincent et al. 2006). In the human, this hippocampal-cortical memory system overlaps core regions of the so-called “default network” (Buckner et al. 2008; Vincent et al. 2006). More recently, correlations were demonstrated between BOLD fluctuations in macaque posterior cingulate/precuneus and bilateral lateral temporoparietal regions that may be anatomic homologues to human lateral parietal regions known to respond during episodic memory retrieval (Margules et al. 2009; Vincent et al. 2007).

The main goal of this study was to determine whether macaque posterior parahippocampal cortex (PPHC) is functionally correlated with regions in posterior limbic and lateral parietal cortex and whether these regions are anatomically distinct from the parietal regions traditionally associated with visual-spatial attention and sensory-motor integration (e.g., Andersen and Buneo 2002; Colby and Goldberg 1999; Heilman and Gonzalez Rothi 1993; Mesulam 1999). A secondary goal was to examine functional correlations in the posterior cingulate/retrosplenial cortex. Hayden and colleagues (2009) have recently shown that firing rates in the macaque posterior cingulate are suppressed during task performance, which is functionally similar to deactivations observed in the human posterior cingulate and the extended default network (Buckner et al. 2008; Gusnard and Raichle 2001; Mazoyer et al. 2001; Shulman et al. 1997). Further, several previous human studies suggest that the posterior cingulate is functionally connected to many of regions that fall within the human default network.
correlation maps are shown in Fig. 1. Figure 1A shows the correlation pattern for the right hemisphere PPHC seed. The top row shows the correlation data overlaid on transverse and sagittal sections of the average anatomy. The bottom row shows the correlation data on lateral and medial views of the inflated F6 cortical surface. The left hemisphere PPHC correlation maps are shown in Fig. 1B. The PPHC was functionally correlated with the contralateral parahippocampal cortex, retrosplenial cortex, the posterior cingulate, and bilateral temporoparietal cortex (including supramarginal gyrus and the superior temporal gyrus). Overall, these results were similar across seed regions and hemispheres. However, the left PPHC correlation with left temporal parietal cortex did not reach significance.

Figure 1C shows the results of left and right PPHC correlations on coronal slices as well as a conjunction map showing voxels correlated with both seed regions in red. The PPHC correlations include parietal cortex lateral to the intraparietal sulcus on the supramarginal and superior temporal gyrus. In the more anterior slices, correlations were found on the superior temporal gyrus. The correlations extended onto the inferior temporal gyrus near V4, possibly as a consequence of spatial blurring. For better localization, we examined correlations in individual subjects.

To further examine the location of functional correlations between the PPHC and temporoparietal cortex, we manually traced the right PPHC on the T2*-weighted image in three macaques (taken from data set 2) and computed functional correlations using those individually drawn PPHC regions as seeds. Figure 2 shows the individual subject maps along side the right PPHC group correlation map. The intraparietal cortex (IPS) and superior temporal sulcus (STS) are traced with black lines. Overall, individuals demonstrated similar patterns of correlation to the group map. These data demonstrate that the PPHC correlation pattern in temporoparietal cortex is largely lateral to the IPS, superior to the STS, and includes the supramarginal and superior temporal gyrus.

Portions of macaque parietal cortex are associated with visuospatial attention and sensory-motor integration. An important question is whether or not the temporoparietal region we identified by functional connectivity with the PPHC corresponds with regions implicated in visual-spatial or sensory-motor functionality. To explore this issue, we compared the temporoparietal region that was correlated with the PPHC to the set of regions activated by a common visual-spatial, sensory-motor task: visually guided saccadic eye movements.

We compared the map of PPHC functional correlations (Fig. 3A, collapsed across hemispheres) to a map of BOLD responses evoked during performance of a visually guided saccadic eye movement task in two awake, behaving macaques (Fig. 3B) (data from Baker et al. 2006). Voxels that overlap in the two maps are shown in yellow in Fig. 3C. There is relatively little overlap, which indicates segregation. The only region of potential overlap lies in or around dorsal-anterior MST. To estimate the areal location of the temporoparietal correlation with the PPHC (Fig. 3A), the correlation data were displayed on a cortical flat map with estimated architectonic area boundaries overlaid (from Lewis and Van Essen 2000a) (Fig. 3D). The temporoparietal region correlated with the PPHC is in or near areas 7a, TPOc, and PA. Areas activated by saccadic eye movements were in or near areas PO, MIP, VIPm, VIP, LIPv, LIPd, 7a, MSTdp, MSTm, MSTda, MT, FST, LOP, and V3a (Fig. 3E). Overall, there are few areas that overlap between the regions activated by saccadic eye movements and the regions
correlated with the PPHC. The only areas that were identified by both analyses were area 7a (and potentially MSTda). However, the correlations with PPHC were located in a more anterior region within area 7a, whereas the activations associated with saccadic eye movements were associated with a more posterior region within 7a. Overall, these data suggest that the regions correlated with the PPHC are likely to be distinct from the regions associated with saccadic eye movements.

In humans, the hippocampal formation and posterior PPHC are functionally correlated with regions in posterior parietal cortex that are activated by recollection (Vincent et al. 2006). The present analyses demonstrate that a qualitatively similar parahippocampal-parietal network exists in macaques. To provide a more objective comparison between the two species, we used a mapping between macaque and human cortex based on a set of 29 landmarks representing known or presumed homologies (supplementary information and Supplementary Fig. S1). Using this mapping, we registered the macaque brain to the surface of the human brain using anatomical and functional landmarks (see supplementary information) and projected the macaque PPHC functional connectivity results (collapsed across left and right seed regions) onto the human atlas surface.

**Fig. 1.** The posterior parahippocampal cortex (PPHC) is functionally correlated with the contralateral medial temporal lobe, retrosplenial cortex, posterior cingulate, and lateral temporo-parietal cortex. The right (A) and left (B) PPHC seed regions are shown in solid blue on a sagittal slice as well as the inflated surfaces. The functional correlations are shown on sagittal and transverse slices as well as the inflated lateral and medial surfaces of the macaque cortex. C: left and right PPHC correlations are shown on sequential coronal slices. A conjunction map (CONJ) shows voxels significantly correlated with both seed regions. Correlation maps are thresholded at $P < 0.05$ (corrected).

**Fig. 2.** Group and individual subject PPHC correlation data are displayed on group and individual T2*-weighted MRI scans to aid in localizing the temporo-parietal region functionally correlated with the PPHC. Left: transverse and a coronal MP-RAGE slice depicting the approximate anatomy that is shown in the T2*-weighted scans to the right. Individual subject (monkeys 1–3; $r \geq 0.01$) and group ($n = 8; P < 0.05$ corrected) PPHC correlation maps. The seed regions are shown above the correlations maps in blue. Black lines trace the intraparietal sulcus (IPS) and superior temporal sulcus (STS).
The deformed monkey PPHC correlation map includes a region in the inferior parietal lobule plus a smaller region in posterior cingulate/retrospenial cortex (Supplementary Fig. S2). For reference, we plot the estimated borders of relevant human Brodmann areas. Based on the results of the deformation, the regions in the macaque that were correlated with the PPHC were in or around human Brodmann areas 39, 31, and 23. This hypothesis, however, is dependent on the validity of the cross-species registration (see DISCUSSION and Supplementary Fig. S1).

The regions functionally correlated with the medial temporal lobe in humans overlap with regions in the default network, including the inferior parietal lobule and posterior cingulate/retrospenial cortex (Buckner et al. 2008; Vincent et al. 2006). The similarity between macaque and human PPHC functional correlation results (Kahn et al. 2008; Vincent et al. 2006) suggest that macaques may have regions that share a lineage with the human default network. Further evidence for this view comes from recent work showing that a region in the macaque PPHC network, the posterior cingulate, shows similar functional responses to the human posterior cingulate during task performance (Hayden et al. 2009). Therefore we also examined functional correlations associated the macaque posterior cingulate/retrospenial (pC/Rsp) cortex. The pC/Rsp was functionally correlated with bilateral posterior medial temporal lobe, parietal cortex (in and around areas 7a, LIP, and DP), medial prefrontal cortex (in and around areas 9, 14r, 10m, 24b, and 32), superior temporal sulcus, superior temporal gyrus, and dorsal lateral prefrontal cortex (in and around areas 6, 8, 9, and 46; Fig. 4). To further examine the correlations in medial prefrontal cortex, the data were projected onto the cortical surface, and boundaries around functional areas were estimated based on the schema of Ferry and colleagues (2000). The pC/Rsp was functionally correlated with regions in and around areas 9, 24b, 10m, 32, and 14r. Thus PPHC is functionally correlated with a region in pC/Rsp cortex that in turn is functionally connected with an additional set of regions throughout the anterior cingulate and medial prefrontal cortex.

DISCUSSION

Overview

This work reports the BOLD functional correlations of the PPHC and pC/Rsp. The main finding is that specific regions within lateral temporo-parietal, posterior cingulate, and retrosplenial cortex are functionally correlated with the medial temporal lobe (Fig. 1). This system was largely distinct from the network of regions activated by a saccadic eye movement task, which suggests that it is unlikely driven by spatial attention or oculomotor performance (Fig. 3). Individual subject results and detailed anatomical analyses suggest that the medial temporal lobe has functional connections to supramarginal and superior temporal gyrus in or near areas TPOc, PA, and 7a (Figs. 2 and 3). Cross-species registration between macaque and human suggested that the parietal region correlated with the PPHC in macaques might be in or around human Brodmann area 39 (Supplementary Fig. S2). Finally, although we found no direct functional connectivity between the PPHC and medial prefrontal cortex, evidence for indirect functional connectivity with the medial prefrontal cortex did emerge when pC/Rsp cortex was explored as an intermediate (Fig. 4).
POSTERIOR CINGULATE / RETROSPLENIAL CORTEX

FIG. 4. The posterior cingulate/retrosplenial (pC/Rsp) cortex is functionally correlated with bilateral posterior medial temporal lobe, lateral temporoparietal cortex, superior temporal sulcus and gyrus, dorsolateral prefrontal cortex, and medial prefrontal cortex. The seed region is shown in solid blue on a sagittal slice. The functional correlations are shown on sagittal, transverse, and coronal slices as well as the inflated lateral, inflated medial, and fiducial antero-medial surfaces of the macaque brain. As can be seen from the correlations displayed on the sagittal slice and caret surfaces, the pC/Rsp is robustly correlated with medial prefrontal regions in and around areas 9, 24b, 10m, 32, and 14r. All correlations $P < 0.05$ (corrected). Borders are adapted from Ferry et al. (2000).

Limitations and caveats

Resting state functional correlation patterns measured using fMRI are consistent across acquisition sessions within a participant (Honey et al. 2009; Meindl et al. 2009; Shehzad et al. 2009; Van Dijk et al. 2009) as well as across participants and groups (e.g., Desmoiseaux et al. 2006; Van Dijk et al. 2009; Vincent et al. 2006). While functional correlations appear to be constrained by anatomical connectivity (Honey et al. 2009; Margulies et al. 2009; Vincent et al. 2007), the correlation strength between regions also reflects polysynaptic connectivity (e.g., Habas et al. 2009; Krienen and Buckner 2009; O’Reilly et al. 2009) and may be influenced by common driving inputs (see Van Dijk et al. 2009 for discussion). Thus the methods applied here provide information about large-scale brain systems and the relationship of medial temporal structures to distributed cortical systems, but the details of anatomic connectivity will require further exploration using direct measures of anatomic connectivity.

Functional correlations can also be modified by the cognitive state of the participant. For example, the strength of functional correlations can be modified by task performance (Fransson 2006; Newton et al. 2007), sleep stage (Horovitz et al. 2009), and anesthesia (Supplementary Figs. 4–6 of Vincent et al. 2007). The anesthetized state of the macaques in this study may have caused a reduction in the correlation strength between some nodes in the PPHC and pC/Rsp correlation networks. For example, an unexpected finding in our study was the weak functional connectivity between the PPHC and the medial prefrontal cortex and anterior temporal lobe. In humans, the default network (of which PPHC and pC/Rsp are a part) is known to exhibit significantly decreased connectivity with the medial prefrontal cortex during loss of consciousness characterized by deep sleep (Horovitz et al. 2009). The present finding that the macaque medial prefrontal cortex was not correlated with the PPHC and weakly correlated with the pC/Rsp may be due to the anesthesia. Another possibility for the weak or nonsignificant correlations with prefrontal and anterior temporal regions is that the BOLD data were distorted and had low signal in the anterior temporal lobe and the medial prefrontal cortex. For these reasons, we are cautious when interpreting weak or nonsignificant correlations with these anterior regions.

Supplementary Fig. S2 plots the macaque PPHC functional correlation data on the human cortical surface using a nonlinear monkey to human registration technique based on a previously published schema (Denys et al. 2004) with additional landmarks in the prefrontal cortex (Supplementary Fig. S1). Based on the current set of landmark constraints, the temporal-parietal region correlated with the macaque PPHC may be functionally related to a region in the human Brodmann area 39. However, one should be cautious when drawing conclusions from this analysis due to the paucity of landmarks driving the cross-species registration in parietal cortex.

Relation to anatomical connectivity

Information about human anatomical connectivity is scarce. Therefore other methods, including functional connectivity mapping of spontaneous BOLD fluctuations, have been used to study potential anatomical networks in humans. Functional connectivity methods alone cannot unambiguously designate functional pathways, determine the directionality of a projection, or discern whether a pathway is direct or indirect. Nevertheless, despite these caveats, functional correlation mapping has successfully generated functional and anatomical predictions about the human brain. For example, we have previously shown that the regions functionally correlated with the human medial temporal lobe during the resting state overlapped those regions activated by episodic memory retrieval (Vincent et al. 2006). The study of functional connectivity in the macaque is useful for refining our understanding of the relation between functional and anatomical connectivity. Previously we reported similarities between functional and anatomical connectivity maps in the oculomotor system as well as functional correlations in visual cortex and known sub-areal, retinotopic organization (Vincent et al. 2007). Here we compare and contrast known anatomical tract tracing work in macaques in relation to our functional correlation results from seed regions in PPHC and pC/Rsp.

The PPHC is strongly anatomically connected to the posterior limbic cortex. Parahippocampal cortex (area TF) has light to moderate projections to area 29 and moderate to heavy projections to areas 30, 23, and retrosplenial area 23v (Lavenex et al. 2002). Morris et al. (1999) also reported that posterior...
The parahippocampal cortex (areas TF and TH) sends projections to retrosplenial area 30. The parahippocampal cortex (area TF) receives strong input from areas 30, 29l, and 29m of the retrosplenial cortex (Suzuki and Amaral 1994). Blatt et al. (2003) used separate retrograde tracer injections in parahippocampal regions TF and TH and showed that injections in both regions result in uptake in posterior cingulate area 23 and retrosplenial cortex (areas 29 and 30). Finally, Kobayashi and Amaral (2003, 2007) demonstrated reciprocal connections between the parahippocampal cortex and areas 23, 29, and 30. Therefore our reported functional correlations between PPHC and posterior cingulate and retrosplenial cortex are consistent with known anatomical connectivity.

The PPHC is anatomically connected to the lateral temporoparietal cortex. Suzuki and Amaral (1994, Fig. 15) demonstrated that retrograde tracer injections into area TF result in uptake in area 7a. In addition, Blatt and coworkers (2003) showed that retrograde tracer injections in parahippocampal region TF resulted in uptake in PG-Opt, which is very similar to area 7a and is near the region that we found to be functionally correlated with the PPHC. In addition, Lavenex and colleagues (2002) reported moderate to heavy anterograde labeling in area 7 after injection in parahippocampal area TF. Perhaps the most convincing data that area 7a is connected to the posterior parahippocampal cortex comes from the work of Cavada and Goldman-Rakic (1989, see Figs. 6 and 7). They injected anterograde and retrograde tracers into parietal area 7a and showed dense, reciprocal connections with the parahippocampal cortex (particularly in TF, but including TH). When taken in conjunction with these anatomical data, our functional correlation data demonstrate a functional pathway between the parahippocampal cortex and the parietal cortex in the macaque.

In addition to consistencies between functional and anatomical connectivity, we also observed inconsistencies. First, the PPHC is known to have connections with the medial prefrontal cortex. For example, the PPHC has both afferent and efferent connections with areas 9, 14, 24, 25, and 32 (Blatt et al. 2003; Lavenex et al. 2002; Kondo et al. 2005; Saleem et al. 2008; Suzuki and Amaral 1994). We did not observe significant correlations between our group PPHC seed region and the medial prefrontal cortex in the monkey. Second, the PPHC is known to have connections with anterior temporal cortex. Specifically, the PPHC has both afferent and efferent connections with dorsal superior temporal sulcus, in particular in the most anterior (Blatt et al. 2003; Lavenex et al. 2002; Suzuki and Amaral 1994) but also in and around MSTdp (Lewis and Van Essen 2000b). While we observed correlations between the PPHC and the superior temporal sulcus (Fig. 1C), we expected the correlations to extend more anteriorly based on previous observations. These negative observations in our data, which we suspect to be false negatives, may be attributable to signal dropout, distortions and/or the anesthetized state of the animals (see Limitations and caveats).

Beyond PPHC, we also examined correlations associated with the pC/Rsp cortex (see also Margulies et al. 2009; Vincent et al. 2007). Correlations with the pC/Rsp were largely in medial prefrontal cortex, dorsolateral prefrontal cortex, superior temporal sulcus, superior temporal gyrus, parietal cortex, and posterior parahippocampal cortex. Posterior cingulate/retrosplenial cortex (including areas 23, 29, and 30) has reciprocal connections with the hippocampal formation and PPHC (including TF and TH), the dorsolateral prefrontal cortex (including areas 9, 10, 11, and 46), medial prefrontal cortex (including area 24), superior temporal sulcus, superior temporal gyrus, and parietal cortex (including 7a, DP, and LIP) (Kobayashi and Amaral 2003, 2007; Morris et al. 1999). The functional connectivity results were consistent with the known connectivity of the posterior cingulate/retrosplenial cortex.

The present work makes two primary contributions to our understanding of macaque functional anatomy. First, although previous papers have demonstrated that the PPHC has reciprocal connections with retrosplenial cortex and the inferior parietal lobule (including area 7a), we extend those observations by demonstrating that the spontaneous BOLD fluctuations in PPHC, retrosplenial cortex, and 7a are robustly correlated. Second, as macaque studies are conducted primarily to better understand the human brain, the present work provides a critical bridge between the anatomical connectivity work in the macaque and the functional connectivity and functional activation literature in the human (Fig. 5).

Relation to the default network

A “default mode” of human brain function (Raichle et al. 2001) was proposed from the observation that a particular set of cortical regions is more active in the passive state than during performance of most attention demanding tasks (Andreasen et al. 1995; Binder et al. 1999; Buckner et al. 2008; Ghanad et al. 1995; Mazoyer et al. 2001; McKiernan et al. 2003; Shulman et al. 1997). Additional research has suggested that this network is not only engaged during passive tasks but is activated during the act of remembering (Wagner et al. 2005), thinking about the future (Schacter et al. 2008), scene construction (Hassabis and Maguire 2007), and social cognition (Saxe and Kanwisher 2003; Vogele and Fink 2003). An alternative hypothesis is that the default network may involve monitoring the external environment and is attenuated during focused attention (Gilbert et al. 2007; Hahn et al. 2007; Raichle et al. 2001; Shulman et al. 1997; see Buckner et al. 2008 for discussion).
The hallmark of the default network is task-induced deactivation. In support of the hypothesis that macaques may have a default network, covert attention suppresses neuronal responses in macaque lateral parietal area 7a (Steinmetz et al. 1994). Specifically, neurons responded more to stimuli that appear at unattended locations than to those that appear at attended locations. More recently, Hayden and colleagues (2009) recorded single neurons in the macaque posterior cingulate during a working memory task and demonstrated that neurons in the posterior cingulate cortex are reliably suppressed during task performance and returned to baseline levels between trials. The network of regions functionally correlated with the macaque parahippocampal cortex includes the posterior cingulate and area 7a (Figs. 1 and 3). Because of the functional and anatomical similarities, these macaque regions may be homologous to regions within the human default network. Future study of the macaque will be required to establish functional homology. An important next step will be to examine whether the regions here identified as functionally correlated with the macaque PPHC are functionally deactivated during attention demanding cognitive tasks.

Future directions

The present functional connectivity results suggest that the macaque has a potential homologue of the human hippocampal-cortical memory network (Greicius et al. 2004; Kahn et al. 2008; Vincent et al. 2006). Figure 5 shows the macaque PPHC correlation map (left) along with the human PPHC correlation map (middle) (data from Kahn et al. 2008). Both the macaque and human PPHC correlation maps include regions in posterior cingulate/retrosplenial cortex and the inferior parietal lobule. The parietal regions fall within an area of rapid cortical expansion in the human compared with macaque lineage (Van Essen and Dierker 2007) and where it is particularly difficult to identify exact homologies.

In humans, the network correlated with the PPHC is consistently activated by correct recognition (and more specifically recollection) of previously studied items (Cabeza et al. 2008; Cabeza R, Ciaramelli E, Olson IR, Moscovitch M. 2008). Neurons responded more to stimuli that appear at unattended locations than to those that appear at attended locations. More recently, Hayden and colleagues (2009) recorded single neurons in the macaque posterior cingulate during a working memory task and demonstrated that neurons in the posterior cingulate cortex are reliably suppressed during task performance and returned to baseline levels between trials. The network of regions functionally correlated with the macaque parahippocampal cortex includes the posterior cingulate and area 7a (Figs. 1 and 3). Because of the functional and anatomical similarities, these macaque regions may be homologous to regions within the human default network. Future study of the macaque will be required to establish functional homology. An important next step will be to examine whether the regions here identified as functionally correlated with the macaque PPHC are functionally deactivated during attention demanding cognitive tasks.

Acknowledgments

We thank W. Suzuki for valuable discussion; J. Harwell for Caret software enhancements used in data analysis; and K. J. Black for providing the monkey atlas target. We thank G. H. Patel, M. D. Fox, A. Z. Snyder, J. T. Baker, J. M. Zempel, L. H. Snyder, M. Corbetta, and M. E. Raichle for helping to conduct these experiments.

Grants

This work was supported by National Institute of Mental Health Grant R01-MH-60974 and by the Howard Hughes Medical Institute.

References


