

The brain uses single-trial multisensory memories to discriminate without awareness

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Received 20 January 2005; revised 18 March 2005; accepted 8 April 2005
Available online 13 May 2005

Multisensory experiences enhance perceptions and facilitate memory retrieval processes, even when only unisensory information is available for accessing such memories. Using fMRI, we identified human brain regions involved in discriminating visual stimuli according to past multisensory vs. unisensory experiences. Subjects performed a completely orthogonal task, discriminating repeated from initial image presentations intermixed within a continuous recognition task. Half of initial presentations were multisensory, and all repetitions were exclusively visual. Despite only single-trial exposures to initial image presentations, accuracy in indicating image repetitions was significantly improved by past auditory–visual multisensory experiences over images only encountered visually. Similarly, regions within the lateral–occipital complex—areas typically associated with visual object recognition processes—were more active to visual stimuli with multisensory than unisensory pasts. Additional differential responses were observed in the anterior cingulate and frontal cortices. Multisensory experiences are registered by the brain even when of no immediate behavioral relevance and can be used to categorize memories. These data reveal the functional efficacy of multisensory processing.

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Keywords: Multisensory; Cross-modal; Visual; Auditory; Object recognition; fMRI; Memory; Lateral-occipital complex (LOC)

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Available online on ScienceDirect (www.sciencedirect.com).

Introduction

The different sensory systems are specialized for treating assorted environmental signals (light, sound, touch, smell, and taste) that provide bases for our perceptions. Perceptions can be further enhanced when several sensory signals originate from a single object—i.e., under multisensory conditions (e.g., Calvert et al., 2004; Molholm et al., 2004; Murray et al., 2004a). While our perceptions are based on the information provided by our senses, they are also strongly influenced by our past experiences (i.e., memories; James, 1890). Neurophysiologically, this suggests interchange between bottom-up and top-down processes that manifests in the manner in which memory traces are established during encoding and later retrieved and utilized. The multisensory composition of our external world raises the question of the comparative efficacy of multisensory vs. unisensory memories in influencing the discrimination of incoming sensory information.

Increasingly, neurophysiological methods have been applied to the question of how experiences in one or multiple senses alter later processing of stimuli from another sensory modality. Two general patterns of results have thus far been observed. Some have shown that regions involved during the encoding of a multisensory experience can be reactivated by repetition of a component part of that experience. For example, responses in auditory cortex were elicited by repeated visual stimuli that had been studied with sounds (Nyberg et al., 2000; Wheeler et al., 2000; see also Gottfried et al., 2004 for a study of olfactory–visual pairings). By contrast, microelectrode recordings have shown that such differential responses can also occur within a single brain region, with inferotemporal (IT) neurons responding according to learned associations (e.g., Gibson and Maunsell, 1997). Brain responses can thus vary, either within a region or throughout an activated network, according to whether they are part of multisensory or unisensory memories.

More recently, we addressed the requisite conditions for generating such differential responses, as well as the rapidity and facility with which such occur (Lehmann and Murray, *in press*; Murray et al., 2004b). Performance with image repetitions was selectively enhanced if the initial experience had been a semantically congruent auditory–visual pair, was unchanged if the initial experience had been a semantically incongruent auditory–visual pair, and was impaired if the initial experience had been paired with a pure tone relative to images only presented visually. This occurred in the absence of either actively studying or actively classifying stimuli, even though subjects were exposed to the multisensory experience for only a single 500-ms trial, and despite the multisensory aspect of the stimuli being completely orthogonal to their required task. That is, this discrimination was incidental. Electrophysiological effects in the case of semantically congruent pairings began at just 60 ms post-stimulus via a topographic change in the electric field at the scalp. Source estimation analyses further suggested that this difference originated within the lateral–occipital complex (LOC; Murray et al., 2004b). Despite being traditionally considered visual in function (e.g., Malach et al., 1995; Murray et al., 2002, 2004c), the LOC has also been shown to have multisensory properties (e.g., Amedi et al., 2001; Amedi et al., *in press*; Molholm et al., 2004).

These results raise the possibility that the LOC may play a central role in multisensory memory functions. However, despite recent advances in source estimation procedures (e.g., Andino et al., *in press*; Michel et al., 2004), the intracranial spatial resolution of scalp recordings remains limited, particularly in comparison with methods such as fMRI. In order to more precisely confirm the role of the LOC in multisensory processes, including memory functions, as well as to account for the discrepancies between electrophysiological and hemodynamic studies, we conducted an event-related fMRI study, modifying the behavioral paradigm from our prior studies (Fig. 1). Our comparison was between spatial patterns of blood oxygen level-dependent (BOLD) activations from two classes of repeated visual stimuli: those initially presented as semantically congruent auditory–visual multisensory

pairs vs. those initially presented without sounds (V+ and V–, respectively).

Methods

Participants

Ten healthy subjects (8 female), aged 18–33 years (mean \pm SD = 25.0 \pm 5.6), participated. (None of the authors participated in this study.) All subjects provided written informed consent to participate in the study, the procedures of which were approved by the Institutional Review Board of the Nathan S. Kline Institute for Psychiatric Research. All subjects were right-handed (Oldfield, 1971). No subject had a history of or current neurological or psychiatric illnesses, and all reported normal or corrected-to-normal vision as well as normal hearing. Behavioral data from two subjects were lost due to equipment failure. However, fMRI analyses were conducted with the data from all 10 subjects.

Behavioral procedures and task

The experimental paradigm is schematized in Fig. 1. Subjects performed a continuous recognition task comprised of equal numbers of initial and repeated presentations of line drawings of common objects, which were pseudo-randomly intermixed within each block of trials. On each trial, subjects indicated whether the visual stimulus was appearing for the first time or had appeared previously. They were instructed to ignore the sounds and concentrate on the visual task. Visual stimuli were comprised of 108 line drawings selected from either a standardized set (Snodgrass and Vanderwart, 1980) or obtained from an online library (dgl.microsoft.com) and modified to stylistically resemble those from the standardized set. Images were centrally presented for 500 ms and appeared black on a white background. On initial presentations, visual stimuli were either presented with or without a corresponding, but task-irrelevant, sound with equal

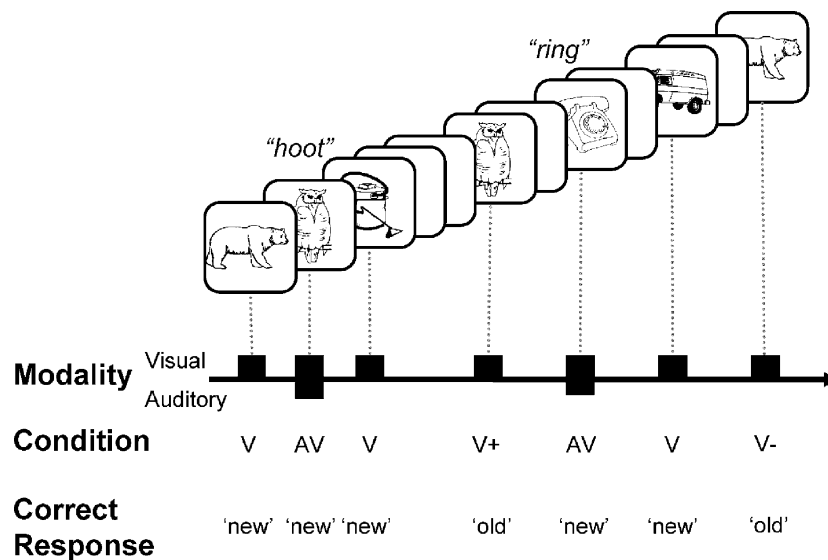


Fig. 1. Experimental paradigm. The continuous recognition task had subjects indicating initial and repeated image presentations. Half of the initial presentations were simultaneously paired with corresponding, but task-irrelevant, sounds (AV trials). The other half contained only images (V trials). All repeated presentations contained only images, but were subdivided for analyses into two conditions—those that initially had been presented with sounds (V+ trials) or only visually (V– trials).

likelihood. That is, the image set was equally divided into two groups: those that upon initial presentation appeared only visually and those that appeared with a corresponding sound as a simultaneous auditory–visual multisensory pair ('V' and 'AV' trials, respectively).

Auditory stimuli were complex, meaningful sounds (16-bit stereo, 44,100-Hz digitization, 500-ms duration), each of which corresponded to one of the visual stimuli in the AV group (e.g., a "hoot" sound with the image of an owl). Sounds were obtained from an online library (dgl.microsoft.com), modified using audio editing software (Adobe Audition version 1.0) so as to be 500 ms in duration. The volume was adjusted to a comfortable and comprehensible level for each subject, such that sounds were clearly, but not uncomfortably, audible in the magnet environment.

On repeated presentations, only the visual stimuli from the initial presentations were displayed. Subjects' task was to indicate as quickly and as accurately as possible, via a right-hand button press, whether or not the image had been seen before. Thus, there were two classes of repeated presentations: (1) those having initially been presented as visual alone and (2) those having initially been presented with sounds ('V-' and 'V+' trials, respectively). These conditions differ only in whether or not the initial presentation of the image was paired with a sound—i.e., whether or not there was an auditory–visual multisensory experience associated with the image. Subjects were not asked to make this distinction and performed the same task with both V+ and V- trials. As such, the context (i.e., whether a sound had been simultaneously presented on the image's initial encounter) was completely orthogonal to the task.

Stimuli were blocked into a series of 72 trials, with equal likelihood of initial and repeated presentations as well as V, AV, V-, and V+ trials (i.e., 18 trials of each per block of trials). During a block of trials, each image was repeated once, independently of how the image was initially presented. Stimuli were presented for 500 ms. The inter-trial interval (ITI) ranged from 6 to 10 s in steps of 2 s, varying randomly from one trial to the next though evenly distributed within each experimental condition to provide adequate temporal sampling of the blood oxygen level dependent (BOLD) response. On average, there were 6 intervening stimuli (range = 1–10 images) displayed between the initial and repeated presentation of any image. Each subject completed 3 blocks of trials. Both behavioral and fMRI data were collected from all conditions throughout the length of the scanning session, and E-prime (Psychology Software Tools, Inc. www.pstnet.com) was used to control stimulus delivery and to record behavioral responses. Each object was presented only once during the course of the experiment.

Anatomical MRI acquisition

High-resolution whole brain images were acquired using a Siemens 1.5-T VISION magnet with a three-dimensional (3D) T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) sequence. Anatomical images (202 slices) were acquired (voxel size = 1 mm³, matrix size = 256 × 256, TR = 11.6 ms, TE = 4.9 ms, flip angle = 8°) for coregistration with the fMRI data.

fMRI Acquisition and analyses

The same Siemens 1.5-T VISION magnet was used for both the functional and anatomical data collection. Information about the

hemodynamic response evoked by the tasks was obtained using single-shot, T2*-weighted, echo planar imaging (EPI) sequences. Images were acquired with a TR of 2 s, a TE of 50 ms, and a flip angle of 90°. Each of the volumes consisted of 22 contiguous axial slices (voxel size = 3.91 × 3.91 × 5 mm; matrix size = 64 × 64 voxels), which allowed for whole brain coverage. Before data analysis, the first five volumes of each block were discarded to account for the time needed for the field to achieve a steady state. Onset of the volume acquisitions was triggered by a transistor–transistor logic (TTL) pulse generated by E-Prime precisely 10 s prior to the presentation of the first experimental stimulus. During this period, subjects were presented with a numerical countdown so as to also prepare for task onset. Stimuli were delivered using an IFIS-SA stimulus delivery system (MRI Devices Corp., Waukesha, WI), which is equipped with a 640 × 480 pixel LCD screen. This shielded LCD screen was mounted on the head-coil, directly in the subjects' line of vision. Head motion was minimized using the standard Siemens head holder. Responses were collected using a Lumina LP-400 MR-compatible serial response pad (Cedrus Corporation, San Pedro, CA). All subjects responded with the index and middle fingers of their right hand to indicate new and repeated images, respectively.

All images were realigned using Analysis of Functional NeuroImages (AFNI; Cox, 1996). Any blocks in which the subject moved more than one voxel in any dimension or more than a degree in pitch, roll, or yaw were discarded. Each raw time-series of signal strength for each subject was first time-shifted so that the slices were aligned temporally (i.e., shifted so that the slices had the same temporal origin), and any linear trends in the data were removed. All volumes in the time-series were then spatially registered using an image midway through the time-series as the canonical image. All voxels outside the brain were eliminated from further analysis. The hemodynamic response was modeled by a delayed γ function, and this function was coded into the design matrix as a regressor. This has been shown to be a robust method of estimating hemodynamic response when the precise timing of the onset of the rise of the hemodynamic response is not known (Ollinger et al., 2001). Contrasts were specified using the General Linear Model, using a corrected voxel-level probability threshold of 0.05. The correction for multiple comparisons was achieved by including a cluster-level threshold of 15 contiguous voxels that was determined using the AlphaSim program (available at <http://afni.nimh.nih.gov>), with Monte Carlo simulations restricted to the gray matter.

Results

Subjects readily performed the task of discriminating between initial and repeated presentations of images. Accuracy on initial image presentations did not significantly differ between multisensory auditory–visual (AV) and unisensory visual (V) conditions (96% vs. 91%; $t_{(7)} = 1.43$; $P > 0.15$), though reaction times were significantly slower on AV than V trials (1120 vs. 1043 ms; $t_{(7)} = 4.18$; $P < 0.005$). We would note at this point that slower reaction times on multisensory trials provide an empirical indication that subjects were unaware of the fact that the mere presence of auditory stimuli signaled a novel image presentation. If this were not the case, faster and/or more accurate performance would be expected for any trial containing a sound, since this signal always indicated that an image was new. This pattern thus also argues

against an explanation in terms of general alerting; a point to which we return in the Discussion. The observed pattern also supports our contention that any effects of these multisensory pairings on repeated image presentations are incidental, in addition to this aspect being orthogonal to the task. Lastly, performance patterns on initial presentations were not mirrored on repeated presentations. Rather, on repeated image presentations, accuracy was significantly higher for the V+ than the V– condition (90.2% vs. 87.8%; $t_{(7)} = 2.76$; $P < 0.03$) in the absence of reaction time differences (975 ms vs. 993 ms; $t_{(7)} = 0.74$; $P > 0.45$). That is, subjects were more accurate at indicating the repetitions of images that had been previously encountered with sounds, though no faster. (This pattern of performance accuracy differences was observed for all but 2 of the participants of this study. One of these individuals showed no difference between the V+ and V– conditions, and the other showed a slight improvement for the V– condition.) This improved accuracy indicates that repeated visual stimuli were differentially processed according to past, task-irrelevant multisensory experiences.

In terms of BOLD responses, analyses were restricted to the V+ vs. V– comparison, reasoning that differences reveal brain mechanisms of multisensory vs. unisensory memory discrimination. This contrast revealed several activations that withstood correction for multiple comparisons. These activations are listed in Table 1 and included the left middle occipital gyrus, the left medial frontal gyrus, the anterior cingulate cortex, and the right inferior frontal gyrus. The maximal activation in the left middle occipital gyrus was located within the LOC (Fig. 2), confirming a role for visual object recognition regions in multisensory memory processes. There was no evidence of activations in auditory cortices, even without applying the cluster-level correction. By contrast, we would note that the differential LOC activation was bilateral, though that in the right hemisphere did not survive cluster-level correction.

Discussion

These data demonstrate that repeated visual stimuli can be discriminated according to whether they were initially encountered in a multisensory (auditory–visual) or unisensory (visual only) manner. This discrimination manifested both behaviorally—in the form of improved accuracy for images with multisensory pasts—and in terms of differential BOLD responses within regions of the lateral–occipital complex (LOC), as well as anterior cingulate and frontal cortices. These effects occurred incidentally. Subjects performed the same decision with all repeated images and showed

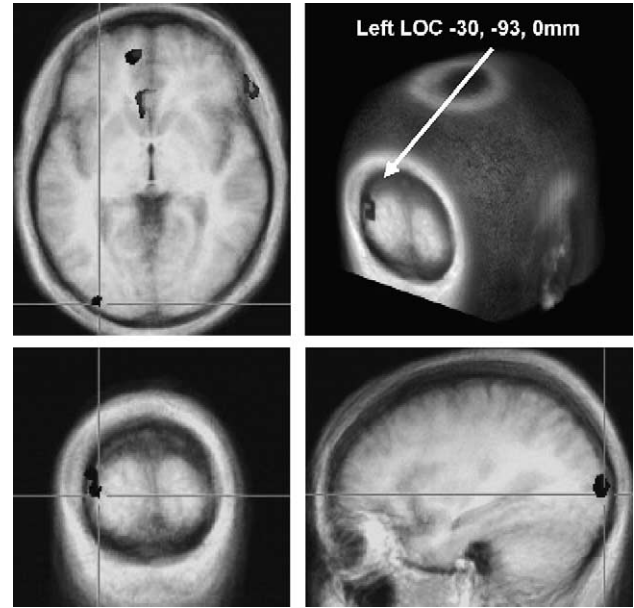


Fig. 2. fMRI results. The V+ vs. V– comparison yielded several activations, including clusters within left LOC, anterior cingulate, and frontal cortex. Talairach and Tournoux (1988) coordinates are indicated for the left LOC cluster. Statistical images have been thresholded at $P < 0.05$ after correction for multiple comparisons (see Methods for details).

no overt signs of being aware of this distinction. These findings support the hypotheses that distinct multisensory memory representations can be incidentally formed following single-trial exposure and that such representations are accessible upon repetition of just the visual component, facilitating behavior on the present task. Most importantly, these data provide evidence that such representations are principally within brain regions traditionally considered visual in their function and that auditory cortex activity is not requisite for auditory–visual memory discrimination, leading to behaviorally significant consequences.

The incidental and single-trial underpinnings of the present behavioral effects and differential LOC activity sharply contrast with previous hemodynamic imaging studies of multisensory memory processes that observed activity within auditory (Nyberg et al., 2000; Wheeler et al., 2000) or olfactory (Gottfried et al., 2004) cortices in response to visual stimuli that had been learned during the experiment as multisensory pairs. For one, the present study observed that repetition discrimination was significantly improved for stimuli with (semantically congruent) multisensory, rather than unisensory, initial exposures. This is our third demonstration of this phenomenon, which here occurred despite nearly doubling the interval between initial and repeated image presentations to be approximately 50 s (relative to 25 s in Lehmann and Murray, in press; Murray et al., 2004b), and also occurred despite the presence of added auditory stimulation from the scanner environment. This behavioral improvement indicates that multisensory memory representations are established after single-trial exposure and are later accessible to facilitate memory. By contrast, the studies of Nyberg et al. (2000) and Wheeler et al. (2000) provide no behavioral evidence that past multisensory experiences were actually beneficial. Rather, the data of Nyberg and colleagues suggest relatively poorer performance for words that had been paired with sounds, with no condition-wise behavioral results reported by Wheeler and colleagues. One possibility, then, is that

Table 1
Activation clusters for the V+ vs. V– contrast

Location	Brodman area	Cluster size	Center of mass	Locus of maximal intensity
Middle occipital gyrus (left)	18/19	29	–34, –89, 7	–30, –93, 0
Anterior cingulate	24	32	–2, 24, –3	2, 23, 0
Medial frontal gyrus	10	27	–12, 44, –5	–14, 31, –8
Inferior frontal gyrus	45	17	56, 34, 0	58, 31, 0

auditory areas were differentially (re)activated in these studies to compensate for the increased task difficulty. A related point is that the design of the present study did not permit extensive studying of the multisensory associations. There were only single-trial exposures, and the continuous recognition task has initial and repeated presentations pseudo-randomly intermixed. The observed performance facilitation does not appear to be contingent upon extensive or explicit encoding. This again contrasts the abovementioned studies, wherein subjects completed separate study sessions prior to testing.

The differential involvement of regions within the LOC in multisensory memory processes is in solid agreement both with microelectrode recordings from IT neurons in macaque monkeys (Gibson and Maunsell, 1997) and also with our previous electrical neuroimaging study (Murray et al., 2004b). Both of these studies provide evidence that distinct neural populations mediate multisensory vs. unisensory memory representations. In the case of the Gibson and Maunsell (1997) study, selective delay activity for specific learned associations was observed at different neurons. In Murray et al. (2004b), differences in the electric field at the scalp were statistically identified beginning at 60 ms post-stimulus, which forcibly result from changes in the configuration of intracranial generators (see e.g., Murray et al., 2004a,b for discussion). Similarly, recent fMRI results are providing evidence that regions of the superior temporal sulcus (STS) might likewise contain a ‘patchy’ distribution for unisensory (auditory or visual) and multisensory (auditory–visual) object representations (Beauchamp et al., 2004). Likewise, increasing evidence indicates that the LOC and surrounding cortices play a substantial role in auditory–visual as well as somatosensory–visual multisensory interactions, particularly with object stimuli (reviewed in Amedi et al., in press; Calvert et al., 2004). The present study further extends the role of the LOC to multisensory memory representations. The activation observed in frontal regions is also consistent with previous studies of multisensory memory retrieval (Wheeler et al., 2000). While one possibility is that this activation reflects a top-down mechanism of retrieval or task goals (e.g., Miller, 2000; see also Calvert, 2001), consideration of the present fMRI results in light of our previous ERP study would suggest that differentiation of incoming visual stimuli according to past experiences might occur first within the LOC and only at later time periods in frontal regions. However, further experiments will be required to more empirically assess this hypothesis.

Some alternative accounts of the observed effects are also worth brief commentary. It is worth noting that in the present study as well as our previous studies with this paradigm (Murray et al., 2004b) or variants examining episodic and semantic factors (Lehmann and Murray, in press), multisensory effects on encoding and retrieval were dissociated. In all cases, multisensory information of all varieties during initial presentations led to slowed reaction times (relative to unisensory stimuli) in the absence of a significant alteration in the accuracy of novelty discrimination. This interference effect from multisensory conditions may be a consequence of the present task being restricted to the visual modality, which would at least partially explain differences between our results and those of others examining semantic congruence in multisensory object discrimination that required fuller processing of both visual and auditory signals (e.g., Molholm et al., 2004). By contrast, it was only performance with repeated images (in particular the accuracy of repetition discrimination) that was significantly affected by the episodic or semantic attributes of the initial multisensory experience. It is thus clear that the effects

observed with stimulus repetitions do not simply reflect a general, long-lasting effect of multisensory interactions between auditory–visual events.

An account of the present results in terms of selective attention to audition or novel context detection (e.g., Ranganath and Rainer, 2003) can thus be discounted, as these would have predicted faster and/or more accurate performance on initial multisensory presentations because of the fact that any auditory information would have been a sufficient cue to correctly indicate novel image presentations. This was not observed here nor in either of our prior studies. A similar argument applies to an explanation in terms of general alerting, wherein multisensory events would have been predicted to produce the fastest and/or most accurate behavior. Rather, the pattern of reaction times on initial stimulus presentations fits well with results suggesting that events in an unexpected modality can lead to slowed reaction times on a detection paradigm (Spence et al., 2001). However, this variety of selective attention still would not account for the performance pattern observed with repeated image presentations. In addition, effects of general arousal and fatigue cannot readily account for the present results. (The different stimulus conditions were approximately homogeneously distributed throughout blocks of trials.) Thus, even if subjects were more engaged in the task during the beginning of a block of trials, this would have applied equally to all stimulus conditions.

In summary, these findings indicate that brain responses to repeated visual stimuli are influenced by how they were previously encountered, even when such is of no relevance to the task at hand. This supports the hypothesis that there is ready access to distinct multisensory and unisensory memory representations within higher-tier regions of the visual cortical processing stream. More simply, we provide evidence that extends the functions of the LOC from visual object processes to multisensory memory processes. These data likewise support similarities between human and non-human primate memory mechanisms. More generally, the brain differentially encodes visual and multisensory experiences and uses this classification for later discriminating component parts of these experiences without our awareness.

Acknowledgments

We thank Marina Shpaner for her excellent technical assistance. The Swiss National Science Foundation (3200BO-105680/1 to MMM), The Leenards Foundation (Prix Leenards 2005 pour la promotion de la recherche scientifique to MMM), and National Institutes of Health (MH63915 to GRW; MH65350 and MH63434 to JJJ) provided financial support.

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