Multisensory experiences and their impact on memory performance

THELEN, Antonia

Abstract

In this Masters' thesis project, I focused on how multisensory experiences influence later unisensory discrimination performance. Previous studies have provided evidence that single-trial multisensory experiences can influence the ability to accurately discriminate image repetitions during a continuous recognition task (Murray, et al., 2004; Murray et al., 2005; Lehmann and Murray, 2005). It has been shown that pairing visual objects with their corresponding sounds can enhance subsequent visual discrimination, whereas pairing visual objects with an identical pure tone leads to an impaired subsequent visual discrimination compared with performance with objects only encountered visually. Despite their opposing polarity, these effects indicate that incoming visual stimuli access multisensory memory traces established through single-trial learning. One open issue is the role of semantic versus episodic multisensory experiences, because prior work was confounded by pairing different visual objects with an identical pure tone (Lehmann and Murray, 2005). In the present masters’ project, I determined the role of episodic [...]
Multisensory experiences and their impact on Memory performance

Antonia Thelen
Faculté de Psychologie et des Sciences de l’Education (FPSE)
Université de Genève
Master interdisciplinaire en Neurosciences
(2009 – 2011)

Direction:
Dr. Micah Murray

Supervision:
Dr. Céline Cappe

Jury members:
Dr. Claire Bindschaedler Orliange
Prof. Dimitri Van de Ville
Acknowledgements

I would like to thank my supervisor Dr. Céline Cappe and my thesis director Dr. Micah Murray for their support and the great emphasis they have put into my education.

I appreciate the faith they have put into me.

Jean-François Knebel for the statistical analyses on luminance and spectra of the visual stimuli. He has also been of great help in resolving technical and statistical conundrums, other than being somebody who always lends a helping hand.

Marzia de Lucia, for additional computer programming.

Giovanni Battistella, who has been an exceptionally patient bench neighbor.

Also Rosanna de Meo, for being a model roommate.

And of course

The whole research group at the CHUV for their support and suggestions.

I would also like to thank my subjects, without whom this thesis would not have been possible.
Table of Contents

Introduction ........................................................................................................................................... 4

1 Multisensory learning .......................................................................................................................... 6

2 Multisensory Interactions ................................................................................................................... 12

   2.1 Rules of Multisensory integration: Evidence from Single-Unit Recordings ................................. 14

      1.1.1 Spatial rule ............................................................................................................................ 16

      1.1.2 Temporal rule ......................................................................................................................... 16

      1.1.3 Principle of Inverse Effectiveness ......................................................................................... 17

   2.2 Multisensory integration at early stages of information processing ............................................... 19

Master Project ....................................................................................................................................... 23

1 Previous findings ................................................................................................................................ 23

   1.1 Rapid discrimination of visual and multisensory memories revealed by electrical neuroimaging (Murray, Michel, Grave de Peralta, Ortigue, Brunet, Andino, & Schnider, 2004, NeuroImage) .......................................................................................................................... 23

   1.2 The brain uses single-trial multisensory memories to discriminate without awareness (Murray, Foxe, & Wylie, 2005, NeuroImage) .......................................................................................................................... 25

   1.3 The role of multisensory memories in unisensory object discrimination (Lehmann & Murray, 2005, Cognitive Brain Research) ......................................................................................................................... 28

2 The role of single-trial, episodic multisensory learning in unisensory object discrimination (Thelen, Cappe, & Murray, 2010, submitted) ........................................................................................................... 30

   2.1 Material and Methods ................................................................................................................... 32

   2.2 Results ........................................................................................................................................ 35

   2.3 Discussion ................................................................................................................................... 37

3 Ongoing Study ..................................................................................................................................... 40

   3.1 EEG acquisition and analyses ..................................................................................................... 40

   3.2 Results ........................................................................................................................................ 42

   3.3 Control Experiment ....................................................................................................................... 45

References ............................................................................................................................................... 49
Multisensory experiences and their impact on memory performance  

Antonia Thelen

Introduction

In this Masters’ thesis project, I focused on how multisensory experiences influence later unisensory discrimination performance. Previous studies have provided evidence that single-trial multisensory experiences can influence the ability to accurately discriminate image repetitions during a continuous recognition task (Murray, et al., 2004; Murray et al., 2005; Lehmann and Murray, 2005). It has been shown that pairing visual objects with their corresponding sounds can enhance subsequent visual discrimination, whereas pairing visual objects with an identical pure tone leads to an impaired subsequent visual discrimination compared with performance with objects only encountered visually. Despite their opposing polarity, these effects indicate that incoming visual stimuli access multisensory memory traces established through single-trial learning. One open issue is the role of semantic versus episodic multisensory experiences, because prior work was confounded by pairing different visual objects with an identical pure tone (Lehmann and Murray, 2005). In the present masters’ project, I determined the role of episodic multisensory experiences by pairing (on their initial encounters) visual objects with meaningless, but unique sounds. Subjects discriminated initial from repeated presentations of images of common objects. Half of the initial presentations of images were presented in a unisensory visual manner. Each of the remaining half of the images was paired on its initial presentation with a distinct but meaningless sound in a multisensory context. All repeated presentations were exclusively unisensory visual. The results of the psychophysical investigation showed that accuracy in recognition of repeated images was impaired for those that had been initially presented in a multisensory context. This decrement was dissociable from performance during initial image presentations, ruling out explanations in terms of attention or direct transfer from encoding to retrieval. Instead, the results indicate that the direction of the impact of single-trial multisensory memories on visual object discrimination is linked to the semantic versus episodic contingencies between the senses.

The thesis is organized as follows. The first section will introduce multisensory learning and how this process impacts further unisensory discrimination and recognition performance. For this purpose several studies will be presented briefly. The second half of the introduction focuses on
multisensory integration. The main principles of integration will be elucidated. Thereafter evidence supporting the model for early, low-level multisensory integration will be presented.

The second section is build around the Master’s project. The previous findings which led to the present investigation will be presented and the open questions will be illustrated. Subsequently, the submitted version of the manuscript which resulted from our psychophysical study is inserted.

The third section is dedicated to the presentation of the ongoing electrical neuroimaging study. The preliminary results will be presented. Further future directions, in the form of a control experiment, will be presented.
1 Multisensory learning

As I focused on a discrimination task in the present Master thesis, the following paragraphs treating learning processes will elucidate a specific type of learning: i.e. perceptual learning. In other words, I investigated the processes by which subjects achieve improvements in their performance when confronted with a perceptual task (e.g. recognition of a learned sensory percept). Perceptual learning is thus something that is linked to experience and improves the more often we are confronted with a given type of stimulus. I will also introduce studies investigating the role of multisensory experiences in unisensory object discrimination.

It has been argued that perceptual learning in one sensory modality can be enhanced, when the learned percept is coupled to a redundant supplementary sensory cue in a different modality during the learning episode (e.g. combining the heard song of a bird to a picture of the same bird facilitates later identification). This view is not a recent finding, despite what might be thought. Maria Montessori (1870 – 1952), founded the multisensory learning movement at the beginning of the 20th century (Montessori, 1912). She integrated auditory, visual, tactile and kinesthetic approaches to her educational methods. In the same line other multisensory approaches were developed over the last century (e.g. Birsh, 1999).

Language acquisition is one of the major fields of interest when studying the effect of multisensory learning during development. In order to acquire a language visual (reading), auditory (hearing/understanding) and motor (vocalization) abilities have to be integrated. Further, this type of learning appears to be implicit during early development and it occurs by exposure to heard speech together with the visual perception of the speaker (Kuhl and Meltzoff 1982). Contrariwise, learning to read, that is to associate letters to speech sounds, requires explicit instructions. Sparks, Ganshow and colleagues have investigated the efficacy of multisensory structured language (MSL) approaches when teaching a foreign language (FL) (for review of these studies (Sparks and Miller 2000). This kind of approach includes the simultaneous use of visual, auditory and tactile skills. The authors have shown that students with or without native language (English) learning difficulties benefit from such MSL approaches while being confronted with the acquisition of a foreign language (Spanish).

The interest of studying perceptual memory has also risen from clinical evidence. Patients with memory impairments such as amnesia show strong impairment of episodic memory. They cannot explicitly retrieve autobiographic experiences. On the other hand, perceptual memory
seems to remain intact in such patients (Hamann and Squire 1997). Perceptual memory traces are linked to (explicit) episodic memory trace retrieval, but they appear to be retrieved in an implicit manner and independently of an explicit, conscious recognition. In a subsequent study (Stark and Squire 2000) the dissociation between repetition priming and recognition and recall was shown. The patient E. P., with severe anterograde and retrograde amnesia showed impaired performance in a delayed recognition task, but performed normally on a stem completion task and perceptual identification priming, other than intact category learning. The authors argued that these findings suggest that intact memory traces formed during repetition priming, are not accessible for familiarity-based recognition. These findings were also supported by studies showing that patients with focal lesions in the occipital cortices did not benefit from visual perceptual priming tasks, while they performed normally on recognition memory tasks (Gabrieli, et al., 1995; Keane, et al., 1995).

These findings support the model which states that recognition memory comprises two independent processes. The first process is linked to recognition and recall of the previous experience. The second is involved in familiarity detection. While the first process depends on explicit episodic memory, the second appears to be accessed implicitly.

Evidence for benefits of multisensory learning has also come from studies that investigated learning situations that were not related to language acquisition. Studies on perceptual learning have shown that the presentation of multisensory stimuli can enhance the training outcome compared to unisensory learning conditions.

A study comparing auditory-visual to visual training of perceptual learning in a motion detection task showed that the group of subjects that was confronted with multisensory training conditions outperformed the group that had been learning in a visual-only training condition (Seitz, Kim et al. 2006). Complementary results were found in a study focusing on auditory recognition (von Kriegstein & Giraud, 2006). The authors found that voice recognition improved when subjects were presented with auditory-visual stimuli during the training session. Further, these authors manipulated the ethological validity of such multisensory associations. One group of subjects was presented with videos of voices and faces, while the other group of subjects was exposed to associations between pictures of cell phones and ringtones. While ringtones are not forcibly linked to a specific brand of cell phones, voices are person (and therefore face-) specific.
Multisensory experiences and their impact on memory performance

Antonia Thelen

Figure 1 (taken from Shams and Seitz, 2008, adapted from Seitz et al., 2006) shows the results of multisensory facilitation of visual learning in a visual motion detection task. Congruent (blue) auditory-visual training results in faster within-session learning (a) and greater across-session learning (b), compared to visual-only training (red). Incongruent (green) training does not show the same benefits as congruent learning.

![Figure 1](image)

Figure 1: The benefit of congruent multisensory learning (blue line ± SD) versus unisensory learning (red line ± SD). The green line shows the effect of incongruent multisensory learning.

Figure 2: (taken from von Kriegstein & Giraud, 2006) shows recognition scores for two groups of subjects for voice and ring tone recognition before and after learning. During the learning session both groups were presented with the same auditory stimuli (voices or ring tones), while the visual stimuli differed between groups. Group 1 saw videos, of either faces (coupled to voices) or of cell phones (coupled to ring tones), while group 2 saw written names or brand names of cell phones. When tested in the subsequent recognition task, subjects in group 1 showed a bigger learning effect than the subjects in group 2.

![Figure 2](image)

Figure 2: shows the benefits from multisensory learning related to ethological validity of the stimulus association. Group 1, which was presented with videos showed greater learning benefits than subjects in Group 2.
Further, studies have investigated the role of congruent multisensory experiences in subsequent unisensory object discrimination. Van der Linden and colleagues (2010), studied the effect of multisensory category learning and its effect on the formation of multisensory object representations. They used an auditory-visual paradigm, where subjects performed a one-back task. The training session consisted of the presentation of images of birds that were coupled to auditory sounds. Subjects were presented with a series of multisensory trials, where they had to indicate whether two consecutive birds were the same type or not. During the post-training scanner session unisensory (auditory-only or visual-only) or multisensory stimuli were presented. The multisensory stimuli could be congruent or incongruent. Further, during the scanner session novel stimuli were intermixed to the previously studied bird types. The results indicated that stimuli that had been previously presented were discriminated faster and more accurately. The fMRI data showed that the superior temporal sulcus (STS) becomes involved in multisensory object representation. Interestingly this training effect did not generalize to the incongruent multisensory pairings. In fact the STS did not show differential responses to incongruent associations compared with novel stimuli (van der Linden, van Turennout et al. 2010).

A more recent study investigated multisensory auditory-visual semantic processing (Chen and Spence 2010). The study was based on the hypothesis that a common semantic system can be accessed by visual information and its congruent auditory counterpart. They found that a semantically congruent sound can influence the discrimination accuracy of a masked visual image. More specifically, they found that identification performance was enhanced for those masked images that were presented simultaneously with a congruent sound, compared to those that had been presented with a burst of white noise or no sound at all. An opposing effect of discrimination impairment was found when the images were paired to an incongruent sound. In addition to the congruency effect the authors showed that the facilitations occurred when the auditory stimulus was presented either simultaneously or was delayed a little bit more than 300ms. When the sound was presented 533ms after the visual masked stimulus, no congruency effect was observed. These findings lead to the conclusion that the semantic systems of visual and auditory systems are not completely independent.

Further, these authors refer to the theory of conceptual short-term-memory (CSTM)(Potter 1993). According to this model the meaning of visual information is accessed rapidly (within 100ms), and is retained in CSTM for 300ms. If another redundant sensory cue is presented within this retention period, the semantic representation is consolidated an encoded into memory.
could explain the findings of Chen and Spence (2010). In fact, the authors argue that the observed enhancement of object discrimination when presenting a congruent sound within a time window of 0 – 300ms after the presentation of the visual stimulus can be explained by a facilitated access to the meaning of the visual stimulus. The presentation of white noise or an incongruent auditory stimulus would interfere with the access to said meaning.

**Figure 3** (taken from Chen and Spence, 2010) illustrates the semantic congruency effects as a function of the stimulus onset asynchrony (SOA) between the visual and the auditory stimuli. The effects were calculated by subtracting the accuracy in semantically congruent or incongruent conditions from that in the noise condition. Positive values indicate the improvement in the semantically congruent condition, whereas negative values indicate impairment in the semantically incongruent conditions relative to the noise condition. (* denotes $p<0.05$ and **$p<0.01$)

**Figure 3:** shows the effect of semantic congruency as a function of the stimulus-onset-asynchrony (SOA).
All of these studies highlight the importance of auditory-visual congruency (Seitz et al., 2006; van der Linden, et al., 2010; Chen and Spence, 2010) and ethological validity (von Kriegstein & Giraud, 2006) in order to enhance subsequent unisensory discrimination. In fact, congruent stimuli might enhance perceptual learning because the redundant sensory information enhances the representation of the other sensory cue, thus facilitating memory trace formation. In my Master Project I investigated the effect of pairing a meaningless auditory stimulus to a meaningful visual object, and the results are in agreement with the abovementioned statement (see Master Project). The controversy arises from a second statement, because these authors have argued that multisensory congruency did not only enhance subsequent unisensory retrieval, but that congruency was necessary to form a perceptual/memory trace. In this Master thesis and former investigations (Lehmann and Murray, 2005), it was found that although incongruent or meaningless associations might not enhance subsequent recognition performance, this association still interacts with the formation of the memory trace; a point to which I return when presenting the main experiment of the Master thesis below.
Multisensory experiences and their impact on memory performance

Antonia Thelen

2 Multisensory Interactions

When studying perception, most investigations have been conducted on single sensory modalities (e.g. vision, audition, taste, olfaction, touch). While this approach might be advantageous for the investigation of the mechanisms underlying the separate pathways along which sensory information processing transpires and how these pathways might be affected in lesion and/or stroke patients, these studies do not reflect everyday situations. Indeed, in our everyday experience we continually integrate information about the surrounding world that is brought to us by different sensory organs. These receptor organs then transmit the information to the brain, where a unified and coherent percept is formed. The formation of a coherent experience by combining this information is commonly known as multisensory integration.

This ability to integrate different modalities of a same object at low levels of sensory treatment is of advantage to the organism because it helps to reduce ambiguity and to enhance stimulus location detection, in addition to reduce reaction times (Calvert, Spence, and Stein, 2004; Stein and Meredith, 1993).

Multisensory integration can be crucial to social interactions, where the ability to integrate information brought to us by different sensory cues has a great behavioral valence for the organism. For example, seeing the lip movements of our conversational partner can enhance the perception of what he or she is saying in a crowded environment. In terms of survival, hearing a bird sing can facilitate its localization by a predator. Picking up the scent of a lion can facilitate its localization by the antelope, anticipating the (probably fatal) attack. Further, multisensory interactions may reduce reaction times when subjects are confronted with (experimental) discrimination tasks. For example, auditory cues that do not contain any spatial information can nonetheless improve subjects’ performance in a visual search task (Van der Burg, Olivers et al. 2008).

By contrast, even though multisensory integration is a process facilitating behavior in most circumstances, incoherent sensory information may result in illusory percepts. The most used examples illustrating illusory multisensory integration and its impact on perception are the ventriloquist illusion and the McGurk effect. The ventriloquism effect is a phenomenon where visual dominance is easily explained as the observer perceives the sound (spoken word) to be emanating from the puppet, while the ventriloquist tries not to move his or her lips whilst
Multisensory experiences and their impact on memory performance

Antonia Thelen

It consists of a spatial mislocalization of the auditory stimulus towards a temporally correlated but displaced visual stimulus. The McGurk effect on the other hand consists in the illusory interaction between vision and auditory perception, where the perceived sound of speech is influenced by the seen lip movements (McGurk and MacDonald 1976). For example a seen /ga/ in terms of lip movement combined with a heard auditory stimulus /ba/ results in the impression of perceiving /da/ by the observer.

The interest of studying multisensory interactions also arises from studies on schizophrenia and other neurological disorders. In fact, patients with schizophrenia show deficits in their ability to derive benefit from visual articulatory motion when presented to speech stimuli in a noisy environment, where multisensory gain is known to be maximal in healthy subjects (Ross, Saint-Amour et al. 2007). Multisensory deficits have also been observed in patients presenting visuospatial hemineglect. This deficit is common after stroke lesion in the right presylvian brain lesion, including the inferior parietal, superior temporal and inferior temporal lobes (Karnath 2001). Patients with this type of deficits typically fail to detect or orient to stimuli presented controlaterally to the damaged hemisphere (Driver and Vuilleumier 2001). The auditory deficits in these patients have been predominantly described for auditory detection tasks, where stimuli are presented bilaterally. Further there is no explication in terms if mere left-ear suppression can account for the findings, and it has been argued that higher-level spatial factors must be implicated. It seems that this deficit is due to attentional deficits to the contralateral site of the brain injury, suggesting that there must be a supra-modal attentional mechanism implicated in these deficits (for a review (Pavani, Husain et al. 2004).

A very promising field of investigating multisensory integration and its development comes from studies with congenitally blind humans. Although they do not seem to exhibit lower auditory sensory thresholds, it has been repeatedly reported that congenitally blind outperform sighted subjects in pitch discrimination tasks (Gougoux, Lepore et al. 2004). Further, it has also been reported that blind musicians often show a higher “absolute pitch” than sighted musicians (Hamilton, Pascual-Leone et al. 2004). These findings, among others, support the hypothesis that the enhancement of the auditory discrimination abilities in congenitally and early blind humans could be due to a reorganization of the auditory cortices (Hotting and Roder 2009).

Although the importance of multisensory integration is commonly accepted, research has traditionally focused on unisensory processing. This approach is based on the assumption that sensory information is treated in a hierarchical manner. According to this view, multisensory
Multisensory experiences and their impact on memory performance

Antonia Thelen

treatment takes place in the higher order association cortices, after extensive unisensory treatment in low-level, sensory-specific cortices (e.g. (Jones and Powell 1970)).

However, recent studies challenged this view, providing evidence for direct anatomical connections between lower-tier sensory cortices and between higher level association cortices (Falchier, Clavagnier et al. 2002; Cappe and Barone 2005; Smiley and Falchier 2009; Falchier, Schroeder et al. 2010). Therefore, besides integration sites situated in the parietal, frontal and temporal regions, multisensory interactions already take place in sensory specific areas of the brain.

2.1 Rules of Multisensory integration: Evidence from Single-Unit Recordings

Current multisensory research is based on a body of work that has been provided by Stein and colleagues (Stein & Meredith, 1993). Stein and colleagues studied (single) neurons in the superior colliculus (SC), a structure in the brainstem, which is known to be involved in visual-motor coordination. In the cat this structure supports its ability to orientate its gaze in direction of an auditory and/or somatosensory stimulus, or vice-versa. This structure receives ascending and descending information from visual, somatosensory, auditory and motor inputs, and cells in the SC appear to be multisensory. Consequently, this structure provided a model for investigating multisensory processes and its governing principles.

In order to introduce the principles put forth by Stein & Meredith (1993), we must clarify that these rules emerged from observations of changes in the firing rate of single neurons, i.e. response enhancement or depression. Further sensory neurons respond to stimuli occurring in their receptive fields. A receptive filed is a region in space (i.e. environment or body surface) in which the presence of a stimulus will alter the firing rate of the neuron. These receptive fields for different sensory modalities of a multisensory neuron overlap, so that it responds to stimuli from the same region in space. Across many cells in the SC, their receptive fields are arranged to provide a functional map of the outside world (Stein and Meredith, 1993).
Figure 4: illustrates the changes of the neural response of a multisensory neuron in the SC. The bar graphs summarize the quantitative difference of the firing rate of the measured neuron.

The following principles of multisensory integration have been described on a single-neuron basis. In order to clarify the above mentioned notions of receptive fields and supradditivity, the following Figure 4 (taken from (Wallace, Meredith et al. 1998)) illustrates how neurons in the SC change their firing rate in the presence of unisensory stimuli (A: auditory, B: visual) compared to multisensory stimuli (C). The bar graphs in (D) summarize the measured neuronal response. The circles represent the receptive field of the neuron. If the sensory cue (here an auditory or visual stimulus) falls inside this receptive field, the neuron will respond by firing action potentials. While the neuron responds weakly to either unisensory stimulation, the combined auditory-visual cue generates a supradditive response. This is depicted in the bar graphs, where the multisensory (AV) stimulus elicits a response that is bigger than the sum (dotted line) of the two unisensory responses taken separately.
1.1.1 Spatial rule

“Spatially coincident multisensory stimuli tend to produce response enhancement, whereas spatially disparate stimuli produce either depression or no interaction.”

(Stein & Meredith, 1993)

A given multisensory neuron in the SC can respond to different combinations of two or three sensory modalities (visual, auditory and somatosensory). If the receptive field of this neuron receives the input of said sensory modalities, its’ firing rate may change in response to whether the inputs are spatially aligned or disparate. In other words, if two sensory stimuli are originated in the same region, the neuronal response is enhanced. This means that the response to one sensory modality impacts the response to the other sensory input. Consequently, spatially coincident stimuli that fall into the neurons’ excitatory receptive fields will enhance one another’s effects, while a depression or no interaction is observed when one of the sensory inputs falls outside the neuron’s receptive field (see Figure 4). This interaction between enhancement and depression of cell activity will generate a “code”, which will be translated into a spatial position. Recent findings suggest this may likewise be a dynamic process, in that the specific excitatory zones can change across time (e.g. Carriere et al., 2008)

1.1.2 Temporal rule

“Maximal multisensory interactions are not dependent on matching the onset of two different sensory stimuli, or their latencies, but on how the activity patterns resulting from the two inputs overlap.”

(Stein & Meredith, 1993)

There are two temporal features that characterize the multisensory interactions in the SC. First, the temporal window in which response enhancement or depression occurs may be very large. Second, if the peak activity periods (i.e. maximal enhancement or maximal depression) of two unisensory stimulations overlap, their interaction is increased.

Figure 5 (taken from (Meredith, Nemitz et al. 1987)) illustrates the response pattern, in terms of firing rate of a multisensory neuron in the SC when stimulated by two sensory cues (visual
Multisensory experiences and their impact on memory performance

Antonia Thelen

and auditory) with different onset latencies. The neuronal response is strongest in a time window where the auditory cue is delivered 50ms before or after the visual stimulus for this particular neuron (A 50 V, A=V, and V 50 A). The key point is that interactions and integration are linked to temporal profiles of neural activity, rather than to the presentation of stimuli in the external world or their arrival at the sensory epithelia.

![Neuronal response image]

**Figure 5**: illustrates the change in firing rate of a multisensory neuron in the SC, when presented with an auditory and a visual stimulus with different stimulus-onset-asynchronies.

1.1.3 **Principle of Inverse Effectiveness**

"Maximal enhancement occurs with minimally effective stimuli."

*(Stein & Meredith, 1993)*

In order to understand what Stein & Meredith (1993) imply when they use the term enhancement, we need to return upon the notion of a “Multisensory Enhancement Index”. This index is calculated as follows:

\[
\text{Multisensory} - \frac{\text{Unisensory}_{(\text{max})}}{\text{Unisensory}_{(\text{max})}} \times 100\%
\]

**Multisensory**: the number of impulses evoked by the multisensory stimulus  
**Unisensory\_max**: the response to the most effective unisensory stimulation

The inverse effectiveness rule states that the response enhancement of a neuron is biggest, when the unisensory stimuli presented independently to the same neuron show minimal
Multisensory experiences and their impact on memory performance

Antonia Thelen

activation patterns.

Figures 6 and 7 (Taken from (Perrault, Vaughan et al. 2003)) illustrate the inverse effectiveness rule. In Figure 6 a neuron is shown, which responds strongly to either of the unisensory stimulations (visual and auditory). When the combined sensory stimulus is presented to the same neuron, it will enhance its’ firing rate, but to a lesser degree than the neuron shown in Figure 7, which only responds weakly to either unisensory stimulus. The extent of the response enhancement is depicted in the bar graphs.

Figure 6: Example for a Low enhancement index

Figure 7: Example for a High enhancement index
2.2 Multisensory integration at early stages of information processing

As mentioned above, research had traditionally focused on multisensory integration in higher-level association cortices or in sub-cortical structures that are dependent on cortical inputs for their multisensory responses. In line with this view, sensory information is treated in sensory-specific cortices (auditory-specific, visual-specific, etc.) and is then merged into a unified percept in the parietal, temporal and frontal cortices or subcortically.

Recent development in this research area has challenged this view (Calvert, Hansen et al. 2001; Falchier, Clavagnier et al. 2002; Foxe, Wylie et al. 2002; Molholm, Ritter et al. 2002; Cappe and Barone 2005; Cappe, Rouiller et al. 2009; Falchier, Schroeder et al. 2010; Sperdin, Cappe et al. 2010). These studies collected evidence from different approaches (e.g. from anatomical tracing techniques, functional neuroimaging and behavioral approaches such as the signal detection theory) either in humans or in animals. Anatomical studies have collected evidence for the existence of feedforward, feedback or lateral axonal projections between the sensory-specific areas and between these areas and the associative areas. Neuroimaging studies have shown activations in low-level sensory when subjects were presented with multisensory detection or recognition tasks. Also behavioral approaches producing faster reaction times in multisensory versus unisensory stimulus discrimination conditions have supported the existence of early multisensory interactions. From the results collected by these different approaches, a more complex view emerged, where multisensory interactions take place, first in low-level sensory cortices and then in higher-level associative cortices. Consequently, it seems clear that the traditional models cannot account, nor integrate these latter findings, which leads us to elaborate much more complex models of sensory integration.

Figure 8: This figure (taken from: (Ghazanfar and Schroeder 2006)) illustrates (a) a classical view of cortical multisensory areas of the primate brain, where multisensory information is merged in higher-level association cortices. Whereas (b) depicts a modern scheme of the anatomy of multisensory areas of the primate brain. In fact, this new model represents the (visual) occipital areas as being auditory-visual integration sties as well as the auditory cortices receiving somatosensory and visual inputs.
Multisensory experiences and their impact on memory performance

Antonia Thelen

Figure 8: On the left the classic model of multisensory integration sites in the parietal, temporal and frontal regions is depicted. On the right, the modern model is shown, where multisensory interaction occur at early low-level stages of sensory processing.

The evidence supporting the model postulating the existence of multisensory connections between different cortical sensory areas has been collected and replicated repeatedly by anatomical studies done in monkeys, ferrets, rats and cats (in the monkey: (Watanabe and Iwai 1991; Schroeder, Lindsley et al. 2001; Cappe, Rouiller et al. 2009); in the ferret: (Bizley, Nodal et al. 2007); in the rat: (Barth, Goldberg et al. 1995); in the cat: (Miller and Vogt 1984; Innocenti, Berbel et al. 1988).

Further, recent studies have also shown that multisensory interactions might be gated by thalamic interconnections (In the gerbil: (Budinger, Laszcz et al. 2008); in the monkey: (Cappe, Morel et al. 2007; Hackett, De La Mothe et al. 2007). This implies that multisensory interaction take place at even earlier, pre-cortical stages, and that part of the information that is transmitted to the low-level sensory areas has already been merged within subcortical structures. The thalamus is considered to be a relay structure between peripheral sensory organs and the central nervous system. This structure gates ascending and descending information to and from the brain.

In classical models of sensory integration, the thalamo-cortical connections have been seen as feedback projections, by which cortical areas control thalamic nuclei from which they receive ascending inputs. However, recent studies have shown the existence of feedforward connections
Multisensory experiences and their impact on memory performance

Antonia Thelen

originating in the thalamic nuclei (Sherman, 2007). Further evidence for these feedforward projections, arises from studies labeling neurons with anterograde and retrograde tracers in monkeys (Cappe, Morel et al. 2007). Cappe et al. (2009) found the existence of an overlap between thalamo-cortical connections (input into cortical areas) in the thalamus and cortico-thalamic (output from cortical areas) connections.

Figure 9: (taken from (Cappe, Rouiller et al. 2009); modified with permission of C. Cappe) (A) shows a schematic representation of multisensory cortico-cortical connections between different low-level sensory areas, which have been thought to be unisensory until recently, and connections between several levels of sensory processing of sensory information. Further the existence of thalamo-cortical connections is schematically illustrated. (B) depicts thalamo-cortical connections originating from different thalamic nuclei to distinct sensory areas. The differently color-coded areas show overlapping thalamo-cortical connections, where a single thalamic nucleus projects to different sensory areas.

Figure 9: (A) illustrates a schematic representation of the model that has emerged from anatomical studies, which provided evidence for monosynaptic connections between unisensory cortices and higher-level association cortices. Also connections from the thalamus to the low-level unisensory cortices are schematically indicated. (B) shows overlapping areas in the thalamus that project to different sensory cortices.
Evidence for multisensory interactions taking place in early and low-level cortices in humans comes from different kinds of imaging approaches. Certain techniques like magnetic resonance imaging (MRI) and positron emission tomography (PET) have very high spatial resolution and let us investigate the areas in which sensory interactions take place. A recent fMRI study investigated multisensory effects within the primary visual cortex, when meaningless, rudimentary auditory stimuli were included into a simple detection task. The results showed that multisensory interactions take place in primary visual and auditory cortices. Further, the authors argue that their findings, in addition to those of previous studies (e.g. (Schroeder and Foxe 2005)) provide evidence for direct multisensory interactions within early sensory processing stages (Martuzzi, Murray et al. 2007), confirming several other studies (Ghazanfar and Schroeder 2006; Kayser and Logothetis 2007).

Further studies using transcranial magnetic stimulation (TMS), which has been shown to permit the investigation of neuronal processes by interacting with cortical excitability (activity enhancement) or provoking so called virtual lesions (activity decrease), has provided evidence for low-level sensory interactions. A recent study, combining auditory looming sounds with TMS pulses over the visual cortices investigated the modulation of activity in these visual areas (Romei, Murray et al. 2009). They found that acoustically structured looming sounds selectively enhanced visual cortex excitability at pre-perceptual latencies.

Other techniques like electroencephalography (EEG) and magnetoencephalography (MEG) might not provide us with such precise spatial information, but these techniques have a high temporal resolution, thus untangling the moments in time at which sensory information interacts. An example for the high temporal resolution of EEG, is a recent study which investigated the time course of auditory-visual integration (Cappe, Thut et al. 2010). This study aimed at resolving an ongoing debate about the time course of early multisensory interaction. While certain studies showed interactions at latencies of ~50ms after stimulus onset (Giard and Peronnet 1999) when comparing multisensory event-related potentials (ERPs) to the sum of unisensory responses, other groups claimed that these findings were not free of the so called “common” activity including anticipatory potentials and motor responses (Teder-Salejarvi, McDonald et al. 2002). Cappe et al. (2010) found effects in timing and scalp topography that replicated the prior findings with nonlinear neural responses between multisensory and unisensory stimulations at ~40 – 50ms.
In order to introduce my Masters project, the previous work leading to this research will be briefly presented. The aim of each study and its’ result will be elucidated.

1.1 Rapid discrimination of visual and multisensory memories revealed by electrical neuroimaging (Murray, Michel, Grave de Peralta, Ortigue, Brunet, Andino, & Schnider, 2004, *NeuroImage*)

Preceding investigations focused on how past multisensory experiences interact with present unisensory retrieval (Nyberg, Habib et al. 2000; Wheeler, Petersen et al. 2000). These studies showed that upon unisensory retrieval the same regions showed activation that were implied during multisensory encoding, thus supporting the theory of “redintegration” (Hamilton, 1859). According to this theory a component part is sufficient to reactivate the whole consolidated representation of the experience. In both studies subjects had extensive training sessions (over several days) and the retrieval performance was tested either in a MR scanner (Wheeler, et al., 2000) or while a PET scan was acquired (Nyberb, et al., 2000). Nevertheless these findings were confounded by the retrieval task, were subjects had to explicitly remember the context in which they had encountered the stimuli during encoding (unisensory or multisensory).

Therefore this study wanted to shed a light on the time course (when) and where an incidental effect of past multisensory experiences on current unisensory retrieval takes place when subjects neither dispose of a prolonged time period to study the auditory-visual stimulus pairs, nor had to classify the stimuli according to their initial presentation modality.
Multisensory experiences and their impact on memory performance

Antonia Thelen

While the investigated multisensory pairings differed between this and the following studies, the procedure was identical to the one of the present master thesis (see section 3, Materials and Methods) and in the other papers that will be presented hereafter.

Figure 10: (taken from Murray et al., 2004) is a schematic representation of the paradigm that was employed

 Subjects performed a continuous recognition task, which required the discrimination of initial from repeated presentations of images. Upon initial presentation the stimuli were either unisensory (V, visual-only) or multisensory (AV, auditory-visual) presentations. Repeated presentations were always unisensory (V-, for the repeated V stimuli, and V+ for the initially multisensory stimuli). It is important to note that this study investigated the effect of multisensory congruent semantic pairings. Thus the auditory stimuli were complex meaningful sounds (16 bit stereo, 44,100 Hz digitization, 500ms duration), each of which corresponded to one of the visual stimuli in the AV group.

High-density electrical neuroimaging techniques were applied to the aim of determining the time course and compute the source estimation of the underlying neuronal processes. EEG was acquired from 123 scalp electrodes, and only trials leading to correct responses were included in the analysis.

The behavioral results showed that stimuli are rapidly discriminated according to their past multisensory or unisensory association (overall accuracy for all conditions = 91 ± 1%; V+ = 88.5%, V- = 86.1%, t(10) = 3.18, p<0.01). In addition this discrimination appeared to be made as early as ~60 – 136ms post-stimulus onset in the regions of the lateral-occipital complex (LOC) (shown in Figure 11). This system is part of the ventral visual (what) pathway, which is involved in object recognition.
Multisensory experiences and their impact on memory performance

Antonia Thelen

(Malach, Reppas et al. 1995). From this observation, the authors concluded that multisensory memories are formed in an incidental manner, and that they alter subsequent unisensory recognition at very early processing stages in visual information treatment.

Figure 11: shows the results from the source estimation and statistical differences between the V+ and the V- conditions are shown.

1.2 The brain uses single-trial multisensory memories to discriminate without awareness (Murray, Foxe, & Wylie, 2005, NeuroImage)

The main reason for this follow-up study was that despite advances in source estimation procedures (Michel, Murray et al. 2004; Gonzalez Andino, Murray et al. 2005) intracranial spatial resolution of scalp recordings remained limited. Thus in order to confirm the role of the LOC in multisensory processes, Murray and colleagues conducted an fMRI study, which procures a much higher spatial resolution than EEG. The behavioral paradigm was modified in order to adjust to the time course of the hemodynamic response. More precisely this implicated that the main difference
was the inter-trial interval (ITI) which was longer than in the previous study (6 – 10 seconds, instead of 1200 – 1500ms).

**Figure 12** depicts the schematic representation of the paradigm. As in the former study, subjects performed a continuous recognition task, discriminating between initial and repeated presentations of the images. The experimental conditions were the same as in the before, where half of the initial presentations were unisensory, visual-only presentations (V) and the other half was composed of congruent multisensory auditory-visual (AV) stimulus pairs. When repeated all images were presented in a visual-only manner (V- and V+).

The behavioral results showed that subjects performed well even when having to perform in the noisy environment of the scanner (Accuracy: AV=96 %, V=91%, $t(7) =1.43; p>0.15$; V+=90.2%, V-=87.8%, $t(7) = 0.74, p< 0.03$). Further slower reaction times on multisensory trials indicated that subjects were unaware of the fact that the mere presence of auditory stimuli signaled a novel image presentation.

In terms of the Blood oxygenation level (BOLD) responses, the contrast between the repeated V+ and V- trials, SHOWED activations in 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 in the LOC (see **Figure 13**). This result confirmed the findings of the former study arguing that this region is in fact involved in visual object recognition and its role in multisensory memory processes.
The results of the fMRI are shown in Figure 13. While the LOC showed a significantly different activation between the V- and the V+ trials, no activation in the auditory cortices was found. These findings are thus in contrast with the model proposed by Nyberg et al. (2000) and by Wheeler et al. (2000).

Figure 13 (taken from Murray, et al., 2005). The table in the left is a list of the activations found in the fMRI analyses when contrasting the V+ and the V- conditions. The right picture shows the results from the same comparison. Statistical images have been thresholded at $p < 0.05$. 

<table>
<thead>
<tr>
<th>Location</th>
<th>Brodmann area</th>
<th>Cluster size</th>
<th>Center of mass</th>
<th>Locus of maximal intensity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle occipital</td>
<td>18/19</td>
<td>29</td>
<td>−34, −89, 7</td>
<td>−30, −93, 0</td>
</tr>
<tr>
<td>gyrus (left)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anterior cingulate</td>
<td>24</td>
<td>32</td>
<td>−2, 24, −3</td>
<td>2, 23, 0</td>
</tr>
<tr>
<td>Medial frontal</td>
<td>10</td>
<td>27</td>
<td>−12, 44, −5</td>
<td>−14, 31, −8</td>
</tr>
<tr>
<td>gyrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inferior frontal</td>
<td>45</td>
<td>17</td>
<td>56, 34, 0</td>
<td>58, 31, 0</td>
</tr>
<tr>
<td>gyrus</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
1.3 The role of multisensory memories in unisensory object discrimination (Lehmann & Murray, 2005, *Cognitive Brain Research*)

Having clarified the neuronal mechanism underlying the mechanism of multisensory experiences impact subsequent unisensory retrieval the aim of the investigations of the present study was to determine what kinds of multisensory experiences produce distinct perceptual/memory traces. The authors argued that the results previously established could have been confounded because of the use of exclusively meaningful, congruent auditory-visual multisensory stimulus pairs. In fact the possibility that the mere presentation of any auditory-visual stimulus pair could suffice to establish such a perceptual/memory trace must be taken into account because the presentation of any other multisensory stimuli could result in similar perceptual/memory trace formation.

To address this issue, the authors conducted two experiments. The first addressed the question of whether a purely episodic multisensory experience, where a somatosensory (haptic stimulation) or a meaningless auditory stimulus (1000Hz tone) is coupled to images could produce similar effects than the previous investigations (see von Kriegstein and Giraud, 2006). In the second experiment the importance of semantic congruency was manipulated, where the meaningful auditory stimuli either matched or did not match the visual object (see Seitz et al., 2006).

Figure 14 shows the paradigms and behavioral results found in the two experiments.
Multisensory experiences and their impact on memory performance

Antonia Thelen

The most left columns depicts the experimental paradigm and the behavioral results of the effect of a pure tone associated to visual images in the initial presentation condition. The second column shows the association of a haptic 50Hz stimulation to each multisensory trial, and the right column corresponds to the semantic congruency manipulation paradigm. \( AV_c \) (V+c upon repetition) stands for multisensory congruent auditory-visual associations, while \( AV_i \) (V+I upon repetition) are incongruent pairs of stimuli.

The principal finding of this study was that past multisensory experiences can influence the ability to accurately judge image repetitions during a continuous recognition task. Specifically accurate discrimination performance during unisensory object recognition, (1) was significantly impaired for images that had been presented with a 1000Hz tone, (2) was not affected when images had been presented with a 50Hz vibration, (3) was not affected for images that had been coupled with incongruent meaningful sounds, and (4) selectively improved for images initially presented with a semantically congruent sound.

Together these results reveal an opposing effect of episodic and semantic contexts for auditory-visual multisensory experiences. In addition episodic multisensory effects on perceptual/memory trace formation seem to be confined to auditory pairing.
2 The role of single-trial, episodic multisensory learning in unisensory object discrimination (Thelen, Cappe, & Murray, 2010, submitted)

We experience our environment through distinct and specialized sensory systems. However, perceptions are often affected by combining information from several sensory modalities, i.e. under multisensory conditions (Calvert, Spence, et Stein, 2004; Stein and Meredith, 1993). Furthermore, multisensory perceptual experiences at one point in time can impact unisensory processing during latter encounters (Stein, Huneycutt et al. 1988; Gottfried, Smith et al. 2004; Murray, Michel et al. 2004; Amedi, von Kriegstein et al. 2005; Lehmann and Murray 2005; Murray, Foxe et al. 2005; Kim, Seitz et al. 2008; Shams and Seitz 2008). However, the circumstances under which such multisensory memory traces impact subsequent unisensory retrieval remain unresolved and were the focus of the present study. This issue falls within the larger framework of whether (and how) performance and brain responses can engender stimulus discrimination through (single-trial) multisensory versus unisensory learning (Shams and Seitz, 2008; Murray and Sperdin, 2010).

Accuracy in reporting repeated presentations of visual objects is incidentally affected according to whether they were initially encountered in a multisensory or unisensory context (Murray, Michel et al. 2004; Lehmann and Murray 2005; Murray, Foxe et al. 2005). Specifically, performance was enhanced for stimuli that had been initially encountered in a semantically congruent multisensory context, was unchanged if initially encountered in a semantically incongruent context, and was impaired if initially encountered with a meaningless sound (i.e. pure tone). All of these effects were relative to performance with images that were initially encountered in a unisensory context (i.e. the same image repeated once). These effects on accuracy were in the absence of parallel modulations in reaction times (in fact, reaction times did not differ) and were not the consequence of carry-over effects from encoding (reviewed in Murray and Sperdin, 2010; see also (Baier, Kleinschmidt et al. 2006) for similar work on multisensory expectancy).

The performance impairment observed by Lehmann and Murray (2005), however, is confounded by the fact that it cannot be discerned whether their effect was due specifically to the episodic nature of the multisensory context and/or because the same tone was associated (across multiple trials) with multiple images. This latter possibility would have likely resulted in repeated
association and dissociation of sounds and images that in turn may have impaired participants’ memory performance. It is important to note that despite the opposite direction of the effects observed across the studies by Murray and colleagues (Murray et al., 2004, 2005; Lehmann and Murray, 2005) incoming visual stimuli are discriminated according to past multisensory experiences. This discrimination is made irrespective of how the stimuli were initially encountered, and does indeed result in differential visual object processing.

The main proposition from these findings was that semantic and episodic associations between the senses modulate the fidelity with which object representations can be activated. In the case of semantically congruent auditory-visual objects, distinct perceptual/memory traces can be established that can be (differentially) accessed upon subsequent presentation of just the object’s image. This may arise through the enhanced activation of a singular object representation via multiple, redundant sources that in turn effectively yields a higher fidelity in the object representation (or alternatively a lower threshold for activating this representation) when the object system is subsequently confronted with just the visual component. No such enhanced traces are established for semantically incongruent pairs relative to those established under unisensory conditions (and by extension no behavioral effect is observed). The visual stimulus activates one object representation and the sound an altogether other (see e.g. (Molholm, Martinez et al. 2007; Fiebelkorn, Foxe et al. 2010) for considerations of this issue based on attentional spreading). Because multiple objects are routinely treated in parallel and can be simultaneously encoded via distributed neuronal representations (Rousselet, Fabre-Thorpe et al. 2002), no effect on performance is observed relative to the visual-only condition. In the case of images paired with tones, it was proposed that the association of a single sound with multiple visual objects over trials effectively leads to the introduction of ‘noise’ into the establishment of distinct multisensory perceptual/memory traces for any one individual object. That is, the same sound has produced an interactive response with several different object representations. Consequently, the fidelity of perceptual/memory traces for these objects is diminished and comparatively impaired performance is obtained.

The present study sought to resolve the role of episodic pairings on single-trial multisensory memory processes. We paired (on their initial encounters) visual objects with meaningless, but unique sounds in the context of a continuous recognition task requiring the discrimination of initial from repeated presentations of visual objects. If single-trial episodic events are sufficient to generate a behaviorally-relevant perceptual/memory trace performance accuracy
would be predicted to be impaired for repetitions of images that had been paired with sounds on their initial encounter. This would suggest that the observations of Lehmann and Murray (2005) are due to the episodic pairing rather than to the repeated association/dissociation of the same sound with multiple images across trials. Alternatively, no performance differences (vs. images that had only been encountered visually) would be predicted if the unique, meaningless sounds are treated as if they were an incongruent event akin to pairing the sound of one (known) object with the image of another object.

2.1 Material and Methods

Participants

The experiment included 20 (11 females) volunteers aged between 23 and 30 years (mean age ± SD = 26.3 ± 3.1). The study was conducted in accordance with the Declaration of Helsinki, and all subjects provided their informed consent to participate in the study. The experimental procedures were approved by the Ethics Committee of the Vaudois University Hospital Center and University of Lausanne. 19 subjects were right-handed, according to the Edinburgh Inventory (Oldfield 1971). No subject had a history of neurological or psychiatric illness, and all subjects had normal or corrected-to-normal vision, as well as normal hearing.

Procedure

Subjects performed a continuous recognition task, which required the discrimination of initial from repeated presentations of line drawings that were pseudo-randomized within a block of trials. They were instructed to perform as quickly and as accurately as possible. Further, each object (irrespective of whether it was initially presented in a unisensory or multisensory context) was only repeated once throughout the duration of the experiment.

The pictures were subdivided into two groups where there were two types of initial presentations and two types of repeated presentations. Initial presentations were either unisensory or multisensory. Repeated presentations were always unisensory. Thus, half of the repeated presentations had been multisensory when initially encountered and the other half had
be unisensory when initially encountered. We will refer to our stimuli in terms of V, for the visual-only initial condition and V- for the same stimuli in the repeated condition. AV will refer to the initial auditory-visual presentation, whereas V+ will refer to the repeated presentation of the visual component of these stimuli (Figures 15 and 16 depict examples of the stimuli implied in the study and a schematic representation of the experimental paradigm).

The line drawings were taken from a standardized set (Snodgrass and Vanderwart 1980) or obtained from an online library (dgl.microsoft.com), and included a mix of living and non-living stimuli. The pictures were equally subdivided over experimental conditions and blocks as described before. Plus, we distributed them based on their referent object (i.e. animals, musical instruments, human body parts and environmental objects). In order to minimize the possibility that the observed effects were due to low-level visual features, we analyzed the spatial frequency spectra and the luminance between the two image groups (AV and V). The full details of these procedures have been reported by Knebel et al., (Knebel, Toepel et al. 2008). The images were presented centrally and appeared black on a white background. On initial presentations these visual stimuli could (50%) or not be paired with a meaningless sound (created with Adobe Audition 1.0). These sounds differed in their spectral composition, ranging from 100Hz to 4700Hz and were modulated (or not) in terms of amplitude envelopes and/or waveform types (triangular and sinusoid) with 500ms duration (10ms rise/fall, in order to avoid clicks; 16bit stereo; 44100Hz digitization).

All stimuli were presented for 500ms, followed by a randomized inter-stimulus interval (ISI) ranging from 900 to 1500ms. The mean (±SD) number of trials between the initial and the repeated presentation was 9±4 pictures for either presentation condition (V and AV). Also the distribution of old and new pictures throughout the length of the block was controlled, so to avoid response-decision bias. This type of bias refers to subjects being able to calculate predictive probabilities about the upcoming stimuli and responses, which could lead to faster reaction times and/or a drop in attention. The experiment took place in sound-attenuated chamber, where subjects were seated centrally in front of a 20” computer monitor (HP LP2068), located about 140cm away from them (visual angle ~4°). The auditory stimuli were presented over insert earphones (Etymotic model: ER4S), and the volume was adjusted to a comfortable level (~62dB). The stimuli were all presented and controlled by E-Prime 2.0, and all behavioral data were recorded in conjunction with the serial response box (Psychology Software Tools, Inc.; www.pstnet.com).
Multisensory experiences and their impact on memory performance

Antonia Thelen

Visual Stimuli:
Line drawings taken from a standardized set (Snodgrass & Vanderwart, 1980) or they were obtained from an online library (http://dgl.microsoft.com)

Auditory Stimuli:
Meaningless sounds created with Adobe Audition 1.0
Frequency range: 100 Hz – 4700 Hz
Modulated in terms of frequency and amplitude envelop

Pure tone Modulated Sound

Figure 15: Examples of the stimuli

Figure 16: Illustration of the paradigm used to investigate multisensory encoding and recall in working memory
2.2 Results

The data were treated as follows: Mean RT (in [ms]) and accuracy (\% of correct responses) were calculated for each subject and condition (V, AV, V-, and V+) separately. We then performed paired t-tests, specifically comparing the initial encoding conditions (V vs. AV) or the repeated retrieval conditions (V- vs. V+). Finally, we sought to assess whether effects during encoding (i.e. differences between V vs. AV) were directly linked to and/or predictive of effects during retrieval (i.e. differences between V- vs. V+), given that prior studies would suggest that these are dissociable (reviewed in Murray & Sperdin, 2010). As will be made clearer in the Results below, we calculated the correlation coefficient between the differences in reaction time during encoding and the difference in performance accuracy during retrieval.

Analysis of performance accuracy (Figure 17) revealed that participants were equally capable of indicating the initial presentation of stimuli both when presented in a multisensory auditory-visual context (AV=85.4±2.2%; mean±s.e.m.) and also when presented in a unisensory visual context (V=87.6±2.0%; t(19)=1.815; p=0.085; \( \eta^2_p = 0.683 \)). There was therefore no indication of encoding differences in terms of discrimination accuracy. By contrast, performance when indicating image repetitions was significantly impaired when the initial presentation entailed a multisensory vs. unisensory context (i.e. V+ vs. V-; 82.9±2.8% vs. 86.8±2.1%; t(19)=2.49; p=0.022; \( \eta^2_p = 0.694 \)). This difference indicates that image repetitions are incidentally discriminated according to past multisensory experiences.

In contrast with the pattern observed with accuracy rates (but highly consistent with prior work; e.g. Lehmann & Murray, 2005), mean reaction times differed for initial presentations, but not for image repetitions (Figure 18). Specifically, reaction times to initial presentations under multisensory conditions were significantly slower than those to initial presentations under unisensory conditions (AV vs. V = 792±20ms vs. 761±21ms; t(19)=-4.019; p=0.001; \( \eta^2_p = 0.861 \)). Reaction times to image repetitions did not significantly differ (V+ vs. V- = 773±25ms vs. 775±24ms; t(19)=0.218; p=0.830; \( \eta^2_p = 0.953 \)).

Finally, we examined if there was a linear relationship between reaction time differences during encoding and accuracy differences during retrieval. There was no evidence of a significant correlation (\( r_{18} = -0.059; p>0.80 \)), providing no evidence for a carry-over effect.
Figure 17: Group-averaged accuracy (±s.e.m.) for the four experimental conditions: initial presentations of visual (V) and auditory-visual (AV) and their repeated presentation (V- and V+, respectively).

Figure 18: Group-averaged reaction times (±s.e.m.) for the same experimental conditions as in Figure 17. Significant effects (p<0.05) are marked with an asterisk.
2.3 Discussion

We show that the discrimination of image repetitions is incidentally affected by whether or not the initial experience was multisensory versus solely visual. Prior research had demonstrated this type of phenomenon following semantically congruent single-trial exposures, but left unresolved whether such also extended to episodic pairings (Murray, Michel et al. 2004; Lehmann and Murray 2005; Murray, Foxe et al. 2005). Here, we show that memory performance with visual objects is impaired by prior multisensory pairings with unique, but meaningless, sounds and thus does not depend on a specific tone creating the episodic association. Additionally, we show that these effects are not a simple carry-over of effects occurring during the initial memory encoding. In what follows, we discuss our findings in terms of incidental effects of multisensory interactions on memory processes.

There was no evidence that performance (reaction times and accuracy) was mirrored across the initial and the repeated presentations of a given object. This finding contrasts with the models put forwards by Nyberg, et al. (2000) and Wheeler, et al., (2000), which postulated that the same encoding-related cortices are reactivated during retrieval. Rather, the present and our prior findings show that multisensory effects on encoding and retrieval are dissociable (Murray, Michel et al. 2004; Lehmann and Murray 2005; Murray, Foxe et al. 2005). Because we did not find a positive correlation between the difference in discrimination accuracy during retrieval and reaction times during encoding \( (r_{18}=-0.059; p>0.80) \), and thus did not observe mirrored performance, we conclude that discrimination of repeated visual objects previously coupled to sounds is not directly linked to the re-activation of the auditory representation itself. A possible explanation of these opposing findings between our group and the work of Nyberg et al. (2000) and Wheeler et al. (2000) is that the auditory areas were differentially re-activated in these studies to compensate for their increased task difficulty or as a consequence of auditory imagery because the task required the explicit recall of the encoding context. It should also be noted that the experimental design of the present study did not allow a similarly extensive studying of the multisensory associations and likewise implicitly assessed the impact of encoding conditions, because participants only received single-trial exposures to the multisensory associations while performing a continuous recognition task. Taken together, this difference between encoding and retrieval lends further support to the proposition that integration of novel events (either unisensory or multisensory) and subsequent
retrieval of this information may rely on (partially) distinct brain mechanisms.

The question then arises as to the putative brain mechanisms subserving the observed retrieval performance differences. To date, our prior electrical and hemodynamic imaging studies have exclusively examined the case of visual memory retrieval based on prior semantically congruent multisensory associations (Murray et al., 2004, 2005). In these studies differences were observed as early as 60ms post-stimulus onset (as well as during subsequent stages) and within higher-tier lateral occipital cortices. The implication is that incoming visual information is rapidly distinguished within object-sensitive visual cortices (e.g. (Grill-Spector and Malach 2004)) according to how it was initially encountered, even if this aspect is task-irrelevant and also occurred as much as one minute earlier or despite several intervening presentations of other objects. Whether the present effects are relying on a similar mechanism is the topic of ongoing research by our group.

At least two families of hypotheses can be generated based on current knowledge regarding auditory-visual multisensory interactions in humans and non-human primates. On the one hand, it may be the case that discrimination of incoming visual object information according to past multisensory experiences is critically dependent upon first determining the identity (at least at a crude level) of that object. In which case, effects would forcibly rely on object-sensitive visual cortices, including lateral occipital regions, which numerous prior studies have shown to receive not only visual but also auditory and somatosensory inputs (reviewed in Murray et al., 2004). On the other hand, it may be the case that the discrimination observed in this study is an extension of what has been observed with simple visual stimuli immediately preceded by either multisensory or visual stimuli (Meylan and Murray 2007). In their study, responses to visual flashes that had been preceded less than 100ms beforehand by a multisensory vs. visual stimulus were attenuated within lower-tier visual cortices. The present study might reflect a similar mechanism operating on a longer temporal interval between multisensory and subsequent unisensory stimulus presentations.

We could exclude an explanation of our results due to a bias by selective attention or novel context detection facilitating perceptual memory trace formation (Ranganath and Rainer 2003), as well as general alerting. If selective attention could account for our findings faster reaction times would have been expected. Rather our results suggest that participants were not overtly attending to the auditory channel, because we did not observe more accurate discrimination and/or faster reaction times for the initial, multisensory condition, where it would have been very easy to
determine that all multisensory trials were newly-presented objects. In addition, Subjects were slower in the initial, multisensory condition, suggesting that they did not expect auditory events (Spence, Nicholls et al. 2001). We also rule out possible bias due to general arousal and fatigue. Block lengths (i.e. 136 trials for ~5min) could produce a decrease in performance accuracy and/or longer reaction times due to loss of concentration and growing fatigue or disinterest towards the end of the block. In order to prevent such a bias, we presented the stimuli with a 9 ± 4 pictures interval, so that the probability of a “new” object appearing on the screen was maintained in the final quarter of the block. This supports our hypothesis that any observed effect is provoked by the initial multisensory pairing, thus being dependent on our paradigm and not due to chance.

The present findings likewise contrast with the hypothesis that single-trial multisensory interactions impact subsequent unisensory retrieval only in specific situations. Instead of juxtaposing semantic and episodic contingencies between the senses, some have emphasized the role of either object familiarity (van der Linden, van Turennout et al. 2010) or ethological validity (von Kriegstein and Giraud 2006) as a principal factor in whether performance (and in some instances brain responses) would be enhanced by multisensory exposure (though we would note that both of these characteristics are rooted in semantic analysis of the objects). Still, the role of familiarity is not straightforward, because some observed performance decrements even when extensive studying of multisensory object presentations was performed prior to being tested with under unisensory conditions, though statistical analyses were not reported (Nyberg et al., 2000). By contrast, our prior works would suggest that the critical variable concerns the relationship between the sound and image, rather than the familiarity of the image, as all images were highly familiar common objects (Lehmann & Murray, 2005).
Future Directions

3 Ongoing Study

In addition to the psychophysical investigation of the role of episodic multisensory learning in unisensory object discrimination, we have conducted an EEG study with the same paradigm. Subjects had to perform a continuous recognition task, where initial from repeated presentations of images had to be discriminated. On initial presentation half of the stimuli were presented in a unisensory, visual-only manner (V), while the other half were multisensory stimuli and a unique meaningless sound was coupled to every image (AV). Upon repetition, all stimuli were again presented in a visual-only manner (V- and V+ as in the investigations discussed before).

Participants

The experiment included 15 (5 females) volunteers aged between 23 and 33 years (mean age ± SD = 26.3 ± 3.83). The study was conducted in accordance with the Declaration of Helsinki, and all subjects provided their informed consent to participate in the study. The experimental procedures were approved by the Ethics Committee of the Vaudois University Hospital Center and University of Lausanne. 12 subjects were right-handed, according to the Edinburgh Inventory (Oldfield 1971). No subject had a history of neurological or psychiatric illness, and all subjects had normal or corrected-to-normal vision, as well as normal hearing.

3.1 EEG acquisition and analyses

Data were acquired from a continuous EEG from 160 scalp electrodes (sampling rate at 1024Hz). Epochs from 100ms prestimulus and 500ms poststimulus onset were averaged for each of the four experimental conditions and from each subject in order to calculate the event-related potentials (ERPs). In addition to a ±80μV artifact rejection, EEG epochs containing eye blinks or other noise transients were removed on a trial-by-trial inspection of the data. Before group averaging, data from the artifact electrodes of each subject were interpolated (Perrin, Pernier et al. 1987). Data were baseline corrected using the prestimulus period, bandpass filtered (0.1 – 60HZ
using a notch at 50Hz) and recalculated against the average reference.

Our analyses were based on the assumption that a differential neural response was to be found between the V+ and the V- trials. We contrasted the grand average ERPs from all subjects and all trials for the V- and V+ conditions from each electrode as a function of time after stimulus inset in a series of pair-wise comparisons (t tests). For this analysis, only effects of with p-values < 0.05 for at least 11 consecutives data points (or time frames, TF) were considered reliable (equivalent to >10ms for the data acquired at 1024Hz (Guthrie and Buchwald 1991)).

After that the global electric field strength was quantified using global field power (GFP) (Lehmann and Skrandies 1980). This measure is equivalent of the standard deviation of the electrode values at a given time point t, and represents a reference independent measure of the ERP amplitude (Murray, Brunet et al. 2008). GFP was analyzed using a millisecond-by-millisecond paired t test, where only values p < 0.05 were considered reliable. As above, temporal autocorrelation was corrected through the application of an > 11 contiguous TF criterion for the persistence of the differential effects.

Hereafter the global dissimilarity (DISS) was calculated. This measure provides information about periods of topographic modulations. It is an index of configuration differences between two electric fields, independently of their strength. We then performed a TANOVA. This measure is not an ANOVA, even though the name might be misleading. In fact the TANOVA entails a non-parametric randomization test. The DISS value at each time point is compared to an empirical distribution derived from a bootstrapping.

This analysis of topographic changes indicates differences in the configuration of the generators, which are active in the brain (Lehmann, 1987). As in all statistical analyses in this experiment, only effects with p-values < 0.05 for at least 11 contiguous TF were considered.
3.2 Results

We have conducted preliminary analyses on our EEG data. Figure 19 shows the group mean ERPs from the two repeated conditions (V- and V+) at an example electrode (Fz). There is a significant difference between these two conditions at ± 100ms and ± 270ms. The gray box shows the results of the pairwise comparison (t test; p < 5%; TF > 11) of each electrode as a function of time.

Preliminary EEG Data:

Figure 19: The upper panel shows an example electrode of the group ERPs for the two conditions (V+ an V-). The green line indicates the result of the pairwise comparison. The two “waves” indicate significant changes (p < 0.05). The lower panel shows the intensity plot of the pairwise comparison in time. Red lines indicate significant differences on individual electrodes and the length of the significant effect.

Participants:
13 {3 females} volunteers
Aged 23-33

Positive Effects: {[a<5%; TF>11]}
@ -100 ms
@ ~270 ms
The results of the TANOVA are shown in Figure 20. We have found two different topographies for the above mentioned time periods. The black boxes indicate stable topographies for the V+ trials and the red boxes indicate topographies for the V- condition.

Figure 20: the results from the TANOVA are shown. The black bars indicate the time periods of significant differences in changes of topography between the two conditions (V+ and V-). The topographies are shown in the boxes. Black boxes indicate topographies that account for the V+ condition, while red boxes show topographies relative to the V- condition.

Together the results from the pairwise comparison at the single-electrode level and the results from the TANOVA indicate two time periods (± 100ms and ±270ms) where significant differences between the experimental V+ and V- conditions exist. These differences are in terms of ERP amplitude (Figure 19) and of topography (Figure 20). While differences in terms of ERP amplitude suggest a difference in neural activity strength, the results from the TANOVA suggest differences in the underlying generators of the brain.

In comparison to the previous findings from Murray et al. (2004), who investigated semantically congruent multisensory associations, the present findings show later modulations between the repeated unisensory discrimination conditions. This does not exclude the possibility that the modulations take place in the LOC as in the before mentioned studies, but it suggests that
semantic and purely episodic associations impact differently the retrieval of perceptual/memory traces. It is important to notice that even though the analysis of the time course indicates later changes due to the present experimental design, these changes still occur at early stages in sensory information processing. In order to clarify if these modulations occur in the LOC or if other neural circuits are implicated in the observed retrieval mechanism, topographic pattern analysis must be conducted.

The open questions that we will address in the ongoing investigation will be (1) to further clarify how the brain discriminates incoming visual information according to past unisensory and multisensory single-trial experiences. (2) To investigate the neural circuits that underlie this distinction, additionally to investigation whether these circuits are similar to those found by Murray et al. (2004).
3.3 Control Experiment

It could be argued that the previously observed psychophysical effects could not be directly compared, because of possible bias introduction by using different cohorts in the different experiments appearing in the collective prior works. That is, the dissociation of semantic and episodic effects is limited by the fact that different populations took part in the study by Lehmann and Murray (2005) and that presented in this thesis. A further argument regarding the experimental paradigm is that although subjects seemed not to be overtly attending to the auditory stimuli, a possible bias may have been introduced to our previous studies by presenting multisensory stimuli pairs only upon initial presentation. This might have facilitated the recognition of such stimuli compared to the initial and repeated visual-only presented objects, although our results suggest otherwise (Murray et al. (2004), Murray et al. (2005), Lehmann & Murray (2005) and Thelen et al. submitted).

The aim of this control experiment will be to directly compare the effect of different (meaningful and meaningless visual-auditory) multisensory pairings upon subsequent unisensory retrieval in a continuous recognition task. The purpose is to integrate into a single experiment several conditions previously studied by our group (Murray et al (2004), Murray et al. (2005), Lehmann & Murray (2005) and Thelen et al. submitted), in order to directly compare the behavioral patterns (in terms of accuracy and reaction times). While the former investigations focused on visual discrimination performance, we here additionally aim at investigating auditory object discrimination.

Thus, in order to control for such possible bias introduction we will present multisensory pairs not only upon initial but also upon repeated presentations. Further, the probability of multisensory versus unisensory presentations will be kept at 0.5 in both the initial and the repeated conditions. Additionally, we want to exclude a possible effect due to the cohort, and will thus present intermixed pairings throughout the blocks to a unique group of subjects.

In addition to the previously studied visual discrimination task, we will introduce an auditory discrimination task, where subjects are asked to discriminate initial from repeated presentations of sounds and tones. Indeed, the underlying assumption is that if the previously observed effects were due to the multisensory pairing, the directionality of attending either to the visual or the auditory component could result in a similar outcome (in terms of accuracy and
Multisensory experiences and their impact on memory performance  
Antonia Thelen

reaction times) upon the repetition of only part of the previously studied stimulus pair as in the previously studied visual discriminations tasks.

Materials and Methods

The experiment will include a visual and an auditory discrimination task, which will be presented in an alternated manner. Subjects will perform a continuous recognition task, which requires the discrimination of initial from repeated presentations of visual or auditory objects that are pseudo-randomized within independent blocks of trials. This results in alternation of visual discrimination blocks and auditory discrimination blocks (V1, A1, V2, A2, V3, and A3). The subjects will be instructed to perform as quickly and as accurately as possible. Further every target object (irrespective of whether initially presented in a unisensory or multisensory context) is repeated once throughout the duration of the block.

In the visual discrimination task, the pictures will subdivided into fourteen groups, where there are four types of initial and ten types of repeated presentations (see Figure 24).

Figure 24: Experimental design for the visual discrimination task

Upon initial presentation the stimuli are divided into unisensory (visual-only, V) and multisensory (auditory-visual, AVc, AVi and AVe) presentations. The multisensory conditions are further subdivided into three groups depending on the auditory context that is assigned to the visual objects. Two thirds of the multisensory pictures are presented with meaningful sounds, which are either congruent (AVc) or incongruent (AVi) with the depicted object. The remaining third of the multisensory stimuli are pictures that are coupled to meaningless sounds and tones (AVe).

Upon repetition half of the stimuli that are presented in a visual-only manner (V) during the initial presentation are presented in the same unisensory manner (V-). The other half of these pictures are presented in a multisensory manner, were one third is presented with a congruent meaningful sound (AV-c), a third is presented with an incongruent meaningful sound (AV-i) and the remaining third is presented with a meaningless sound or tone (AV-e). The pictures that are

<table>
<thead>
<tr>
<th>Block design</th>
<th>Initial</th>
<th>Trigger</th>
<th>Repeated</th>
<th>Trigger</th>
</tr>
</thead>
<tbody>
<tr>
<td>VISUAL</td>
<td>V</td>
<td>1 V-</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>AV-c</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>AV-i</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>AV-e</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AVc</td>
<td>2 V+c</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>AV+c</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AVi</td>
<td>3 V+i</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>AV+i</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td></td>
<td>AVe</td>
<td>4 V+e</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>AV+e</td>
<td>14</td>
<td></td>
</tr>
</tbody>
</table>
Multisensory experiences and their impact on memory performance

Antonia Thelen

presented in a multisensory manner during the initial presentation (AVc, AVi, AVe), when repeated can either be presented in a unisensory, visual-only (V+c, V+I, V+e) in half of the repetition conditions, or a multisensory manner (AV+c, AV+i, AV+e), where they are repeated in the same context as during the first encounter (see Figure 25).

Figure 25: Experimental design for the auditory discrimination task

<table>
<thead>
<tr>
<th>Block design</th>
<th>Trigger</th>
<th>Repeated</th>
<th>Trigger</th>
</tr>
</thead>
<tbody>
<tr>
<td>As</td>
<td>A-s</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>VAs-c</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>VAs-i</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>VAs-e</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Ae</td>
<td>A-e</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>V Ae-image</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>V Ae-scrambled</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>VAc</td>
<td>A+c</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td></td>
<td>VA+c</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>V Ai</td>
<td>A+i</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td></td>
<td>VA+i</td>
<td>16</td>
<td></td>
</tr>
<tr>
<td>VAe</td>
<td>A+e</td>
<td>17</td>
<td></td>
</tr>
<tr>
<td></td>
<td>VA+e</td>
<td>18</td>
<td></td>
</tr>
</tbody>
</table>

The blocks for the auditory discrimination task, will be constructed as follows. Initial presentation of sounds and tones will be divided into 5 conditions, two unisensory and three multisensory presentation contexts. The first group of initial presentations is composed of unisensory stimuli that are divided into meaningful (As) and meaningless (Ae) auditory stimuli. The other group contains stimuli that are presented in a multisensory manner upon initial presentation. Two thirds of these multisensory stimulus pairs are either congruent (VAc) or incongruent (VAi) pairs of meaningful sounds coupled to visual objects. The remaining third of initial multisensory stimuli is composed by meaningful auditory sounds that are coupled to scrambled meaningless images (VAe).

Upon repetition half of the meaningful sounds (As) are presented in a unisensory manner (A-s), while the remaining half is subdivided into three distinct multisensory groups. The first will include congruent auditory-visual stimulus pairs (VAs-c), the second incongruent pairs (VAs-i) and the third will be composed be meaningful auditory sounds coupled to meaningless (scrambled) images (VAs-e). The stimuli of the Ae group will be divided into three groups upon repetition. Half of the meaningless sounds will be repeated in a unisensory manner (A-e), while the remaining half will be subdivided into two groups of presentations. The first will be composed of meaningless sounds coupled to visual objects (VAe-image) and the second will be composed of meaningless sounds coupled to meaningless visual stimuli (VAe-scrambled).

When repeated the initially multisensory stimuli are repeated in half of their repetitions in a unisensory manner (A+c, A+i, A+e). The other half of the repeated presentations is coupled to
the same visual object as during the initial presentation condition (VA+c, VA+I, VA+e).

**Hypotheses**

From this manipulation we anticipate several possible outcomes. For the visual discrimination task, we expect that we will be able to replicate our previous findings (Murray et al., 2004; Murray et al., 2005; Lehmann & Murray, 2005). In other words, we expect to find that performance in terms of accurate discrimination (1) will be enhanced for those pictures that have been encountered in a congruent multisensory context, (2) will be unaffected for those stimuli that have been previously encountered either in a unisensory manner or coupled to an incongruent meaningful sound, and (3) will be impaired for those images that had been coupled to a meaningless sound during the initial encounter.

For images that are presented in a multisensory context upon repetition several possible outcomes can be imagined. First, representing the visual objects in the same multisensory context as during the initial encounter could improve their accurate discrimination. This would lead to the conclusion that the observed enhancement is due to the additional activation of object representation through the redundant sensory modality. For images that had been experienced in a unisensory context during initial presentation three possible outcomes can be hypothesized. The first there is the possibility that we observe an enhancement of correct discrimination due to a similar mechanism as mentioned above. The redundant sensory cue could thus enhance the accessibility to the perceptual/memory trace. Second, the opposite effect could be observed, were the auditory stimulus could perturb the access to the previously established visual memory trace.

In the case of the auditory discrimination task, the outcome of the manipulations is not as straightforward. Taking into account the before mentioned study focusing on auditory perceptual learning (von Kriegstein & Giraud, 2006), we can hypothesize that auditory stimuli that had been coupled to congruent meaningful visual images during the initial encounter, could be discriminated in a more accurate manner upon repetition, compared to those auditory stimuli that had been coupled to meaningful incongruent or meaningless scrambled images.
References


Multisensory experiences and their impact on memory performance

Antonia Thelen


Multisensory experiences and their impact on memory performance

Antonia Thelen


51
Multisensory experiences and their impact on memory performance

Antonia Thelen


Multisensory experiences and their impact on memory performance

Antonia Thelen


Multisensory experiences and their impact on memory performance


