Cognitive neuroscience research investigating working memory has suggested that item and inter-item relational information are processed by distinct regions of the lateral prefrontal cortex. Recent neuroimaging evidence has suggested that this distinction might hold for LTM memory encoding as well. Interestingly, the question of whether item based and inter-item relational processing can be dissociated behaviorally has long been debated with mixed results in the cognitive psychological literature. Beginning with the pioneering work of G.H. Bower in 1970, many studies have examined whether item-based encoding facilitates memory for individual items, whereas relational encoding facilitates memory for the inter-item associations amongst items. Results from these studies have been mixed, and it is unclear whether the differences between these two processes are just simply quantitative rather than qualitative. However, very few previous studies have used parallel measures to investigate item and inter-item memory. Furthermore, no study has considered the contribution of recollection and familiarity to item and inter-item memory judgments following item based and relational processing. In the present experiment, participants encoded word pairs using either an item-based (separation imagery) or relational (interactive imagery) encoding strategy. They were then given either a 6-point confidence item recognition memory test or a 6-point confidence associative recognition memory test. Stemming from the notion that item-based and relational encoding produce qualititative rather than just quantitative differences in that separation and interactive imagery will lead to similar levels of item recollection, however recollection of inter-item details will be specifically enhanced following interactive imagery. In agreement with these hypotheses, our preliminary results show that separation and interactive imagery produce equivalent estimates of item recollection, yet interactive imagery leads to far greater estimates for the recollection of inter-item associations.
Nicolas Davidenko

A reverse distinctiveness effect in face memory

Nicolas Davidenko & Michael Ramscar
Stanford University

The recognition advantage for distinctive items in memory is a widely reported finding (e.g., Schmidt, 1991; Shepherd et al., 1991; Valentine, 1991, Deffenbacher et al., 2000). The effect is robust and appears as both an increased hit rate for distinctive targets and a reduced false alarm rate for distinctive distractors. Because distinctive items may lie in sparse regions of “representational spaces”, a recognition advantage for distinctive items may potentially be due to the fact that they are more dissimilar than typical items to any randomly chosen set of distractor items. To explore this idea in the domain of face memory, we used a parameterized space of silhouetted face profiles (Davidenko, 2006) that allowed us to control for similarity between target and distractor faces. In Study 1, we replicated the classic “distinctiveness effect.” Participants observed sequences of 4 "training" silhouettes, which were followed by an 8-second retention interval and a sequence of 4 "test" silhouettes (2 targets and 2 distractors, in random order) which they judged as "old" or "new." Consistent with previous studies using front-view face images (e.g., Shepherd et al., 1991), distinctive face silhouettes yielded significantly higher hit rates and significantly lower false alarm rates than typical silhouettes. In Study 2, we used a 3AFC delayed match-to-sample paradigm to test whether distinctive faces retained this processing advantage over typical faces when target-distractor distances were matched for the two types of faces. For each target face silhouette, two distractor silhouettes were constructed at a fixed distance in “silhouette face space” from the target silhouette. Participants observed a target for 2 seconds, and after a 4-second delay, selected the correct target from among the two distractors. In Condition A, the sets of typical and distinctive silhouettes were constructed to lie on concentric hyper-spheres in silhouette face space. In Condition B, to control for potential learning effects in the course of the study, typical and distinctive silhouettes were constructed to occupy regions of equal size in silhouette face space, with typical silhouettes centered in the origin of the space, and distinctive silhouettes centered in the periphery. In both conditions, the recognition advantage normally associated with distinctive items reversed: we observed a recognition disadvantage for distinctive face silhouettes. The “reverse distinctiveness effect” we report with faces should not be too surprising. A variety of results from human perception and memory report similar advantages for well-learned regions of representational space: prototypical colors are discriminated better than less prototypical ones (Lucy & Shweder, 1979); realistic chess patterns are better remembered by experts than random assortments of chess pieces (Chase & Simon, 1973); and own-race faces are advantaged in recognition (e.g., Tanaka, Kiefer, & Bukach, 2004). This work illustrates the importance of quantifying target-distractor similarity when interpreting recognition memory performance.
The dual process signal detection (DPSD) model has been used to account for results from a wide range of recognition memory paradigms. However, a number of concerns have been raised about the model, and it has been suggested that the unequal variance signal detection (UVSD) model can provide an equally good, or even better, account of the data. We clarify the core assumptions of the DPSD model, and the way it is applied to different recognition paradigms, to dispel some common misconceptions. We then review the literature and show that the DPSD model provides a better account of recognition memory than does the UVSD model. The reviewed results clarify why pure signal detection models like the UVSD model have generally been rejected in favor of hybrid models that incorporate a signal-detection based familiarity process along with a separate probabilistic threshold process. Finally, we consider possible modifications of the UVSD model that might bring the model more in line with the data.
High-Resolution fMRI of Stimulus-Specific Novelty Encoding and Subsequent Memory Responses in Human Medial Temporal Lobe

Aaron M. Bornstein, Alison R. Preston, J. Benjamin Hutchinson, and Anthony D. Wagner

The medial temporal lobe (MTL) is critical for declarative memory, though the functions of specific MTL subregions remain underspecified. Given known differences in anatomical connectivity and inputs to particular subregions, MTL substructures may differentially support memory encoding, depending on the content of the experience. Using high-resolution fMRI (voxel size: 1.71 mm x 1.71 mm x 3 mm), the present experiment investigated the topographic organization of stimulus-specific encoding processes in human MTL, focusing on encoding responses related to novelty processing and subsequent memory performance. During scanning, subjects performed a novelty-encoding task on classes of stimuli (e.g., unfamiliar faces and scenes) that differed according to perceptual domain (e.g., visual-object and visuo-spatial). A post-scan recognition memory test assessed memory for stimuli presented at encoding. Analysis of novelty encoding (Novel>Repeated) and subsequent memory (Remembered>Forgotten) responses revealed differential activation along the anterior-posterior axis of MTL cortex. Parahippocampal cortex demonstrated encoding responses associated with novelty and subsequent memory during scene presentation, whereas perirhinal cortex demonstrated such responses during presentation of faces. Within hippocampus proper (CA1, CA3, dentate gyrus, subiculum), segregation of stimulus-specific novelty and subsequent memory responses was less differentiated, with hippocampal subfields demonstrating novelty and subsequent memory responses across multiple stimulus classes. These results suggest that MTL contributions to encoding vary across experience, with certain classes of stimuli/events being differentially processed by specific MTL subregions. Support Contributed By: NSF, NIH (MH071092)

Unitization increases neural and behavioral correlates of familiarity in an associative recognition task

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Recent data from neuroimaging, human amnesics, and animal models suggest that different medial temporal lobe subregions may differentially contribute to familiarity and recollection. More specifically, many results have supported the idea that the hippocampus may disproportionately support recollection, whereas the perirhinal cortex may support familiarity-based recognition. However, some findings suggest that the perirhinal cortex may be sufficient to support associative recognition under some circumstances. Although previous behavioral studies have indicated that associative recognition relies heavily on a recollection
process and is not strongly supported by assessments of familiarity, there is evidence that familiarity can support associative recognition as long as the paired items are treated as a single coherent unit. We conducted an event-related functional magnetic resonance imaging (fMRI) study to examine the role of "unitization" in associative recognition and to determine the degree to which different MTL subregions contribute to associative recognition based on familiarity and recollection. Participants were scanned while performing two encoding tasks, one in which they were instructed to unitize word-pairs (high-unitize), and another in which they encoded the items as an association (low-unitize). Subsequent recognition data showed that word pairs studied in the high-unitize condition yielded receiver operating characteristics (ROCs) at test that were consistently more curvilinear than ROCs from the low-unitize condition. Analysis of these ROCs shows that unitization increased both familiarity and recollection, with a disproportionately large increase in familiarity.

Preliminary fMRI analysis suggests that the high-unitize condition recruits a different network of brain regions, compared with the low-unitize condition. Parametric analysis of functional data additionally provides support for previous findings that different networks encode information that supports associative recognition based on familiarity and recollection.

Heekyeong Park

Determinants of successful recollection – study task versus study context

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Numerous fMRI studies employing the ‘subsequent memory procedure’ have demonstrated that successful episodic encoding recruits a variety of cortical regions, notably, prefrontal and fusiform/parahippocampal cortex. Findings from a number of studies indicate that the loci of subsequent memory effects depend on study task; for example, effects associated with semantic study judgments overlap regions identified as supporting semantic processing more generally, while the effects associated with a syllable judgment task localize to regions that support online syllabic judgments. Here, we investigate whether these task-based differences in subsequent memory effects extend to circumstances where subjects must encode and retrieve specific contextual features in addition to the item information sufficient to support a simple test of recognition memory. In two separate study sessions, subjects viewed visually-presented words and were required to make animate/inanimate judgments (in one session), or odd/even syllable judgments (in the other session). In both tasks, words were presented either in an orange frame on the left side of screen or in a purple frame on the right side. Subjects were instructed to pay attention to the details of each word’s presentation context in anticipation of a later memory test. Memory for study items and their source (i.e., color/location at study) were tested immediately after each study phase. Across tasks, highly robust subsequent memory effects were identified in bilateral extra-striate visual cortex and left inferior frontal gyrus. Task-specific subsequent memory effects were relatively modest and primarily driven by larger effects in the animacy task than in the syllable task. We interpret these data as consistent with the proposal that subsequent memory effects reflect those cognitive operations most salient for the on-line processing of a study item. In the present case, these operations involved the perceptually-based processing required to associate study items with their background contexts. Variation in this processing was a more important determinant of later recollection than variation in processing engaged in service of the ostensible study task. Thus, subsequent memory effects reflecting perceptual processes
common to the two study tasks overshadowed effects that would have reflected task-specific elements.

**Melina Uncapher**

*Modulation of the fMRI correlates of episodic encoding by divided attention depend on the nature of the secondary task*

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Dividing attention between a study task and a secondary task has a detrimental impact on later memory for the studied items. Two previous fMRI studies employing the 'subsequent memory procedure' came to different conclusions about the functional loci mediating the disruptive effects of divided attention on encoding. Kensinger et al. (2003) concluded that divided attention disrupts what appear to be task-specific study processes, whereas Uncapher and Rugg (2005) reported that competition between study and secondary tasks was manifest in neural regions supporting task-general, executive processes. The present study further addresses this issue by contrasting the neural correlates of successful encoding when the same study task competes with a secondary task for either task-general or task-specific processing resources. fMRI data were acquired as 15 volunteers made semantically-oriented (animacy) judgments to visually-presented words while concurrently performing one of three tasks on auditorily-presented words: male/female voice discrimination (control task), 1-back voice comparison (executive task), or indoor/outdoor judgment (semantic task). Using the 'remember/know' procedure, memory for the study words was assessed after a 15 min delay. Later recollection of items studied concurrently with the executive and the semantic secondary tasks was equivalently reduced relative to the control task. Subsequent memory effects (greater activity for words later remembered vs. later forgotten) in several regions varied according to the nature of the secondary task, indicating that the tasks disrupted encoding in different ways. These findings indicate that divided attention can disrupt episodic encoding through interference at multiple functional loci in the 'encoding pathway', and that the identity of these loci depends on the nature of the processing resources shared between the study and secondary task.

**Kaia Vilberg**

*Dissociation of the cortical correlates of recollection and familiarity: Further evidence from fMRI*

Kaia L. Vilberg, & Michael D. Rugg
UC Irvine

In two very similar fMRI studies (N=14 in each), the neural correlates of recognition memory for pictures were investigated with a test task that allowed studied items to be segregated according to whether recognition was associated with recollection or was based on familiarity alone. At study, participants viewed pairs of pictures of everyday objects. In experiment 1, study exposure varied up to a maximum of 8 seconds per trial, whereas in experiment 2 exposure duration was constant at 3 seconds. The test phase, which was identical across the two experiments, followed approximately 15 minutes later. Using a modified ‘Remember/Know’ procedure, participants were required to indicate whether a test item was new, familiar (known), elicited recollection of general contextual details from the study episode, or elicited a specific recollection of the picture with which it was paired.
Participants were encouraged to use the three latter response options only when they were confident an item was old. Regions sensitive to recollection were defined as those that showed greater fMRI BOLD activity for studied items endorsed as recollected rather than known. Regions sensitive to familiarity were defined as those showing greater activity for studied items endorsed as known rather than incorrectly endorsed as new (misses). Recollection was associated with enhanced activity in posterior cortex, most notably left BA 39/19 and medial parietal cortex (precuneus). The former region was further sensitive to amount of information recollected. Familiarity was associated with enhanced activity in left lateral parietal cortex, anterior to the parietal/occipital region associated with recollection, as well as in several regions of inferior and anterior left prefrontal cortex. These results strongly support the proposal that recollection and familiarity engage distinct cortical networks. They are difficult to reconcile with models of recognition memory in which recollection and familiarity are conceptualized as reflecting variations along a single continuum of memory strength.

Ellen Klostermann Wallace

Parietal activation during the successful retrieval of abstract and concrete auditory information

Ellen C. Klostermann Wallace, Ari Kane, and Arthur P. Shimamura
University of California Berkeley, Department of Psychology

In previous fMRI studies, successful recognition performance has been associated with a left frontal-parietal network that includes prefrontal, inferior parietal and precuneus regions. As nearly all fMRI studies use visual stimuli or visualizable auditory stimuli, it is unclear whether activations in parietal regions are specifically associated with memory or if they reflect visuospatial processing. Here, we investigated recognition performance—and particularly the status of parietal activations—for abstract and concrete nouns presented auditorally. Greater activation was observed in virtually identical left inferior parietal areas (BA 40) for the successful recognition of both abstract and concrete nouns. Successful recognition was also associated with activity in anterior cingulate (BA24), bilateral prefrontal cortex (BA 45/46) and precuneus (BA 7). These findings suggest that parietal activations during retrieval are not simply related to bottom-up visuospatial processes but may be more directly related to memory processes.
Talk Session II

Rachel Diana

The low frequency encoding disadvantage: Word frequency affects processing demands

Rachael Diana
UC Davis

Low frequency words produce more hits and fewer false alarms than high frequency words in a recognition task. When tasks other than item recognition are used, such as recall or associative recognition, the low frequency advantage is not seen. The low frequency hit rate advantage has sometimes been attributed to an advantage for low frequency words during the recollection process of recognition (e.g. Reder et al., 2000). We tested the hypothesis that, in addition to the advantage of low frequency words during recollection, there is a low frequency disadvantage during encoding. That is, low frequency words require more processing resources to be bound to episodic information than do high frequency words. When processing resources are reduced at encoding, low frequency words show a larger decrement in recognition than high frequency words. Words of either high or low frequency are not remembered as well when studied simultaneously with a low frequency word as opposed to a high frequency word.

Jeffrey Johnson

Recollection and the reinstatement of encoding-related neural activity

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Several functional neuroimaging studies have reported differences in the neural correlates of episodic retrieval (‘recollection’) according to the type of information retrieved from memory. These content-specific differences are often held to reflect the reinstatement of cortical activity elicited when the information was initially encoded. The present study (N = 20) used event-related fMRI to directly test this ‘reinstatement hypothesis’ by contrasting activity during the encoding and subsequent recollection of words studied in the context of two different study tasks. In the ‘scene’ task, a word was superimposed on a picture of a landscape scene, with the requirement to imagine the object denoted by the word occupying a suitable location in the scene. In the ‘sentence’ task, words were presented on a blank background, and the requirement was to silently generate a sentence incorporating the word. On a later memory test employing a ‘Remember/Know’ procedure, the neural correlates of recollection were operationalized by contrasting the activity elicited by studied words receiving ‘Remember’ versus ‘Know’ responses. Recollected words that had been encoded in the scene task elicited activity in regions of bilateral extrastriate and parahippocampal cortex that overlapped with regions where activity was greater for the scene compared to the sentence study task. Conversely, the loci of activity elicited by words recollected from the sentence task overlapped with regions in left middle temporal and medial frontal cortex where activity at encoding was greater for the sentence task. These task-specific associations
between encoding- and retrieval-related neural activity lend strong support to the reinstatement hypothesis of episodic retrieval.

Elizabeth Race


E.A. Race¹, D. Badre², C. Jones², A.D. Wagner¹,²

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Initial stimulus processing facilitates subsequent processing and classification. Perceptual repetition and conceptual repetition facilitate behavior and modulate neural activity. Recently, it has been proposed that rapid stimulus-response learning can account for components of these behavioral and neural repetition effects, though the electrophysiological correlates of such response-based repetition has not been delineated. The present ERP study aimed to (a) distinguish the electrophysiological signatures of perceptual repetition, conceptual repetition, and response repetition, and (b) examine possible contributions of response learning and response conflict to repetition-based changes in neural activity. During initial exposure, participants performed one of two semantic classification tasks with words. Subsequently, a mixed block was presented in which these words were represented along with a set of new words. Importantly, half of the old words were processed in the same manner as previously processed, and half were processed with the other classification task. Of the old words processed with the other classification task, half required the same response as was previously appropriate. ERPs from this mixed block were analyzed for new words, words that were repeated with the same task (perceptual, conceptual, and response repetition), words that were repeated with a different task but that required the same response (perceptual and response repetition), and words that were repeated with a different task and that required a different response (perceptual repetition and response conflict). Perceptual repetition was associated with reduced ERP amplitude over posterior electrode sites from ~400-550ms, while conceptual repetition effects emerged at ~550-700ms over left lateralized sites. Two response-related components were identified: (a) An earlier effect (~400-650ms) onsetting before the average response time and situated over fronto-central and right-lateralized scalp sites, and (b) a later effect (~900-1250ms) onsetting around the time of response over bilateral frontal sites, resembling the correct response/conflict-related negativity (CRN). These results suggest that repetition-induced response learning and response conflict modulate response selection demands at multiple times during stimulus classification.

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Talk Session III

David Badre

*FMRI evidence for a hierarchic organization of control in prefrontal cortex*

D. Badre & M. D’Esposito
UC Berkeley

Recent neuroimaging studies in humans, as well as electrophysiology and lesion studies in non-human primates, have reported regional distinctions in the prefrontal cortex (PFC) based on the level of abstraction at which multiple alternative representations compete to guide the selection of a response. Moreover, some evidence suggests that this organization may be hierarchic, in that more abstract, superordinate representations maintained in anterior PFC constrain the selection of less abstract, subordinate representations processed in posterior PFC subregions. To test this hypothesis, four fMRI mini-experiments parametrically manipulated the number of alternatives at increasing levels of representation during a response selection task. From subordinate to superordinate, we manipulated (a) the set of relevant manual responses, (b) the set of features of a stimulus (e.g., upward orientation versus downward orientation) that determine a manual response, (c) the set of perceptual dimensions (e.g., orientation versus texture) that determine the relevant features of a stimulus, and (d) the set of temporally distinct task contexts (e.g., block number) that determine the relevant perceptual dimensions. Parametric and additive increases in reaction time were evident across experimental manipulations. Furthermore, consistent with the hierarchy hypothesis, fMRI results revealed a systematic posterior to anterior gradient within PFC depending on the manipulated level of representation. More specifically, left premotor cortex was associated with the response set manipulation, lateral frontal regions with the feature and dimension set manipulations, and the left frontal pole with the manipulation of the task context. However, these regions also appeared to differ qualitatively in their temporal profiles, suggesting that this organization may reflect both distinctions in process as well as content.

Daphna Shohamy

*Novelty Differentially Modulates Medial Temporal Lobe and Basal Ganglia Contributions to Learning and Transfer*

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Dept. of Psychology and Neurosciences Program, Stanford CA

Extensive converging evidence suggests that the medial temporal lobe (MTL) supports rapid learning from single episodes, while the basal ganglia (BG) support incremental learning of stimulus-response associations. Recent evidence, however, suggests that these systems may interact during learning. Studies further suggest that both systems may play an important role in processing novelty. Taken together, these findings raise important questions regarding how novelty modulates different forms of memory, and the interaction between them. In this study, we used functional imaging (fMRI) to examine the impact of novelty on MTL and BG dynamics during associative learning and transfer. In this two-phase learning task, subjects first engaged in a concurrent, forced-choice discrimination, where they learned to associate between faces and scenes. This learning phase was followed by a transfer phase, where subjects were probed to transfer previously learned knowledge to a new context. Previous patient studies indicate that the first phase of learning this task depends on the BG, while the ability to transfer depends on the MTL. Here, prior to learning, subjects were pre-exposed to
a subset of the stimuli. Subjects were subsequently scanned during learning and transfer, allowing a comparison of brain activity related to learning of novel vs. familiar stimuli. Results indicate that novel stimuli were associated with better learning, and with increased MTL activity during learning, especially early on. By contrast, BG activity increased during learning of both novel and familiar stimuli. Performance on the transfer phase was less impacted by novelty, overall, although performance was somewhat lower for the novel stimuli compared with the highly familiar stimuli. These data suggest that MTL-based learning mechanisms are heavily modulated by whether the learned information is novel or familiar. By contrast, BG-based learning mechanisms appear to contribute more generally to incremental, stimulus-response learning.

Bradley Buchsbaum

Repetition suppression and reactivation in short-term recognition memory

Bradley R. Buchsbaum
UC Berkeley

A great deal of recent work on the neural underpinnings of recognition memory has shown that, in regions known to be important for sensory processing, a novel stimulus elicits a stronger response than a repeated one; and, moreover, the smaller response to the second stimulus the greater the subjective report of item familiarity. However, this phenomenon, often called "repetition suppression", would seem to stand at odds with another oft-proposed neural mechanism for recognition memory: namely, that perceptual traces established during stimulus encoding are "reactivated" upon a subsequent encounter of the same stimulus. Moreover, in short-term memory, at least, it is thought that memory traces established during initial stimulus perception undergo a rapid temporal decay. In the present work we examined, first, whether at short repetition lags, and using verbal stimuli, reactivation or repetition suppression is observed in sensory cortical regions known to be involved in memory for words. Second, we investigated whether both phenomena: repetition suppression and trace reactivation, are modulated by the number of intervening items (1-5) between an item and its repeat. Lastly, we examined how the phenomena of repetition suppression and reactivation are affected by a change in modality (auditory-to-visual or visual-to-auditory) between repetitions. Subjects performed a continuous verbal recognition task (ISI = 2.5 s), with randomly ordered auditory- and visual-verbal stimuli and repetition lag varied between one and five items. Pronounced repetition suppression was observed for both auditory and visual items in auditory and visual sensory cortices, respectively. Moreover, the degree of suppression was modulated by lag such that the degree of repetition suppression decreased with the number of items intervening between presentation and repeat. Reactivation (greater activity for a repeated item) was observed in the auditory association cortex of the middle superior temporal gyrus, and this effect was modulated by the modality-correspondence between item and probe. Our results indicate that neighboring cortical regions in the superior temporal lobe exhibit repetition suppression and reactivation, respectively, and that these effects are modulated by the intervening lag between item and probe in short-term recognition memory.

Deborah Hannula

Medial temporal lobe activity related to successful allocentric spatial working memory

Deborah Hannula & Charan Ranganath
UC Davis
Classic studies of amnesia led to characterization of hippocampal function emphasizing differential involvement in short-term (or working) versus long-term memory tasks. However, recent neuroimaging data suggest that the hippocampus is sometimes active during working memory maintenance. Furthermore, recent neuropsychological investigations have shown that hippocampal amnesia results in a deficit in memory for relations among co-occurring items, even at short lags. Here, we use functional magnetic resonance imaging to determine whether the hippocampus and adjacent medial temporal lobe structures are active when relations among co-occurring items must be maintained in working memory. Participants were scanned during performance of a working memory task that required memory for the locations of objects within scenes. Critically, we examine at what stage of processing (encoding, maintenance, retrieval) medial temporal lobe structures are recruited, and whether activation in these regions is correlated with successful working memory performance.
Craig Brozinsky

*Do amnesics recency effects rely on rehearsal?*

Craig Brozinsky
Department of Psychology, UC Davis

Numerous studies have shown that even patients with dense amnesia can show an intact recency effect in list learning tasks. Such findings are popularly interpreted to reflect the intact contribution of rehearsal to recall performance in amnesics. However, in healthy controls, there is little evidence to suggest that covert or overt rehearsal contributes to recency effects. In this study, we tested whether amnesic’s recency effects can be explained by rehearsal, a factor that has not previously been shown to be necessary for normal control’s recency effects. Amnesic patients with medial temporal damage and aged-matched controls studied twenty-eight lists of disyllabic nouns, and their recency effects were compared. In a within-subjects manner, subjects were presented lists under conditions of articulatory suppression or not, and in either auditory or visual modalities. Subjects were directed to output terminal items first in order to control for group based output order strategies. Critically, amnesic subjects showed a recency effect even under conditions of articulatory suppression. Furthermore, articulatory suppression did not significantly interact with group, suggesting that rehearsal does not guide amnesic’s recency effects to a larger extent than it does in normal controls.

Tracy DeBoer

*Electrophysiological indices of memory for temporal order during early childhood*

Tracy DeBoer
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Multiple Memory Systems Theory asserts that dissociable subsystems exist for memory for individual items and memory for contextual details (e.g., temporal order of the stimuli) within the episodic memory system (Schacter, et al., 2000). Findings from functional neuroimaging studies in typical adults and behavioral research in adults with lesions to specific brain regions support this claim with findings that item memory and memory for item-context relations rely on 1) separable and distinctive neural systems and 2) different mnemonic processes (Eichenbaum & Cohen, 2001). Memory for individual items relies relatively more on perirhinal and entorhinal cortices and is associated with familiarity of the items, whereas item-context memory is relatively more dependent on the hippocampus and recollective processes (e.g., Ranganath et al., 2003). To date, little is known about the development of these memory subsystems and how they relate to individual differences in performance on complex memory tasks during early childhood.

Evidence from electrophysiological investigations of memory in infants and young children has shown that item-memory effects can be detected in the electrophysiological response. Specifically, these measures reliably distinguish old/familiar items from novel items (e.g., Carver et al., 2000; Marshall et al., 2002). However, the contribution of memory for item-context relations to this effect has not yet been addressed. The purpose of the present investigation was to assess which aspects of the electrophysiological response were related to memory for individual items (i.e., familiarity processes supported by cortices surrounding
the hippocampus) and which were related to memory for context as indicated by temporal order memory (i.e., hippocampally-mediated recollection processes).

Participants included 21 3- to 4-year-old typically developing children. The paradigm consisted of teaching children 3 different 9-item event sequences. In order to induce variability in recall of temporal order difficulty of the event sequences was manipulated by altering the number of enabling connections between the items. One week after learning the sequences, children returned to the laboratory and both electrophysiological and behavioral measures of memory were obtained. Children viewed pictures of familiar and novel items while event-related potentials (ERPs) were recorded from 32 sites on the scalp and subsequently recalled the event sequences behaviorally.

Preliminary findings from analyses of behavioral measures suggest that memory for individual items was equivalent for each of the 3 event sequence types. However, memory for temporal order varied as a function of sequence difficulty: ordered recall was greater for sequences with more enabling connections between the items. Preliminary findings from electrophysiological analyses indicate that differences in ERPs to familiar and novel stimuli were related to memory for temporal order of the events sequences. Specifically, amplitude differences between responses to familiar and novel stimuli significantly predicted recall of order information after the 1-week delay.

Together these results suggest that subsystems of the episodic memory system are present in early childhood and that indices of memory reflected by differential electrophysiological responses to old and new stimuli during this developmental period are influenced by recollective, hippocampally-mediated mnemonic processes.

Sandrine Duverne

Age-related differences in neural correlates of retrieval of visual episodic information

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Previous findings from functional neuroimaging studies of age-related differences in the neural correlates of episodic memory suggest that healthy young and older adults recruit a common set of neural regions in association with successful episodic retrieval. Relative to young subjects, however, older subjects often demonstrate greater retrieval-related activity (‘old/new’ effects) in a sub-set of these regions (‘over-recruitment’). In the present study, we investigated age-related differences in episodic retrieval using a source memory procedure. At study, young and older healthy adults encoded a set of pictures of objects that were presented in one of two visually distinct contexts. Half of the pictures were presented once (hard condition), and the other half twice (easy condition), thus manipulating the difficulty of the subsequent memory test. At test, studied pictures were presented intermixed with new (unstudied) pictures. For each picture, participants were required to indicate whether it was previously studied in one or the other context, or whether the picture was new. A further response category was available for pictures that were judged old, but for which no source information was available. Older subjects’ source accuracy for the easy condition approximated the performance of the young subjects in the hard condition. Thus, these two conditions were employed for the primary age-related contrasts of retrieval-related activity. Consistent with previous findings, analyses of event-related fMRI BOLD activity revealed a network of regions that exhibited robust and equivalent old/new effects in the two age groups. These regions included bilateral medial and lateral parietal cortex, as well as left
anterior prefrontal cortex. There were no regions where old/new differences (in the sense of elevated old item activity relative to new items) were greater in young than in older subjects. In several visual extrastriate and medial temporal regions, however, old/new effects were of greater magnitude in the older subjects. These age-related effects primarily took the form of crossover interactions, such that the effects reversed in direction between the two age groups. These findings add further weight to the proposal that episodic retrieval in older subjects is associated with neural over-recruitment. The functional significance of this phenomenon is unclear.

April Hebert

*Role of the Entorhinal Cortex in Contextual Fear*

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Several studies have delineated a role for the hippocampus in fear conditioning. However, the role of the entorhinal cortex (EC), the main input-output structure for the hippocampus, in this task is uncertain. The extracellular-signal regulated kinase (ERK) cascade has been shown to be a molecular correlate for long-term memory, and its activity is required for various types of memory storage, including fear memory. In this report, we show that ERK activity in the medial entorhinal area (MEA) increases 90 minutes following fear conditioning. Post-training intra-EC infusion of ERK inhibitors at 40 min, but not at 10 min, resulted in an increase in freezing to the context, but not to the tone, during a 48 hr retention test. This enhancement was not due to a generalized increase in freezing behavior. Interestingly, both PD098059- and UO126-infused animals demonstrated anticipatory freezing in the context, freezing maximally at the time the shock was given during training. This anticipatory behavior was also seen in naïve animals receiving multiple training trials. Taken together, these results suggest that ERK-mediated plasticity in the EC normally suppresses context-specific fear memory, especially the temporal nature of the freezing response, and that blocking this plasticity mimics the effects of additional training.

Antonio Jaeger

*ERP correlates of the incidental retrieval of emotional information: effects of study-test delay*

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Prior experiments have established that event related potentials (ERPs) elicited by emotionally neutral pictures differ according to whether the pictures were encoding in association with an emotionally arousing or emotionally neutral study context. These studies employed only a single, relatively brief (ca. 10 min) study-test delay. Here, we contrasted these ERPs emotional retrieval effects as a function of a short vs. a long delay. Neutral pictures were initially encoded in association with either an emotionally negative or emotionally neutral backgrounds. In a repeated measures design, half the pictures were
subjected to a recognition memory test 10 min after the study phase, whereas the remainders were tested 24 hrs later. ERPs were recorded during both test phases. The ERPs data elicited by correctly judged recognition test items closely replicated previous findings: relative to new items, studied pictures elicited early frontal and left parietal old/new effects that did not vary according to study history (negative vs. neutral). A late-onset, fronto-centrally distributed positivity was however markedly larger for items encoded against the negative backgrounds. This effect was attenuated, and barely present, in the second test phase 24 hr later. These findings suggest that ERPs incidental retrieval effects are relatively transient. This transience likely reflects the time-limited effectiveness of the retrieval cues eliciting the emotional memories, rather than fragility of the memories themselves.

Diane Marian

*Effects of Emotional Facial Expression on Memory and Attention*

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Prior research examining attention to emotional facial expressions suggests that attention is drawn to threatening faces (i.e. those with angry expressions). These experiments typically employ paradigms in which two or more are presented simultaneously, and thus several stimuli compete for attentional resources. In another line of research, emotional faces are presented one by one and memory for the faces is evaluated later by way of surprise recognition tests. These studies find that happy faces are remembered better than faces displaying other emotional facial expressions (for non-clinical populations). The current studies were an attempt to integrate the two seemingly conflicting phenomena (preferential attention to threatening faces and superior memory for happy faces) within a single experiment by measuring both attention and memory for emotional faces. We combined an encoding phase in which groups of faces are presented and participants must identify whether one face displays a different emotional expression than the others (The Face In The Crowd paradigm) with a subsequent memory test that measures recognition accuracy for individual faces.

In Experiment 1, threatening faces among neutral crowds were detected more quickly than happy faces among neutral crowds, thus replicating the ‘Face in the Crowd’ effect. However, there was not a significant difference in recognition accuracy for the different facial expressions. In Experiment 2, more potent happy faces were chosen as stimuli in order to equate the intensity of the threatening and happy faces. Although there was no response time difference for detecting discrepant emotional expressions within neutral crowds, a memory difference emerged. Recognition accuracy was higher for threatening faces than for happy faces. The inconsistency of this result with previous findings may be due to the different encoding tasks. The influence of stimuli choice is highlighted by the different results obtained by the two experiments. Further research is needed to better understand the complexity of memory for emotional faces and its interaction with attention.

Adriane Mayda

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Age-related changes in memory are often associated with prefrontal cortex (PFC) dysfunction. One mechanism to explain this dysfunction is disconnection of white matter
tracts connecting prefrontal cortex with its anatomical targets. White matter hyperintensities (WMH) are associated with decrements in cognitive performance, particularly in working memory tasks, in both normal elderly and mild cognitive impairment (MCI) patients. WMH can disrupt working memory tracts and have been shown to have a periventricular distribution that changes with disease status; however, this non-specific marker of white matter injury may not be specific to white matter tract integrity. In this study, we examined diffusion tensor imaging, a more specific marker of white matter tract integrity, in a mixed group of elderly individuals ranging from normal cognition to MCI. We correlated average fractional anisotropy (FA) values in a periventricular white matter hyperintensity frequency map region of interest with performance on working memory and episodic memory tasks. Periventricular white matter tract disconnection correlates with performance on item recognition working memory tasks in elderly adults with and without mild cognitive impairment. FA values in our region of interest do not correlate with performance on an episodic memory task. In a multivariate model, total white matter hyperintensities, hippocampal volume, and total brain volume do not affect this relationship. These results suggest that periventricular white matter tract disconnection may explain some of the age-related working memory deficits in elderly individuals.
Talk Session IV

Fenna Krienen

Cross-modal differences in response inhibition.

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Response inhibition has been prominently conceptualized as a domain general, central capacity and as independent of the pathway that leads to the emission of a response. In a series of experiments using the stop-signal task, we investigated the hypothesis that there may be cross-modal differences in response inhibition. Subjects responded to Go signals and attempted to inhibit the initiated response to occasional Stop signals. For each of the four conditions, stimuli required either spatial or semantic judgments (Content), and subjects responded with manual key presses or verbal utterances (Output). While there was strong within-subject correlation in stop signal reaction time (SSRT) across Content, there was no correlation across Output; it appears that there are significant cross-modal differences in stopping time. We explore the implications for the independence assumption between going and stopping processes in the stop signal task, as well as the central capacity formulation of response inhibition.

Moriah Thomason

Development of working memory in the child's brain: evidence from functional magnetic resonance imaging

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We used fMRI to study the development of verbal and spatial working memory (WM) in a group of children and adults. We quantitatively varied WM capacity, or load, to determine whether children holding a larger number of items in mind would show regional activation similar to what has been observed in adults. In adults it has been observed that increasing WM task difficulty or complexity causes more significant and widespread activation in the WM system. We found that college-aged adults demonstrated the expected increases in activity with increased demands on memory capacity, but 7 to 12 year old children did not. For both spatial and verbal WM significant interaction effects were observed (between groups across load conditions). For spatial WM interactions occurred in left inferior parietal cortex (BA 40), right superior parietal cortex (BA 40), left inferior frontal cortex (BA45), left medial frontal gyrus (BA 6), and right inferior frontal cortex (BA 44). For verbal WM significant interaction effects occurred in left and right inferior parietal cortex (BA 40), left inferior frontal gyrus (BA 45 and BA 9), and left middle frontal gyrus (BA 46). Further, individual performance differences in children were correlated to magnitude of fMRI response. It appears that children are unable to marshal neural resources as well as adults in order to meet the demands of maintaining a large amount of goal-related information in WM.
Previous findings suggest the operation of selective information processing tendencies in older adults that favor positive over negative stimuli in both memory and attention (for a review see Mather & Carstensen, 2005). This study used eye tracking to investigate older adults’ use of selective visual attention as one of the cognitive control processes supporting the implementation of their emotional goals. Younger and older adults (N = 60) viewed emotional-neutral and emotional-emotional pairs of faces and pictures while their gaze patterns were recorded under full or divided attention conditions. Consistent with our cognitive-control-based account of the positivity effect in older adults’ information processing tendencies (Mather & Knight, 2005), relative to younger adults, older adults allocated less of their visual attention to negative stimuli in negative-neutral stimulus pairings in the full attention condition than younger adults did. Older adults’ tendency to avoid negative stimuli was reversed in the divided attention condition. Relative to younger adults, older adults’ limited attentional resources were more likely to be drawn to negative stimuli when they were distracted. While successful emotion regulation is likely under the control of a range prefrontally-mediated strategic processes, these findings demonstrate that selective allocation of visual attention is among them.