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Multisensory context portends object memory

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Multisensory processes facilitate perception of currently-presented stimuli and can likewise enhance later object recognition. Memories for objects originally encountered in a multisensory context can be more robust than those for objects encountered in an exclusively visual or auditory context [1], upturning the assumption that memory performance is best when encoding and recognition contexts remain constant [2]. Here, we used event-related potentials (ERPs) to provide the first evidence for direct links between multisensory brain activity at one point in time and subsequent object discrimination abilities. Across two experiments we show that individuals showing a benefit and those impaired during later object discrimination could be predicted by their brain responses to multisensory stimuli upon their initial encounter. These effects were observed despite the multisensory information being meaningless, task-irrelevant, and presented only once. We provide critical insights into the advantages associated with multisensory interactions; they are not limited to the processing of current stimuli, but likewise encompass the ability to determine the benefit of one's memories for object recognition in later, unisensory contexts.

The contexts in which learning and retrieval of memories occur can refer to external or internal states (e.g., being in a particular room inebriated) or alternatively to fine-grained stimulus features (e.g., their colour or position) [2, 3]. Traditionally, memory has been scientifically investigated under unisensory conditions, despite most real-world situations being multisensory and despite multisensory information oftentimes benefiting perception and thus being well-poised to facilitate memory [4]. Investigations of memory from a multisensory perspective have yielded discrepant results [1]. Some observed that multisensory contexts are beneficial to memory formation and retrieval, while others

obtained the opposite pattern [1, 5]. Individual factors and/or trial-to-trial variability may therefore determine whether multisensory learning will be beneficial. Here, we tested whether multisensory processes related to perceptual salience at one point in time predict an individual's later memory performance.

Participants completed a continuous recognition task involving the presentation of individual images and requiring the discrimination of initial ("new") from repeated ("old") items. Unbeknown to them, half of the initial images would be presented together with a meaningless sound, resulting in two encoding contexts (Figure 1). Accuracy differences in recognizing (unisensory) image repetitions showed there were individuals who either improved with or were impaired by prior multisensory vs. visual encoding. Notably, there was no evidence for a general difference in behaviour between these sub-groups; performance was indistinguishable on both initial and repeated encounters as well as in same and different contexts, arguing against general attention or arousal difference. Rather, only the relative performance difference between types of repeated encounters distinguished participants (significant interaction; Supplemental Information). These accuracy differences were directly linked to processes specifically during the encoding of multisensory information.

Electrical neuroimaging analyses of ERPs [6] focused on differences in the processing of multisensory stimuli (Figure 1). No group differences were observed in response to visual stimuli (Supplemental Information), ruling out general differences in stimulus processing across individuals. ERPs significantly differed between individuals later improving from versus being impaired by the initial exposure to multisensory stimuli, being stronger in individuals who later exhibited improved recognition. This was further substantiated by a correlation analysis between ERPs in response to initial encounters with multisensory stimuli and later differences in object discrimination accuracy as a function of time. These modulations appear to be elicited implicitly; there were no group differences in explicit awareness of or selective attention to the multisensory aspect of the experiment. Source modelling showed that this ERP enhancement was localized to bilateral posterior parietal cortices. Prior findings have implicated these regions in perceptual benefits of multisensory object recognition [7]. In other words, brain activity in response to single-trial multisensory events was indicative of how well an individual would later recall the constituent unisensory elements.

Critically, this pattern of results generalized to a separate experiment involving another set of 15 participants, who instead performed the task in the auditory rather than visual modality (Supplemental Information). The pattern of behaviour and brain activity in this follow-up experiment was strikingly

similar to that observed in the main experiment and confirms the predictive value of multisensory processes for later memory performance.

These findings provide an additional important challenge to the longstanding belief that recognition is best when encoding and retrieval contexts are identical [2, 3]. Previously, we showed that single-trial exposures to multisensory contexts are sufficient to improve recognition performance relative to purely unisensory contexts. We originally observed this improvement exclusively when the multisensory context involved a semantically congruent object pairing [1]. Here, we show for the first time that improvements can be elicited even when the multisensory context involves meaningless stimuli and can be predicted by specific patterns of brain responses to previously-experienced multisensory information.

However, this memory facilitation depended on individual factors. Some participants improved with context changes, and others were impaired by such changes compared to unchanged and exclusively unisensory contexts. Our results suggest it is how the brain responds to multisensory information that translates into later memory function (at least in the present task). One possible explanation is that some people are more prone to multisensory interactions, even when successful task completion does not require it. By contrast, others are less prone to multisensory interactions, particularly when selectively attending to one modality either due to task context and/or instructions (Supplemental Information).

By focusing on inter-individual variations, we provided the first evidence for a direct link between brain activity in response to multisensory information at one point in time and later visual object discrimination abilities. This demonstrates the behavioural relevance and the ethological value of multisensory processes even in situations where the importance of these processes might not be readily observed at the group level. Notably, a particularly effective strategy for learning may in fact rely on (implicit) processing of task-irrelevant stimuli presented to another sensory modality. A fuller understanding of the behavioural and neural bases of inter-individual differences will undoubtedly be a critical step in applying our findings. Such notwithstanding, multisensory information does confer substantial learning benefits across the lifespan and in health and disease [8-10].

Supplemental Information

Supplemental Information including experimental procedures, two figures, one table, and discussion can be found with this article online at *bxs

Supplemental Information

Document S1. Experimental procedures, two figures, one table, and discussion

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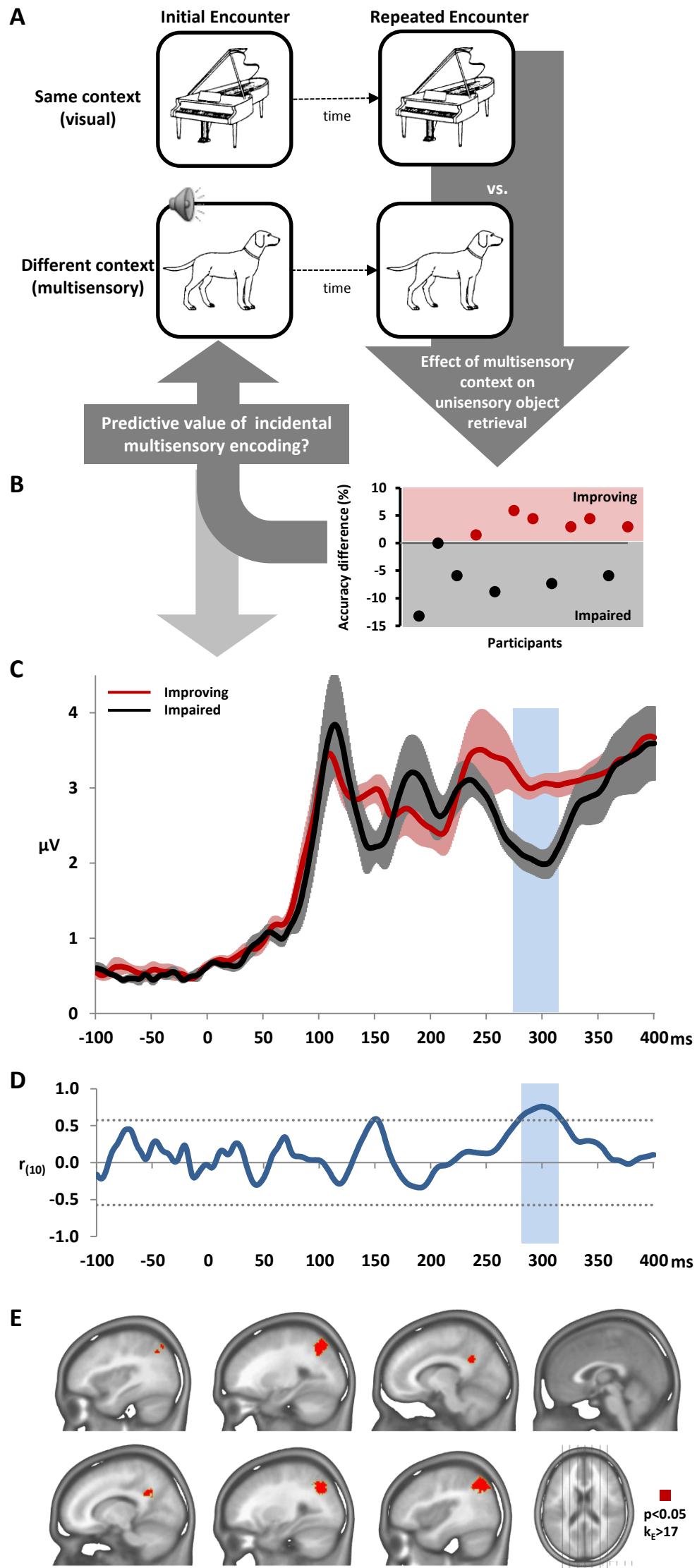
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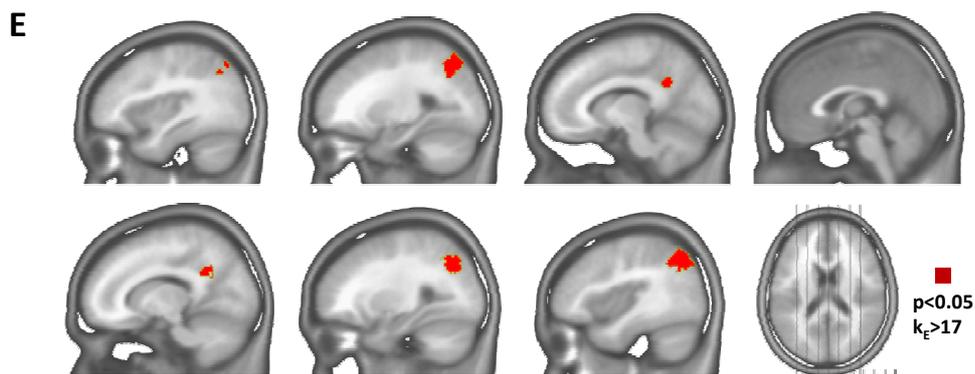
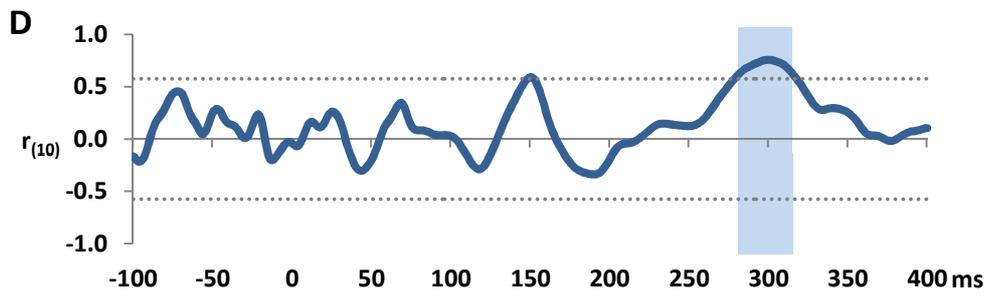
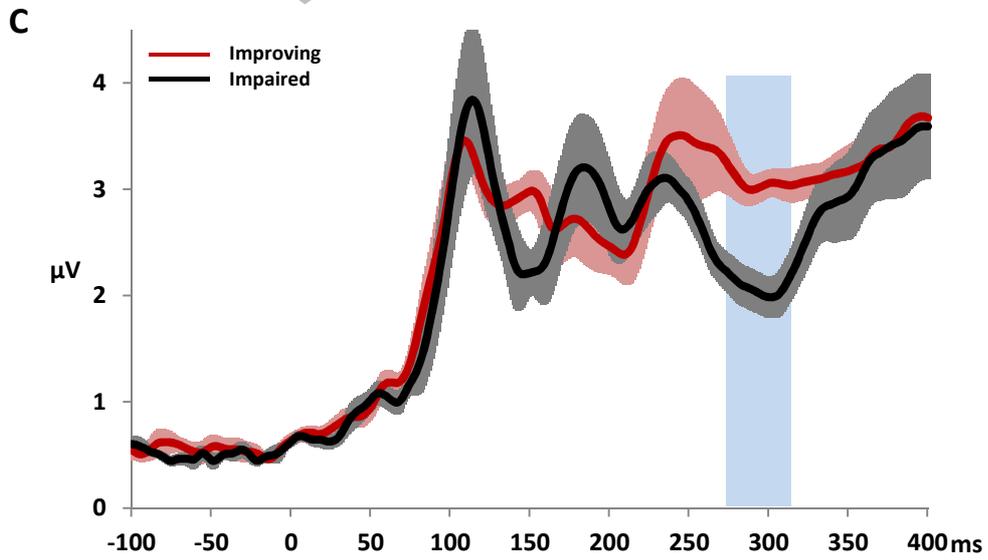
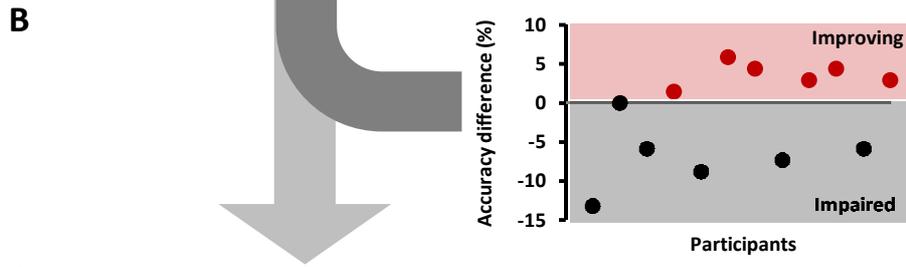
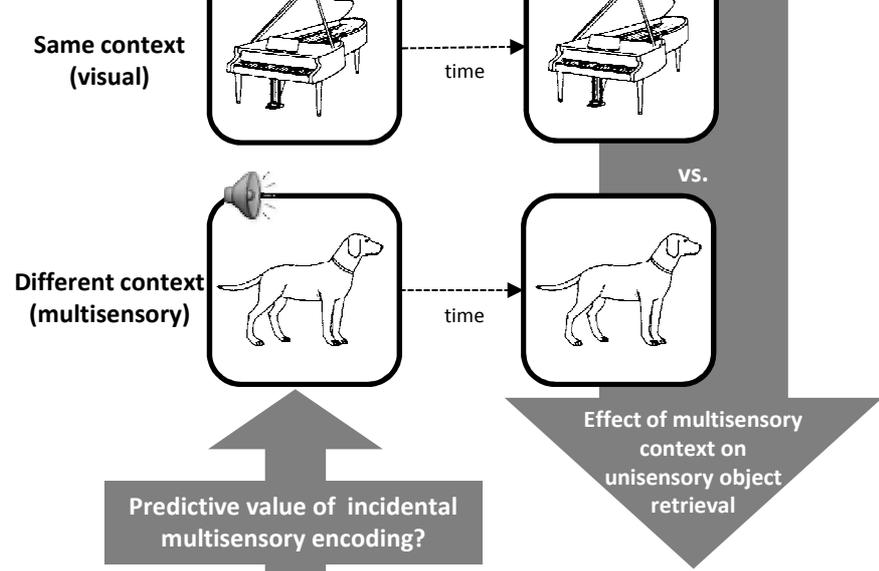
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Figure 1. Paradigm and results of main experiment

(A) A schematic depiction of the continuous recognition task involving the discrimination of repeated from initial image presentations. The context either remained the same across the image presentations (which were separated by intervening trials) or differed, such that initial presentations were paired with a meaningless sound. Further details of the paradigm are provided in the Supplemental Information. (B) The behavioural results obtained from repeated image presentations indicated that some participants improved with different contexts between the initial and repeated image presentations involving multisensory pairings, and some participants were impaired by such context changes (red and black dots, respectively). (C) In order to determine the predictive value of multisensory contexts during encoding for later unisensory memory performance, ERP strength was quantified using Global Field Power triggered by initial image encounters. Individuals improving with context changes showed significantly stronger Global Field Power in response to multisensory stimuli than did individuals impaired by context changes (red versus black waveforms, respectively; mean \pm s.e.m. shown; $p < 0.05$ for contiguous > 10 ms indicated by the shaded blue period). This difference was observed over the 270-316 ms post-stimulus period, and no differences whatsoever were found in response to unisensory visual stimuli (Supplemental

Information). (D) Correlation analysis between Global Field Power to multisensory stimuli and later differences in object discrimination accuracy as a function of time was performed and revealed significant positive correlation over the 273-316 ms post-stimulus period ($r_{(10)} > 0.575$; $p < 0.05$ for continuous > 10 ms indicated by the shaded blue period). (E) Significant differences in distributed source estimations were observed within the inferior parietal sulcus bilaterally and are displayed on a set of sagittal slices ($p < 0.05$; $k_E > 17$ nodes). See Supplemental Information for further details.





Supplemental Information

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Supplemental Experimental Procedures

Main Experiment

Participants

Twelve healthy adults (3 women; mean age \pm SD = 27.1 \pm 3.4 years; 10 right-handed according to the Edinburgh handedness inventory [S1]) participated in the study. These individuals are the subset of participants from [S3] who partook in both the behavioural as well as the EEG acquisitions. The study was conducted in accordance with the Declaration of Helsinki, and all subjects provided written informed consent to participate in the study. The experimental procedures were approved by the Ethics Committee of the Vaudois University Hospital Centre and University of Lausanne. No subject had a history of a neurological or psychiatric illness, and all subjects had normal or corrected-to-normal vision as well as reported normal hearing.

Task and Procedures

Subjects performed a continuous recognition task, which required the discrimination of initial (i.e., 'new') from repeated (i.e., 'old') presentations of line drawings that were pseudo-randomized within a block of trials. That is, on each trial a single image was presented (with or without a sound) that required a judgment regarding whether it was "new" or "old" (c.f., Figure 1 in [1]). Participants were instructed to perform as quickly and as accurately as possible. Each object (irrespective of whether it was initially presented in a unisensory or multisensory context) was repeated only once throughout the duration of the experiment. Furthermore, the pictures were subdivided into two groups: Initial presentations were either unisensory or multisensory. Repeated presentations were always unisensory. Thus, half of the repeated presentations were multisensory when initially encountered and the other half were unisensory when initially encountered (different and same contexts, respectively).

The line drawings were taken from a standardized set [S2] or obtained from an online library (dgl.microsoft.com) (see Appendix 1 in [S3] for a full list). The pictures were equally subdivided across experimental conditions and blocks. Images were controlled to equate spatial frequency spectra and luminance between image groups (AV vs. V), according to the procedures described in [S4]. They were black drawings presented centrally on a white background. On initial presentations, the visual stimuli could be presented simultaneously with a meaningless sound or displayed alone (each 50% of all trials). The sounds were generated using Adobe Audition 1.0 (16 bit stereo; 44100 Hz digitization; 500 ms duration; 10 ms rise/fall to avoid clicks), differed in their spectral composition (ranging from 100 Hz to 4700 Hz), and sometimes were modulated in terms of amplitude envelopes and/or waveform types (triangular and sinusoid).

Stimulus presentation was 500 ms, followed by a randomized inter-stimulus interval (ISI) ranging from 900 to 1500 ms. The mean (\pm SD) number of trials between the initial and the repeated presentation of the same image was 9 \pm 4 pictures for both presentation conditions (V and AV). Importantly, the distribution of old and new pictures throughout the length of the block was controlled. An equal probability of "new" objects across all quartiles within a block ensured that subjects could not determine the predictive probabilities of the upcoming stimuli. This, in turn, prevented the results from confounds

related to a response-decision bias, reflected, for example, by faster reaction times. Blocks consisted of 136 trials each, equally divided between V, AV, V-, and V+ conditions (i.e., 34 trials each). Notably, the same the block length was used in our prior studies [S3, S5, S6]. All participants completed 2 blocks of training.

The experiment took place in a sound-attenuated chamber, where subjects were seated centrally in front of a 20" LCD computer monitor that was located about 140 cm away from them to produce a visual angle of ~4°. The auditory stimuli were presented over insert earphones (Etymotic model: ER4S), and the volume was adjusted to a comfortable level (~62 dB). All stimuli were presented and controlled by E-Prime 2.0, and all behavioural data were recorded in conjunction with the serial response box (Psychology Software Tools, Inc.; www.pstnet.com).

EEG acquisition and pre-processing

Continuous EEG was acquired from 160 scalp electrodes (sampling rate at 1024 Hz) using a Biosemi ActiveTwo system. Data pre-processing and analyses were performed using Cartool ([S7]; <http://sites.google.com/site/fbmlab/cartool>). Event-related potentials (ERPs) were calculated by averaging epochs from 100 ms pre-stimulus to 500ms post-stimulus onset for each of the four experimental conditions and each subject. In addition to a ± 80 μ V artefact rejection criterion, EEG epochs containing eye blinks or other noise transients were removed based on a trial-by-trial visual inspection of the data. Before group averaging, data from artefact electrodes of each subject were interpolated using 3-D splines [S8]. On average, 5 of the 160 channels were interpolated (range 2–12). The ERP data were baseline corrected using the pre-stimulus period, band-pass filtered (0.1–60 Hz including a notch filter at 50 Hz) and recalculated against the average reference.

Electrical neuroimaging analyses

The ERP analyses were based on the hypothesis that a differential neural response would be found between individuals with memory performance that was improved by multisensory contexts and individuals whose memory performance was impaired by such multisensory contexts. The approach we employed here has been referred to as “electrical neuroimaging” and is based largely on the multivariate and reference-independent analysis of global features of the electrical field at the scalp that in turn informs the selection of time periods for analyses of source estimations [S9-S12]. These electrical neuroimaging analyses allowed us to differentiate the effects following from 1) modulations in the strength of brain responses within statistically indistinguishable brain generators, 2) alterations in the configuration of these generators (viz. the topography of the electric field at the scalp), as well as 3) latency shifts in brain processes across experimental conditions. Additionally, we applied the local auto-regressive average distributed linear inverse solution (LAURA [S13, S14]) to these ERP data to visualize and statistically contrast the likely underlying sources of the effects identified during the preceding steps of analysis of the surface-recorded ERPs.

The strength of the electric field across the whole scalp was quantified using Global Field Power (GFP; [S15]). This measure is equivalent to the standard deviation of the voltage potential values across the entire electrode montage at a given time point and represents a reference-independent measure of the ERP strength [S9]. The formula for GFP is:

$$GFP_u = \sqrt{\frac{1}{n} \cdot \sum_{i=1}^n u_i^2}, \text{ where } u \text{ is the measured potential at the } i^{\text{th}} \text{ electrode among } n \text{ electrodes.}$$

GFP was statistically contrasted using a millisecond-by-millisecond paired t-test, in conjunction with a >10 ms contiguous temporal criterion for significant effects that corrects for multiple contrasts [S16]. While this dependent measure provides an assay of ERP strength, it is inherently insensitive to spatial (i.e., topographic) variation in ERPs across conditions.

In order to test the ERP topography differences independently of strength differences, we used Global Dissimilarity (DISS [S15]). DISS is equivalent to the square root of the mean of the squared difference between the potentials measured at each electrode for different conditions, normalized by the instantaneous GFP. It is also directly related to the (spatial) correlation between two normalized vectors (cf., Appendix in [9]). We then performed a non-parametric randomization test (TANOVA, [9]): The DISS value at each time point is compared to an empirical distribution derived from permuting the condition label of the data from each subject. Because changes in topography forcibly follow from changes in the configuration of the underlying active sources [S17], this analysis can reveal at which points in time the experimental conditions activate distinct sets of brain networks. Because topographic differences were not observed in the current experiments, we do not discuss these analyses further here.

We estimated the sources underlying our GFP effects using a distributed linear inverse solution (minimum norm) together with the LAURA regularization approach ([S13, S14]; see also [S18] for review). LAURA selects the source configuration that better mimics the biophysical behavior of electric vector fields (i.e., according to electromagnetic laws, activity at one point depends on the activity at neighboring points). In our study, homogenous regression coefficients in all directions and within the whole solution space were used. LAURA uses a realistic head model, and the solution space included 4024 nodes, selected from a 6x6x6mm grid of 4024 nodes equally distributed within the gray matter of the Montreal Neurological Institute's average brain (courtesy of R. Grave de Peralta and S. Gonzalez Andino; <http://www.electrical-neuroimaging.ch/>). Prior basic and clinical research by members of our group and others has documented and discussed in detail the spatial accuracy of the inverse solution model used here (e.g., [S14, S18-S21]). In general, the localization accuracy is considered to parallel the matrix grid size (here 6 mm). The results of the above GFP analysis defined the time periods for which the intracranial sources were subsequently estimated and statistically compared between conditions (here 270-316ms post-stimulus). Prior to calculation of the inverse solution, the ERP data were down-sampled and affine-transformed to a common 111-channel montage. Statistical analyses of source estimations were performed by first averaging the ERP data across time to generate a single data point for each participant and condition. This procedure increases the signal-to-noise ratio of the data from each participant. The inverse solution was then estimated for each of the 4024 nodes. These data were then submitted to an unpaired t-test. Here, we considered a difference reliable if it fulfilled a spatial extent criterion of at least 17 contiguous significant nodes (see also [S3, S22-S27]). This spatial criterion was determined using the AlphaSim program (available at <http://afni.nimh.nih.gov>) and assuming a spatial smoothing of 6mm full-width half maximum. The described criterion indicates that there is a 3.54% probability of presence of a cluster of at least 17 contiguous nodes, which gives an equivalent node-level p-value of $p \leq 0.0002$. The results of the source estimations were rendered on the Montreal Neurologic Institute's averaged brain.

Follow-up Experiment

Participants

A new set of fifteen healthy adults (9 women; mean age \pm SD = 26 \pm 3.9 years; 13 right-handed according to the Edinburgh handedness inventory [S1]) participated in the follow-up study. The study was conducted in accordance with the Declaration of Helsinki, and all participants provided written informed consent to participate in the study. The experimental procedures were approved by the Ethics Committee of the Vaudois University Hospital Centre and University of Lausanne. No subject had a history of neurological or psychiatric illness, and all subjects had normal or corrected-to-normal vision as well as reported normal hearing.

Task and Procedures

Participants performed a continuous recognition task with complex, meaningful sounds, rather than with images (as in the main experiment). Subjects heard a sound and were instructed to indicate as quickly and as accurately as possible (by right-hand keyboard button press) whether the sound was being heard for the first or second time within a given block of trials.

The sounds of 60 common objects were obtained from an online library (<http://dgl.microsoft.com>) or from prior experiments (e.g., [S28]) and modified with Adobe Audition to be 500 ms in duration (10 ms rise/fall to prevent clicks; 16 bit stereo, 44100 Hz digitization) and to have normalized mean volume. The average sound intensity during the experiment (comprised of stimuli and background noise between stimuli) was adjusted to 53.1 dB (s.e.m. \pm 0.2 dB). These sounds were presented through stereo loud speakers (Logitech, Speaker System Z370) placed on both sides of the computer monitor that was located directly in front of the participants.

When presented for the first time, sounds could be presented alone (A), with a semantically congruent image (AVc) or with a meaningless, abstract image (AVm). Repeated sound presentations were always unisensory (auditory-only), and were labelled according to their past presentation context: previously presented alone (A-), previously presented with a congruent (A+c) or with a meaningless image (A+m). This yielded six experimental conditions in total. The present analyses focused exclusively on ERPs in response to the AVm and A conditions, based on the performance differences across the A+m and A- conditions.

For the AVc condition, visual stimuli consisted of line drawings of common objects obtained from a standardized set [2] or from an online library (dgl.microsoft.com). For the AVm condition, visual stimuli were abstract drawings of lines and circles or scrambled versions of the line drawings (the latter of which were produced by dividing the images into 5×5 squares and randomizing pixels within these squares with an in-house MATLAB script (www.mathworks.com))

To familiarize participants with the sounds, subjects underwent a habituation block before the beginning of the experiment, in which all the sounds were coupled with their corresponding visual image (e.g., an image of a dog together with the sound of a barking dog) and presented twice. No responses were recorded for this block. All the remaining experimental procedures, such as the number of blocks or counterbalancing of the task-relevant stimuli within the block were similar to the procedures employed in the main experiment, with the obvious difference that now the task-relevant objects were auditory, while the irrelevant stimuli were visual in nature.

EEG acquisition, pre-processing, and analyses

Continuous EEG was recorded at a sampling rate of 500 Hz with 63 scalp electrodes (EasyCap, BrainProducts), positioned according to the international 10-20 system. An electrode on the tip of the nose served as the online reference. The electrode-skin impedance was monitored throughout the experiment and averaged 4.5 k Ω across electrodes and individuals. Incorrect trials (erroneous responses and misses) were removed from the analysis. On average, less than one electrode was interpolated per participant (range 0-3). EEG data pre-processing steps and the ERP analyses followed the same procedures as described above. The source estimations were again based on LAURA, though in the present experiment data were down-sampled to a 61-channel montage. The array of 4024 solution points and the statistical analysis of the source estimations remained identical.

Supplemental Figures

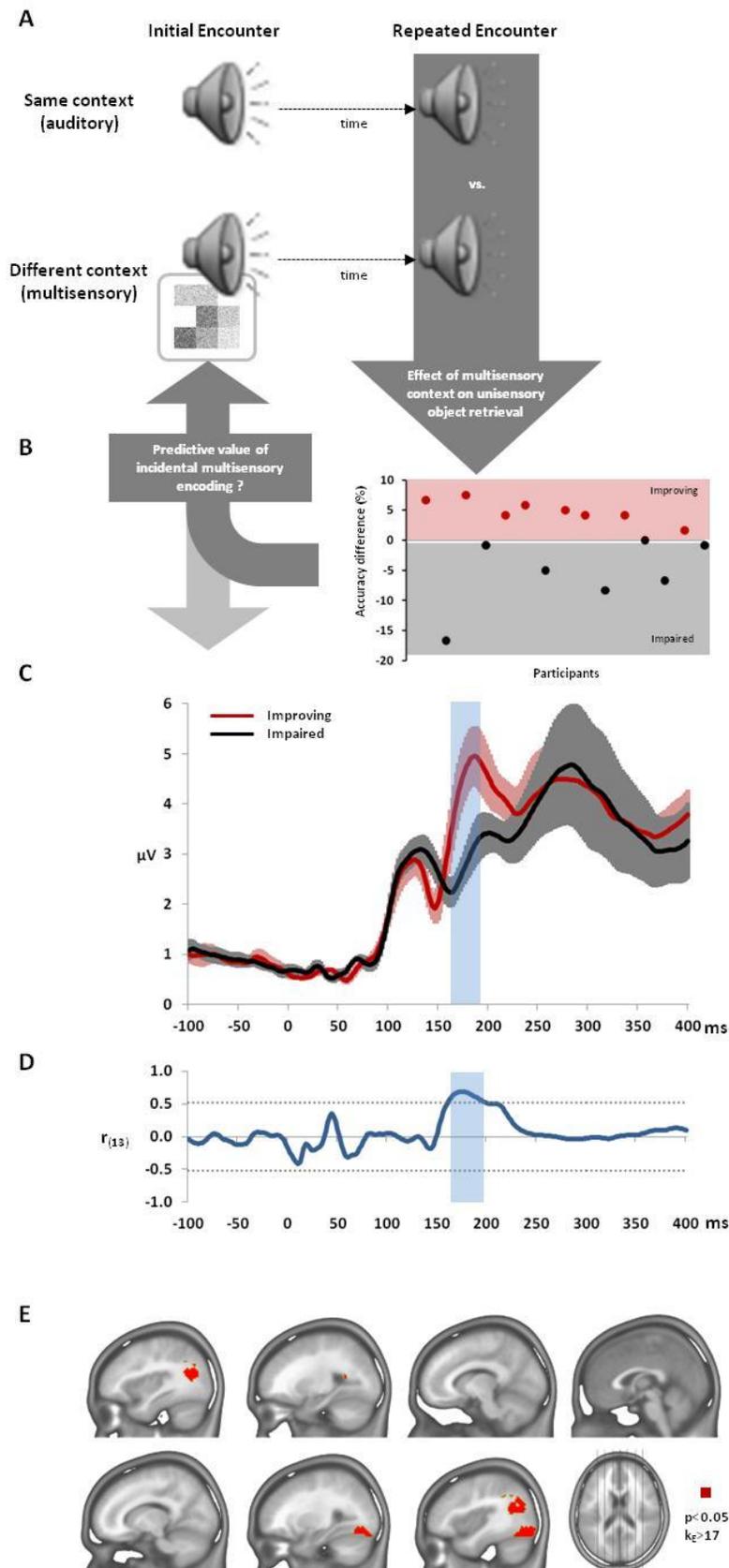


Figure S1. Paradigm and results from the follow-up study

(A) A schematic depiction of the continuous recognition task, here involving the discrimination of sounds (initial vs. repeated). As in the main experiment, the context across the sound presentations remained the same or differed, such that the initial presentations were sometimes paired with a meaningless image. (B) The behavioral results from repeated sound presentations indicated that between the initial and repeated sound presentations that involved multisensory pairings some participants improved with different contexts and some participants were impaired by such context changes (red and black dots, respectively). (C) In order to determine the predictive value of multisensory contexts during encoding for later unisensory memory performance, ERP strength was quantified using Global Field Power triggered by initial sound encounters. Individuals that improved with context changes showed significantly stronger Global Field Power in response to multisensory stimuli than did individuals impaired by context changes (red versus black waveforms, respectively; mean \pm s.e.m. shown; $p < 0.05$ for > 10 ms contiguously indicated by shaded blue period). This difference was observed over the 160-190 ms post-stimulus period. No such differences were observed in response to unisensory auditory stimuli (see Figure S2). (D) The correlation between Global Field Power to multisensory stimuli and later differences in object discrimination accuracy as a function of time identified significant positive correlation over the 162-200ms interval. Thresholds for significant correlations ($p < 0.05$) are indicated by the dotted lines. (E) Significant differences in distributed source estimations were observed within the inferior parietal sulcus bilaterally as well as within the right inferior occipital cortex, here displayed on a set of sagittal slices.

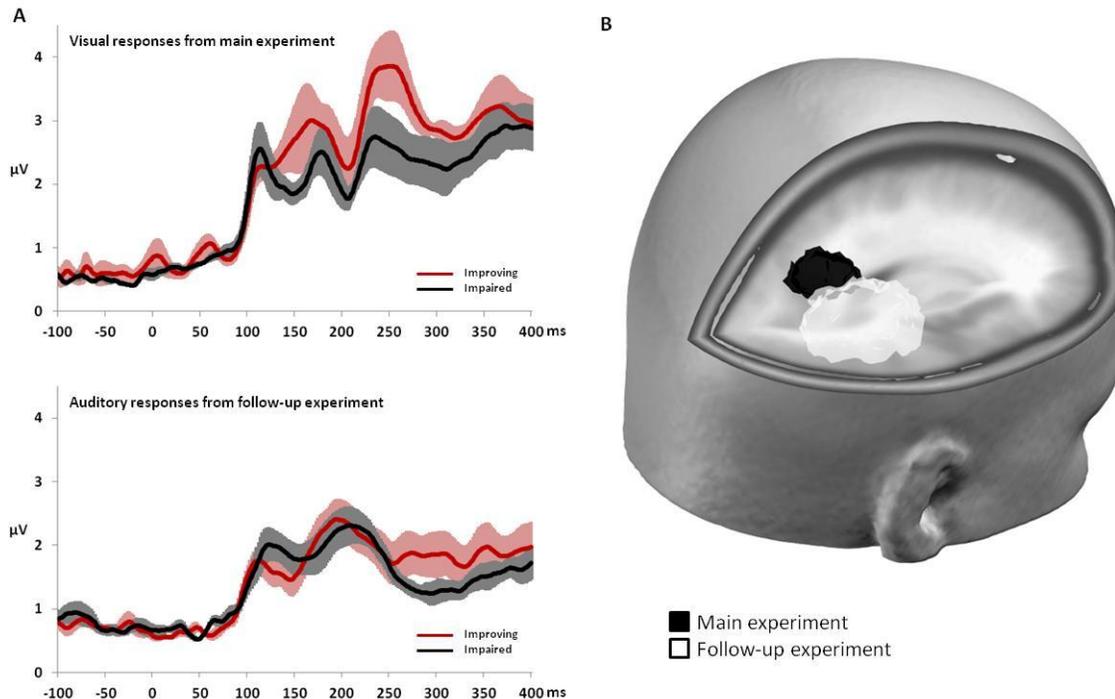


Figure S2. Global Field Power in unisensory conditions and overlay of source estimations

Panel A displays controls for general differences in stimulus processing between the individuals improving from versus those impaired by prior multisensory contexts. We compared ERPs in response to unisensory visual stimuli (main experiment, top) as well as those triggered by unisensory auditory stimuli (follow-up experiment, bottom). In neither case did the Global Field Power reliably differ between these groups of participants (mean \pm s.e.m. displayed). The minimal p-value in these analyses was >0.10 across all time points. Panel B displays the overlay in source estimations from the main experiment (black) and follow-up experiment (white) within the left hemisphere, though a similar overlay was obtained in the left hemisphere.

Supplemental Table

Table S1.

Accuracy rates across conditions and experiments as a function of whether an individual's memory performance was improved by or impaired by multisensory contexts. There was no evidence for general performance differences across groups in either experiment.

Main Experiment				
		Improving	Impaired	<i>Between groups t-test</i>
Initial presentation	Multisensory	91±1.5	86±4.8	$t_{(10)}=1.0$; $p=0.32$
	Visual	90±1.8	85±5.5	$t_{(10)}=0.8$; $p=0.45$
	<i>Within-group t-test</i>	$t_{(5)}=0.2$; $p>0.83$	$t_{(5)}=1.6$; $p>0.17$	
Repeated presentation	Had been multisensory	88±2.4	82±4.4	$t_{(10)}=-1.2$; $p=0.26$
	Had been unisensory	85±2.6	89±3.3	$t_{(10)}=1.2$; $p=0.27$
	<i>Within-group t-test</i>	$t_{(5)}=6.3$; $p<0.002$	$t_{(5)}=-3.9$; $p<0.02$	
ANOVA on initial presentations				
Main effect of context: $F_{(1,10)}=0.69$; $p>0.40$				
Main effect of group: $F_{(1,10)}=0.83$; $p>0.38$				
Group x context interaction: $F_{(1,10)}=0.17$; $p>0.68$				
ANOVA on repeated presentations				
Main effect of context: $F_{(1,10)}=1.98$; $p>0.19$				
Main effect of group: $F_{(1,10)}=0.01$; $p>0.9$				
Group x context interaction: $F_{(1,10)}=33.72$; $p<0.001$; $\eta_p^2=0.77$				
Follow-up Experiment				
		Improving	Impaired	<i>Between groups t-test</i>
Initial presentation	Multisensory	72±4.5	78±4.7	$t_{(13)}=-0.9$; $p=0.38$
	Auditory	69±4.8	74±4.3	$t_{(13)}=-0.9$; $p=0.41$
	<i>Within-group t-test</i>	$t_{(7)}=1.9$; $p>0.09$	$t_{(6)}=1.2$; $p>0.26$	
Repeated presentation	Had been multisensory	79±4.9	66±8.3	$t_{(13)}=1.4$; $p=0.13$
	Had been unisensory	74±5.0	71±6.3	$t_{(13)}=0.4$; $p=0.69$
	<i>Within-group t-test</i>	$t_{(7)}=7.7$; $p<0.001$	$t_{(6)}=-2.5$; $p<0.05$	
ANOVA on initial presentations				
Main effect of context: $F_{(1,13)}=4.0$; $p>0.05$				
Main effect of group: $F_{(1,13)}=0.81$; $p>0.38$				
Group x context interaction: $F_{(1,13)}=0.01$; $p>0.85$				
ANOVA on repeated presentations				
Main effect of context: $F_{(1,13)}=0.06$; $p>0.8$				
Main effect of group: $F_{(1,13)}=0.01$; $p>0.9$				
Group x context interaction: $F_{(1,13)}=19.8$; $p<0.001$; $\eta_p^2=0.6$				

Supplemental Discussion

It is worthwhile to provide some considerations regarding the difference in the timing of effects across the two experiments. One possibility is that this timing difference may stem from the brain's faster old/new discrimination of sounds of objects than images. For example, [S29] showed old/new effects with the same auditory stimuli as used in the present study at ~170-200 ms post-stimulus onset. By contrast, most studies of these processes involving images, typically line drawings, observed effects at ~250-300 ms (reviewed in [S30]). The qualitative features of the stimuli presented to each modality – e.g. naturalistic sounds vs. line drawings – may likewise constitute an important contributing factor.

Additional research is clearly required to provide a fuller account. Such notwithstanding, the timing differences should not detract the reader from the principal discovery; namely that brain activity in response to multisensory stimuli at one point in time is predictive of whether an individual's later memory will benefit or be impaired.

Given the above, it is important to consider what precisely leads to an individual improving versus being impaired by prior multisensory contexts (at least in the case of the paradigm employed here). Inter-individual differences have been previously shown to impact multisensory interactions. For example, preferences at the level of perception and/or goal-based attention determine the impact of sounds on visual cortex excitability [S31, S32, see also S33 for influences of game-playing on top-down control mechanisms in vision or S34 for inter-individual differences in multisensory speech processing]. Other findings have linked variations in brain activity to susceptibility to multisensory influences on *current* perception/attention [4, S35]. The present results are consistent with these findings, but also extend them in an important, novel fashion to *later* memory function. The current observation of two distinct patterns of behaviour would suggest there to be contrasting mechanisms at play that were elicited in response to multisensory, but not unisensory, contexts across the two groups in our paradigm.

It is possible that those individuals who show less accurate performance with stimuli that had been previously encountered in a multisensory vs. unisensory context are actually more adept at attending to task-relevant information. Had this been the case, however, a prediction would have been for a general difference across groups in the processing of information. We had no evidence in either experiment for differences in unisensory processing. However, this interpretation would assume that attending to multisensory stimuli can be likened to attending to visual stimuli, which has not been unequivocally established [S36, S37]. If our results can be construed as an enhancement of processing by individuals whose performance increases for stimuli that had been previously encountered in a multisensory vs. unisensory context, then it may likewise be the case that such individuals have a stronger tendency to integrate information across sensory modalities, even in contexts where some of this information is task-irrelevant. Consistent with this proposal is the specificity of our effects for multisensory conditions. Enhanced Global Field Power in response to multisensory stimuli, together with the localization of the effects in both experiments to regions of the parietal cortex that have previously been linked to perceptual benefits in multisensory object recognition [7], provide another line of support for the proposal that performance benefits may stem from enhanced multisensory processing rather than weaker top-down control mechanisms. One derivative hypothesis that is currently being investigated in our laboratory is that individuals improving with multisensory context also exhibit greater multisensory integration during other tasks, such as simple stimulus detection, where notably both visual and auditory stimuli are task-relevant. The hypothesis of enhanced tendency to integrate information across the senses in some individuals compared to others would be in line with recent evidence suggesting that multisensory processes scale across function levels [S38].

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