International Multisensory Research Forum

3rd Annual Meeting

24th-26th May 2002, Geneva, Switzerland

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3rd Annual Meeting
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- The committee would also like to extend its gratitude to Anne Deriaz for her assistance with the conferences, to Xavier Ciana for his help with the conference website, and to the staff of the Hotel Chavannes-de-Bogis for their help and patience with the meeting's organization.

- 3rd Annual Meeting website: http://www.hcuge.ch/~infotec/imrf
- IMRF website: www.wfubmc.edu/nba/imrf

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3rd Annual Meeting

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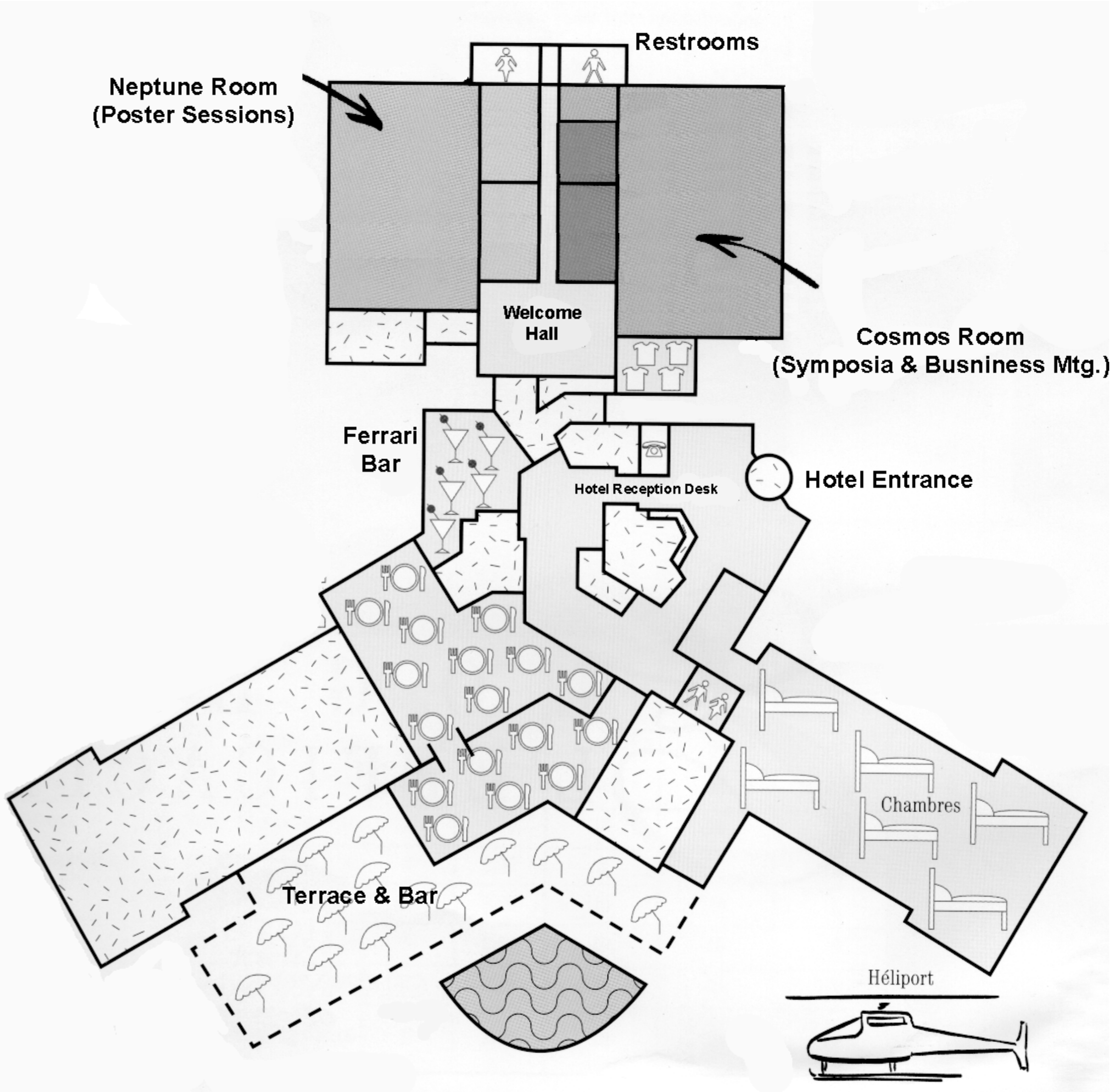

The symposia and business meeting will be held in the Cosmos Room.

The poster sessions will be held in the Neptune Room.

Coffee breaks will be held in the Welcome Hall.

International Multisensory Research Forum
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Scientific Program

Friday, May 24th	
6:00-7:00pm	IMRF Business Meeting
7:00pm onwards	Informal reception, registration, & materials pick-up
Saturday, May 25th	
8:00am onwards	Pick-up of conference materials
8:15am	Welcoming remarks
8:30 - 10:30am	Symposium 1: Defining Multisensory Regions & Pathways *Chaired by Charles Schroeder, The Nathan Kline Institute, USA* <u>*Speakers:*</u> Alex Meredith, *Virginia Commonwealth University, USA* Frank Bremmer, *Philipps University Marburg, Germany* Troy Hackett, *Vanderbilt University, USA* Kathleen Rockland, *RIKEN Brain Science Institute, Japan* Stephanie Clarke, *Division de Neuropsychologie, CHUV, Switzerland* Sara Gonzalez, *University Hospital Geneva, Switzerland*
10:30 - 11:00am	Coffee/tea break
11:00 - 1:00pm	Symposium 2: Temporal & Spatial Aspects of Multisensory Interactions *Chaired by Charles Spence, Oxford University, England* <u>*Speakers:*</u> John Foxe, *The Nathan Kline Institute, USA* Bernd Lutkenhoner, *University of Munster, Germany* Adele Diederich, *International University Bremen, Germany* Ariane Fiesser, *Max Planck Inst. for Brain Research Frankfurt, Germany* Norimichi Kitagawa, *Tokyo Metropolitan University, Japan* Francis McGlone, *University of Wales & Unilever Research, Wales*

Saturday, May 25th (continued)	
1:00 - 2:30pm	Lunch (included with registration fees)
2:30 - 4:30pm	Symposium 3: Multisensory Facilitation, Illusions, & Conflict *Chaired by Alain Berthoz, College de France, France* *Speakers:* Lawrence Marks, *Yale University, USA* Ladan Shams, *California Institute of Technology, USA* Krish Sathian, *Emory University Medical Center, USA* Thomas Brandt, *Ludwig-Maximilians-University, Munich, Germany* Salvador Soto-Faraco, *University of Barcelona, Spain* Paul Bertelson, *Universite libre de Bruxelles, Belgium*
4:30 - 6:30pm	Poster session & coffee/tea break
6:30 - 7:30pm	Keynote address: Prof. Jon Driver, *University College London, England* "Crossmodal Space & Crossmodal Attention"
8:30pm onwards	Banquet dinner (included with registration fees)
Sunday, May 26th	
9:00 - 11:00am	Symposium 4: Development, Plasticity, & Maintenance of Multisensory Systems *Chaired by Mark Wallace, Wake Forest University, USA* *Speakers:* Atsushi Iriki, *Tokyo Medical and Dental University, Japan* Edouard Gentaz, *Universite Rene-Descartes, France* Francesco Pavani, *University College London, England* John Jeka, *University of Maryland College Park, Maryland* Thomas Anastasio, *University of Illinois at Urbana/Champaign, USA* *David Lewkowicz,* New York State Institute for Basic Research, USA
11:00 - 11:30am	Coffee/tea break

Sunday, May 26th (continued)	
11:30 - 12:30pm	Graduate Students Symposium *Chaired by Micah Murray, University Hospital Geneva, Switzerland* *Speakers:* Marie Avillac, *Institut des Sciences Cognitive, CNRS Bron, France* Donna Lloyd, *Oxford University, England* Sophie Molholm, *The Nathan Kline Institute, USA* Sharon Morein-Zamir, *University of British Columbia, Canada* Gilles Pourtois, *Tilburg University, The Netherlands* Oliver Stock, *Philipps University Marburg, Germany*
12:30 - 2:00pm	Lunch (included with registration fees)
2:00-4:00pm	Symposium 5: Neurological & Clinical Multisensory Manifestations *Chaired by Theodor Landis, University Hospital Geneva, Switzerland* *Speakers:* Alessandro Farne, *Universita degli Studi di Bologna, Italy* Peter Brugger, *University Hospital Zurich, Switzerland* Olaf Blanke, *University Hospital Geneva, Switzerland* Yves Rossetti, *INSERM Bron, France* Angelo Maravita, *University College London, England* Christina Krause, *Helsinki University of Technology, Finland*
4:00-6:00pm	Poster session & coffee/tea break
6:00 - 7:00pm	Keynote address: Prof. Jean-René Duhamel *Institut des Sciences Cognitives, CNRS, France* “The Construction of Multisensory Space in the Primate Parietal Cortex”
7:00 - 8:00pm	Conference summary & roundtable discussion between symposia chairs *Moderated by Christoph Michel, University Hospital Geneva, Switzerland*
8:00 – 8:15pm	Concluding remarks
8:30pm onwards	Banquet dinner (included with registration fees)

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Keynote Addresses' Abstracts

Professor Jon Driver, *University College London, England*
"Crossmodal Space & Crossmodal Attention"

A number of behavioral studies in humans have now shown interactions between different modalities in relation to spatial attention, for both endogenous and exogenous cases. I briefly review some of this work, and then turn to ERP and fMRI studies on the neural basis of such effects. These show that crossmodal spatial interactions for attention can affect not only multimodal structures, but also structures or components conventionally considered to be 'unimodal'. In addition to feedforward convergence towards multimodal structures, feedback from such areas to unimodal brain areas may also play a critical role.

I then turn to consider two further issues: the spatial nature of such effects, and the 'control' processes that may produce them. On the first issue, manipulations of posture demonstrate that many crossmodal effects depend on the spatial alignment of multimodal stimuli in external space. On the second issue, recent studies suggest that preparatory shifts of spatial attention, or re-orienting following an event at an unexpected location, may both involve common brain areas across different modalities.

The combination of behavioral, fMRI and ERP studies is beginning to reveal the architecture of crossmodal spatial representation and crossmodal attention.

Professor Jean-René Duhamel, *Institut des Sciences Cognitives, CNRS, France*
"The Construction of Multisensory Space in the Primate Parietal Cortex"

The perception of our surroundings and the preparation of action both imply the capacity to use information gathered though multiple sensory channels. Single-unit recording studies in non-human primates, sometimes in association with mathematical models of the activity of large neuronal populations, have been used to gain a better understanding of the neural substrate of a multimodal representation of space. Two complex problems are at the core of this effort: (1) How does the brain combine sensory inputs that are congruent in space but characterized by divergent encoding formats? (2) How are multiple, simultaneous and at times unreliable stimuli correctly assigned to a common source in the environment? Neurons in different cortical and subcortical structures have spatially limited response fields in several sensory modalities. In the posterior parietal cortex, neurons encode locations in a variety of egocentric reference frames, and their activity is modulated by postural variables such as eye and head position. Computational approaches implementing such properties within a multisensory neural network provide a common theoretical framework to account for both multidirectional coordinate transformations and optimal integration of sensory information across sensory modalities. However, more experimental work is necessary to clarify how such integration is accomplished within the cortex and how these elementary mechanisms relate to psychophysiology of crossmodal interactions.

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Symposium 1:Defining Multisensory Regions & Pathways
Chaired by Charles Schroeder, The Nathan Kline Institute, NY

CORTICAL CONNECTIVITY UNDERLYING INHIBITORY CROSS-MODAL CONVERGENCE

M. Alex Meredith

Department of Anatomy and Neurobiology,
Virginia Commonwealth University School of Medicine, Richmond, VA, USA

For multisensory behavioral and perceptual effects to occur, information from the different sensory modalities must converge onto individual neurons. The most obvious and well known form of multisensory neuron is one which receives excitatory inputs from more than one sensory modality. These neurons respond with excitation to either modality input alone, (usually) integrate the resultant activity when the two modalities are combined, and have been well documented throughout the neuroaxis and across phylogeny. However, recent studies in this laboratory suggest that multisensory convergence may occur in other, fundamentally different forms.

Tract tracing methods identified that projections occur between the auditory field in the Anterior Ectosylvian sulcus (FAES) and the fourth somatosensory (SIV) representation in the cat cortex. Standard electrophysiological recordings in SIV, however, failed to reveal the expected bimodal neurons, suggesting that the auditory inputs from FAES to SIV must either be subthreshold, or inhibitory. These alternatives were tested in chronically prepared, anesthetized cats. Extracellular recordings were made from SIV neurons in response to electrical stimulation of FAES through indwelling electrodes. Orthodromic activation from FAES was not observed in any SIV neuron. Next, repeatable tactile stimulation (modified Ling vibrator) within the somatosensory receptive field and electrical stimulation of auditory FAES were presented alone and in combination in an interleaved fashion. Of the SIV neurons tested, approximately 70% showed a significant reduction in response to a tactile cue when FAES was stimulated, while only 6% showed an increased discharge. Stimulation using control electrodes located in the adjacent auditory area AI yielded no significant SIV response changes; neurons in the adjacent second somatosensory area (SII) were unaffected by FAES stimulation. Furthermore, the suppressive effect of FAES stimulation on SIV neurons was blocked by the application of the GABA-A antagonist, bicuculline methiodide (100 uM).

These data indicate that the cross-modal projection from auditory FAES to somatosensory SIV corresponds to a feedback-type projection. The lack of orthodromic (excitatory) input from FAES to SIV, the suppressive effect of FAES stimulation on a large proportion of SIV responses to tactile stimulation, and the sensitivity of the effect to bicuculline are consistent with the idea that the functional connection between the two regions is inhibitory results in suppression. Thus, multisensory convergence not only occurs in the well known excitatory-excitatory arrangement that leads to integration, but also in an excitatory-inhibitory format that may underlie more subtle forms of cross-modal modulation. Supported by NIH NS 39460 and by the Human Frontiers Science Program.

POLYMODAL SPACE REPRESENTATION IN PRIMATE AREA VIP

Frank Bremmer

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Keywords: *Monkey; Human; Intraparietal; Craniocentric; Self-motion*

The neural circuits underlying normal spatial vision and attentive sensorimotor behavior of primates have been most intensively studied in macaque monkeys. Both electrophysiological and anatomical studies have highlighted the importance of the posterior parietal cortex for the integration of neural signals from different sensory modalities and its use for guiding and controlling action in space. In the monkey, a highly modular structural and functional specialization has been demonstrated within this part of the brain. One such functionally specialized area is the ventral intraparietal area (VIP) located in the fundus of the intraparietal sulcus (IPS). I will review recent studies demonstrating that area VIP contains many neurons which show polymodal directionally selective discharges. A considerable proportion of these neurons encode this polymodal information in a common, probably head-centered, frame of reference. Furthermore, direct anatomical connections between area VIP and an area within the ventral premotor cortex (PMv), which subserves head movements, have been reported recently. Although many specific human behaviors necessitate the convergence and integration of information conveyed through anatomically distinct sensory pathways, to date little is known about polymodal motion information processing and integration in humans. To test for equivalencies between macaque and human polymodal motion processing, we used functional MRI in normals while presenting moving visual, tactile, or auditory stimuli. Increased neural activity evoked by all three stimulus modalities was found in the depth of the intraparietal sulcus (IPS), ventral premotor, and lateral inferior post-central cortex. The observed activations strongly suggest that polymodal motion processing in humans and monkeys is supported by equivalent areas. The activations in the depth of IPS imply that this area constitutes the human equivalent of macaque area VIP.

Supported by DFG (SFB 509/B7) and HFSP (RG0149/1999-B)

MULTISENSORY CONVERGENCE IN MACAQUE AUDITORY CORTEX & ITS RELATIONSHIP TO THE ANATOMICAL ORGANIZATION & BEHAVIORAL FUNCTIONS OF THE AUDITORY SYSTEM

Troy A. Hackett[1], Kai-Ming Fu[2], Taylor A. Johnston[2], Ankoor S. Shah[2], Laurie Arnold[3], John Smiley[2], Preston E. Garraghty[3], Charles E. Schroeder[2]

[1]Dept. of Hearing & Speech Sciences, Vanderbilt Univ. School of Medicine, Nashville, TN
[2]Cogn. Neurosci. Prog., Nathan Kline Inst. & Neurosci. Dept., Albert Einstein Coll. Med., NY
[3]Psychology Dept., Indiana University, Bloomington, IN

keywords: *Auditory, Somatosensory, Primate, Bimodal, Sensory, Cortex*

Current models of auditory cortical organization in primates include a central core region of two to three areas with characteristics of primary cortex, surrounded by belt and parabelt regions containing multiple nonprimary areas. The core, belt, and parabelt regions represent successive hierarchical stages of processing, while subdivisions of each region appear to process at least some inputs in parallel (Hackett et al., 1998). The caudal belt and parabelt areas are preferentially connected with areas in lateral intraparietal and prefrontal cortex associated with the processing of spatial related information, whereas the rostral belt and parabelt areas have stronger connections with ventral and orbital prefrontal domains associated with the processing of nonspatial information. Compared to neurons in the rostral belt areas, neurons in the caudal belt fields have greater spatial selectivity for complex sounds, including species-specific vocalizations. By comparison, neurons in the rostral belt areas exhibit reduced spatial selectivity and are more selective for the type of call (Tian et al., 2001). These findings support the hypothesis that cortical processing of spatial and nonspatial auditory information is performed in specialized streams (Rauschecker & Tian, 2000). The propensity for spatial processing in caudal superior temporal cortex is consistent with growing evidence of auditory and somatic sensory convergence in the temporoparietal region of the primate brain. In addition to connections with caudal belt and parabelt areas of auditory cortex, the temporoparietal area (Tpt) has connections with the superior temporal sulcus, lateral intraparietal cortex, caudal prefrontal cortex, and thalamic nuclei with multimodal inputs (e.g., suprageniculate, limitans, and pulvinar nuclei). Neurons responsive to auditory and somatic or visual inputs were found in Tpt by Leinonen et al (1980), but the multimodal properties of this region had not been explored further until recently. Schroeder et al (2001) sampled multi-unit and current source density profiles in the core area, AI, and a caudal belt area adjacent to AI, known as CM (caudomedial area). Only sites in CM were found to be responsive to both auditory and somesthetic stimulation. In a subsequent study (Fu et al, 2002) single- and multi-unit recordings from AI and CM revealed that single neurons in CM were responsive to both auditory and cutaneous stimulation. These neurons were responsive to pure tone acoustic stimuli, but more broadly tuned than neurons in AI. Cutaneous receptive fields were also broad, often bilateral, and included areas on dorsal hand surfaces, but appeared biased toward a representation of the face, head and neck. CM is known to receive auditory cortical inputs from the core region, especially AI, and is considered to lie in the second tier of the auditory processing hierarchy. Subcortical auditory inputs primarily arise from the dorsal (nonprimary) divisions of the medial geniculate complex. Other inputs to CM include LIP of the posterior parietal cortex (Lewis & Van Essen, 2000) and the magnocellular division of the medial geniculate complex, both of which may be sources of somatic sensory input to CM. The somatic representation in CM is unexpected, given its position at an early stage of auditory cortical processing, but the bias of the somatic input toward the head and neck is consistent with its integration into the proposed stimulus localization (spatial) functions of the caudal auditory cortices. The demonstration of multisensory convergence in CM challenges the view that such processing occurs only in “higher-order” cortical domains.

MULTIMODAL CONVERGENCE IN CALCARINE VISUAL AREAS IN MACAQUE MONKEY

Kathleen S. Rockland and Hisayuki Ojima

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keywords: *Area V1, Area V2, Layer 1, Peripheral vision*

Multimodal convergent inputs and interactions are well-documented in association cortical areas, such as parts of the cingulate cortex, parahippocampal gyrus, or superior temporal sulcus in monkeys. Recently, however, we have found evidence for direct connections to areas V1 and V2 from auditory (Rockland and Ojima, SFN 2001) and parietal (Rockland, SFN 2000) related areas. Connections were demonstrated by injections of anterograde tracer in auditory belt areas (n=3), or in different parts of areas 5, 7a, and 7b (n=5). The auditory injections resulted in projections to V1, in the upper bank of the calcarine fissure (peripheral lower visual field representation). These were primarily in the anteriormost 3.0mm. The parietal projections were widely distributed, with less of a bias for the upper bank. Terminations were in layers 1 and/or 6, and were very divergent (1.0-4.0mm), although sparse. These could be considered "feedback" connections, but other interpretations are possible. Both auditory and parietal areas also projected to dorsal area V2 in the calcarine fissure (peripheral lower visual field). Projections to V2 were denser than those to V1, but less divergent. They were mainly in layer 1, but extended through other layers as well. Retrogradely labeled neurons occurred in layers 3 and 5 of V2, but were not observed in V1. Possible functional roles include vestibular, spatial, or attentional processes. Also relevant is psychophysical evidence for illusory visual motion induced by sound (Shams et al., SFN 2001).

PARALLEL PATHWAYS IN HUMAN VISION AND AUDITION

Stephanie Clarke

Division de Neuropsychologie, CHUV, Lausanne, Switzerland

The human visual and auditory cortex presents several characteristics that are compatible with parallel and hierarchical processing. Chemoarchitectonic and tracing studies revealed that the primary sensory areas are surrounded by several other areas, both in the visual (Clarke and Miklossy 1990; Clarke 1994) and auditory modality (Rivier and Clarke 1997) with a putatively hierarchical organisation (Mesulam and Geula 1994; Hustler and Gazzaniga 1996; Rivier and Clarke 1997). In the primary visual cortex intraareal compartments were identified anatomically in non-human primates (Horton and Hubel 1981) and in man (e. g. Clarke 1994). In the auditory domain, human, but not non-human primate primary area was shown to contain intraareal compartments which can be visualised with cytochrome oxidase histochemistry (Clarke and Rivier 1998). Furthermore, patterns of human cortico-cortical connectivity strongly support parallel processing (Di Virgilio and Clarke 1997; Tardif and Clarke 2001).

Parallel processing is generally believed to play a major role in vision but not in audition. Our recent evidence suggests otherwise.

A sound in natural setting conveys information about the identity of the sound source and about its location. Activation studies with fMRI in normal subjects suggest that the two aspects are processed independently within anatomically distinct pathways (Maeder et al. 2001). Lesions of either of these networks were shown to result in selective deficits of sound recognition or sound localisation (Clarke et al. 2000). Attending to meaningful auditory events in natural setting involves several aptitudes, including auditory spatial attention. Auditory hemineglect, most often concerning left hemispace following right hemispheric lesions, is most commonly diagnosed by the failure to report stimuli presented to the left ear in tasks of dichotic listening. Our recent observations indicate that there are two behaviourally and anatomically distinct types of auditory neglect: i) a deficit in allocation of auditory spatial attention following lesions centred on basal ganglia; and ii) distortion of auditory spatial representation following fronto-temporo-parietal lesions (Bellmann et al. 2001).

SPATIAL AND TEMPORAL ASPECTS OF VISUO MOTOR INTEGRATION STUDIED WITH DISTRIBUTED INVERSE SOLUTIONS

Sara L. Andino Gonzalez, Gregor Thut, Christoph M. Michel, Rolando Grave de Peralta Menendez

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Keywords: *Linear inverse solutions (LAURA), Poffenberger task, visuo-motor integration, time frequency analysis, neuroelectromagnetic inverse problem*

A more comprehensive neuroimaging is essentially linked to the analysis of the fine temporal information available only in electrophysiological techniques (EEG, MEG, ERP). However, these techniques describe neurophysiological processes at the scalp level and possess limited localization value. Here, we present tomographic images of the functioning human brain obtained by solving the electromagnetic inverse problem combining linear distributed models and biophysical constraints. This solution (LAURA, Grave de Peralta et al., 2001) raises the number of sources that can be retrieved with zero localization error without any assumptions about their number and positions (up to 50% from previous 22%). The achieved spatial and temporal resolution permits the dynamic exploration of sensory and cognitive processes. In contrast to hemodynamic techniques, electrically reconstructed tomographic images are directly linked to neuronal processes. Because of their high temporal resolution, these images allow the extraction of information about the short-lived neuronal networks functioning on specific frequency bands and subserving cognitive and sensory events.

Here we present the results of a study aimed at characterizing the spectral and temporal features of visuo-motor integration in a set of normal subjects performing the Poffenberger task. The analysis is performed on the individuals' single trials so as to view spectral features over all frequency bands that might otherwise be obscured by classical averaging procedures. The analysis applies the inverse solution (LAURA) to the single trials and the subsequent analysis of the estimated waveshapes at nodes selected as belonging to specific regions of interest according to the Tailairach atlas. A time-frequency decomposition (complex wavelet) is applied to the estimates at such nodes and the temporal evolution of the energy at the classical frequency bands is obtained, permitting statistical comparisons across conditions and subjects. Such analysis allows us to shed light on the role played by brain oscillations in multisensory interactions. A consistent result over subjects is the presence of statistically significant differences in the alpha and gamma band energy between slower and faster reaction times at the motor area contralateral to hand response execution. An earlier gamma peak at the motor area generally coincident with a gamma burst at the responding visual area is characteristic of the fastest responses. In general, a gamma bursting increase is accompanied by alpha bursting reduction in both scalp and estimated intracranial signals, contradicting the hypothesis that gamma band oscillations are simply harmonics of alpha band.

Grave de Peralta et al. *Brain Topography*. Vol. 14, No 2. Winter 2001, pp 131-137.

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Symposium 2: Temporal & Spatial Aspects of Multisensory Interactions
Chaired by Charles Spence, Oxford University, England

THE CASE FOR EARLY FEEDFORWARD INTEGRATION OF MULTISENSORY INPUTS

John J. Foxe

The Cognitive Neurophysiology Laboratory
The Nathan Kline Institute for Psychiatric Research

A widely held view in the field of multisensory science is that sensory information from a single object (e.g. a barking dog) is first processed extensively through the respective unisensory processing streams before the information is combined in higher-order multisensory regions of cortex. Under this view, multisensory modulations which have recently been found in early sensory cortices during hemodynamic imaging studies have been interpreted as reflecting feedback modulations that occur subsequent to multisensory processing in the higher-order areas. Of course, hemodynamic imaging cannot address the relative timing of such activations. In this talk, I will focus on recent evidence from both human and monkey electrophysiological investigations as well as hemodynamic imaging studies that challenge an exclusively feedback model. Specifically, these studies show that multisensory integration effects are seen at very early latencies relative to the well-established timecourse of sensory activation within the respective unisensory processing streams. In fact, intracranial recordings show that multisensory inputs found in early sensory cortices display a characteristic feedforward pattern of inputs. For many years, it was believed that there were no direct anatomic connections between early sensory cortices of the different sensory modalities but recent anatomic tracer studies have begun to uncover direct connections between early visual and auditory sensory regions, providing the necessary anatomic substrate for such early interactions. In light of these recent findings, it is becoming evident that models of multisensory cortical processing will need to incorporate early feedforward integration mechanisms as well as feedback. These data highlight the tremendous potential of "multimodality" imaging, whereby data from the macrospcopic noninvasive level (fMRI and high-density scalp recordings in humans) are integrated with equivalent data from the more microscopic/cellular level, which we record intracranially in non-human primates.

MAGNETOENCEPHALOGRAPHIC CORRELATES OF AUDIOTACTILE INTERACTION

Bernd Lütkenhöner[1], Christian Lammertmann[1], Cristina Simões[2], and Riitta Hari[2]

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[2] Brain Research Unit, Low Temperature Laboratory,
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Keywords: *Audiotactile Interaction; Secondary Somatosensory cortex; Auditory Cortex; Time course of Interaction; Inhibition*

To seek for correlates of an interaction between auditory and somatosensory processing, the brain's magnetic field in response to simultaneously presented auditory and tactile stimuli (AT) was compared with the sum of the respective unimodal responses (A+T). The stimuli were binaural 1047-Hz tonebursts of 60 dB sensation level and tactile pressure pulses to the right thumb. The mean interval between two stimuli of the same modality was 1.95 s. The magnetic field was recorded using a 306-channel whole-scalp neuromagnetometer. A clear audiotactile interaction was revealed in the hemisphere contralateral to the side of tactile stimulation in six of eight subjects, whereas in the ipsilateral hemisphere an interaction was noticed in only three subjects. The time courses of these audiotactile interaction fields typically showed major deflections of opposite polarities around 140 and 220 ms. The first deflection appeared to arise in the region of the secondary somatosensory cortex (SII). The polarity of this interaction was consistent with the view that the auditory stimulus resulted in a partial inhibition in SII. In two subjects, strong indications were available of auditory contributions to the interaction, although in different hemispheres. The relatively high interindividual variability of the observed interaction, which represents potential neural substrates for multisensory integration, could indicate that the way subjects perceive the simultaneous presentation of auditory and tactile stimuli differs.

MODELING THE TIME COURSE OF VISUAL-TACTILE SPATIAL INTERACTION

Adele Diederich[1] and Hans Colonius [2]

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[2]Department of Psychology, Oldenburg University, Germany

Keywords: visual-somatosensory interaction, saccadic reaction time, two-stage model

Presenting an auditory stimulus in close spatio-temporal relation to a visual target stimulus has been shown to influence saccadic reaction time (SRT) to a visual target even if participants are instructed to ignore the auditory accessory (focused-attention task). Here we investigate whether a tactile stimulus has a similar bisensory interaction effect. A visual target (LED) and a tactile accessory stimulus (vibrator applied to palm) were presented at 20° or 70° eccentricity ipsi- and contralaterally at different stimulus onset asynchronies (tactile stimulus 100 ms, 50 ms, 0 ms before visual, or 50 ms after visual stimulus). Average visual-tactile SRT was up to 80 ms shorter than unimodal (visual) SRT. Specifically, average bimodal SRT was shorter for ipsi- than for contralateral presentation, and shorter for 20° than for 70° eccentricity. SRT facilitation decreased with SOA: response to the visual target was faster the earlier the accessory was presented.

The two-stage model for multisensory interaction (Colonius & Arndt, 2001) distinguishes a peripheral parallel processing stage from a more central decision stage where interaction occurs. Probability of interaction depends on the outcome of the first stage contingent upon unisensory stimulus properties only, while the amount and direction of interaction (facilitation/inhibition) is a function of the spatial configuration of stimuli. A parametric version of the two-stage model gave a satisfactory fit for individual data from 6 subjects. We conclude (1) that presentation of a tactile accessory stimulus has a facilitating effect on SRT to a visual target depending both on the spatial and temporal configuration, and (2) that these effects can be described by the two-stage model.

References

Colonius, H., & Arndt, P. (2001). A two-stage model for visual-auditory interaction in saccadic latencies. Perception & Psychophysics, 63, 126-147.

Diederich, A., Colonius, H., Bockhorst, D., & Tabeling, S. (submitted). Visual-tactile spatial interaction in generating saccadic responses.

SPATIAL INTEGRATION OF AUDIO-VISUAL STIMULATION IN RETINOTOPIC AREAS MEASURED WITH FMRI

Ariane Fiesser, Marcus J. Naumer, Wolf Singer, and Lars Muckli

Max Planck Institute for Brain Research, Frankfurt/M., Germany

Keywords: *audio-visual, spatial representation, crossmodal localization, visual cortex, retinotopic mapping*

We studied the effects of spatially congruent and incongruent audio-visual stimulation on the activity in human visual cortex using functional magnetic resonance imaging (fMRI). Auditory stimulation that fitted one of four locations in space was jointly presented with either a relevant matching visual cue (congruent), a spatially matching but semantically inconsistent visual cue (low incongruity), or a spatially non-matching visual cue (high incongruity). A control experiment with equally relevant visual cues at each of the four spatial locations was designed in order to investigate the direct effect of the auditory stimulation on activity in visual cortex. Data were obtained from seven subjects. Each subject performed two runs for retinotopic mapping (polar angle, eccentricity) and three experiments with audio-visual stimulation. Subjects were instructed to decide about the spatial congruity of the auditory (barking) and visual (barking dog) stimulus by pressing a button. Cortex based fMRI analysis was performed using BrainVoyager 4.6.

Careful positioning of stimuli allowed us to analyze the cortical response to each position separately. Retinotopic mapping of early visual areas confirmed that activity was found for each visual stimulus along the cortical representations of the horizontal meridian in V1 and at the borders of V2/V3. For each cortical representation of a stimulus, the change of MR-signal was analyzed. We were not able to find a direct effect of auditory stimulation on the activity in visual cortex (control experiment). We found higher activity for the incongruent conditions compared to the congruent conditions.

To explain our data we postulate a recurrent feedback process that signals mismatch. According to this model, the feed-forward process of perception is interrupted at multisensory stages of the brain as soon as spatial (or semantic) incongruity is detected between the modalities. This may lead to a redirection of spatial attention to relevant locations in space. In cases of low incongruity, auditory cues are attributed to the spatially congruent visual distractor instead of the semantically better matching, but spatially displaced visual stimulus.

ADAPTATION TO VISUAL MOTION-IN-DEPTH PRODUCES AN AUDITORY AFTEREFFECT

Norimichi Kitagawa and Shigeru Ichihara

Department of Psychology, Tokyo Metropolitan University

Keywords: cross-modal aftereffect, adaptation, auditory, visual, motion-in-depth

It has been implicitly assumed that motion aftereffects reflect fairly low-level neural processing and that they do not occur across sensory modalities. In this study, we report that an auditory aftereffect occurs from adaptation to visual motion in depth. After a few minutes of viewing a square moving in depth (size-changing or retinal-disparity-changing), a steady sound was perceived as changing loudness in the opposite direction. Adaptation to a combination of auditory and visual stimuli changing in a compatible direction increased the aftereffect and the effect of visual adaptation almost disappeared when the directions were opposite. On the other hand, listening to a sound changing in intensity did not affect the visual changing-size aftereffect. The visual effect on the auditory aftereffect was also observed when the test sound was presented to left ear only. However, when the adapting sound was also presented to left ear only, the visual effect disappeared. The results provide psychophysical evidence that, for processing of motion in depth, the auditory system responds to both auditory and visual motion in depth.

MIRRORS AND MIRROR CELLS IN MULTISENSORY PERCEPTION: VISUO-TACTILE AND VISUO-MOTOR INTERACTION AND INTEGRATION

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Keywords: *Visuo-tactile facilitation, learning, mirrors*

Vision of a body site, without proprioceptive orienting of eye and head to that body site, can facilitate tactile perception, when that body site viewed is the hand (which can be seen directly under normal viewing conditions) (Tipper et al., 1998). Subsequent research has shown (i) that vision similarly affects tactile perception at body sites that cannot normally be viewed directly, such as the face or neck (ii) prior experience e.g., with mirrors, influences such visuo-tactile links, and (iii) there is a temporal window within which such visual information can affect tactile target detection.

One explanation for the visuo-tactile effect observed is that a form of visuo-tactile spatial transfer occurs, whereby the subject perceives themselves within the spatial frame of reference of the observed individual. The discovery of mirror neurons (Rizzolatti et al., 1996), cells that respond both during performance of an action and during passive observation of another performing that same action, may support this interpretation. Since their discovery, their function has been speculated to include learning, motor control and empathy to theory of mind and language. The potential importance of the action-observation system in visuo-motor and visuo-tactile transfer will be discussed in the context of this work.

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AUDITORY-VISUAL INTERACTIONS IN SENSORY DISCRIMINATION

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keywords: hearing, vision, interactions, discrimination

Methods of speeded classification have revealed systematic and pervasive cross-modal interactions, especially between hearing and vision (e.g., L. E. Marks, J. Exper. Psychol.: Hum. Percept. Perf., 1987, 13, 384-394; R. D. Melara, J. Exper. Psychol.: Hum. Percept. Perf., 1989, 15, 69-79). Two interactions are noteworthy. First, subjects are slower and less accurate in classifying tones that differ, for example, in frequency when a concurrent visual stimulus varies unpredictably in luminance, compared to a baseline where luminance is constant (orthogonal interference); similarly, orthogonal variation in frequency interferes with speeded classification of lights differing in luminance. And second, orthogonal combinations of frequency and luminance produce congruence effects: subjects are both slower and less accurate in classifying incongruent combinations of tones and lights (low pitch + bright, high pitch + dim) compared to congruent combinations (low + dim, high + bright). The present study asked whether analogous auditory-visual interactions characterize performance when subjects must discriminate very small differences in frequency or in luminance in the face of irrelevant stimulation in the other modality. The first set of experiments used a one-stimulus paradigm: on each trial, the subject used a confidence-rating scale to identify the relevant stimulus as low or high in pitch (or in brightness). The second set used a two-stimulus same-different paradigm: on each trial, the subject judged whether the two relevant stimuli were the same or different in pitch (or in brightness). Two main findings emerged. First, there was little evidence of orthogonal interference in either paradigm. Sensitivity, as quantified by d', was about the same when the stimuli in the irrelevant modality were constant and when they varied orthogonally. And second, congruence effects were evident in the identification judgments, though virtually absent from the same-different judgments. These findings are consistent with information-accrual and criterial models of cross-modal interaction.

VISUAL CORTEX AS A SITE OF CROSS-MODAL INTEGRATION

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Keywords: *cross-modal illusion, auditory-visual perception, multi-modal brain areas*

It has been shown that visual perception can be strongly affected by auditory stimuli. It is unclear, however, what the brain circuitry subserving these inter-actions may be. We used the sound-induced illusory flash effect (a single flash accompanied by two auditory beeps is perceived as two flashes) as a tool to investigate this question. This illusion is much stronger in the periphery than fovea. In a previous study using event-related brain potentials, we had investigated whether this illusion is due to modulation of activity in the visual pathway or a higher perceptual area, such as associative cortex. We compared the visual evoked potentials (VEPs) in the presence and absence of sound. Activity was modulated significantly already prior to 200 ms poststimulus in the illusion trials (periphery) but not in trials where no illusion occurred (fovea). In addition, the VEP associated with the illusory second flash was qualitatively very similar to the VEP associated with a physical second flash, suggesting that similar representations underlie the percept of the illusory and a physical flash. These results suggested that the observed modulation of activity by sound occurs within the visual cortex. In the present study we tried to localize the brain regions involved in the perception of the illusory flash more directly and more accurately using event-related fMRI. We collected the functional images of 3 participants in the following conditions. Unimodal conditions Vp and Vf consisted of visual stimulation: a small disk flashed once in the periphery or fovea, respectively. Bimodal conditions AVp and AVf consisted of auditory-visual stimulation: combination of 2 beeps with visual stimuli Vp and Vf, respectively. In another unimodal condition, Vp2, a physical double flash was presented in the periphery. Trials were randomized. Contrasting the (illusion) condition AVp against Vp resulted in activity in Brodmann's areas 17, 18, and 19. Contrasting (no-illusion) condition AVf versus Vf, however, did not show any activity in the occipital lobe ruling out the possible role of attention in the aforementioned enhanced visual activity. Considering that the visual stimulus was identical in AVp and Vp , the enhanced activity of early visual areas in AVp can only be attributed to the perception of the illusory flash caused by sound. Similar brain areas were indicated when contrasting Vp2 against Vp. The common brain areas involved in these two contrasts confirm our previous ERP results suggesting similar mechanism underlying the percept of a physical and an illusory flash. These results altogether indicate that the activity in the early visual cortical areas is modulated by sound.

VISUAL CORTICAL ACTIVATION DURING TACTILE FORM PERCEPTION

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***Keywords**: Mental imagery, visual cortex, tactile perception*

In a previous positron emission tomographic (PET) study in normal humans, we found that an area of extrastriate visual cortex near the parieto-occipital fissure is active during tactile discrimination of grating orientation (NeuroReport 8:3877-3881, 1997). Further, we showed that interfering with the function of this cortical area using transcranial magnetic stimulation (TMS) selectively disrupted this ability (Nature 401:587-590, 1999). Thus, visual cortical processing is necessary for optimal performance of this tactile task in normally sighted people. Whether it occurs on a top-down basis, due to visual imagery, or on a bottom-up basis, reflecting multimodal inputs, is not clear.

In the present study, we investigated whether visual cortical processing also accompanies tactile form perception. One task we used, requiring mental rotation of tactile stimuli, is a classic mental imagery task. We reasoned that finding activity in similar visual cortical regions during this and other tactile tasks would support the idea that mental imagery underlies visual cortical processing in tactile perception. We used PET scanning with $H_2^{15}O$ while stimuli were applied to the immobilized right index fingerpad. Activations were corrected for multiple comparisons within an *a priori* mask comprising all of occipital and parietal cortex. Two experiments were performed with separate groups of normal subjects.

In the first experiment, uppercase Js were applied using an electromechanical device. Subjects reported whether the J was in a normal or mirror-reversed configuration. In one condition, the angular deviation of the J from the long axis of the finger was either 0° or 30°. Compared to a control condition without tactile stimulation, this condition evoked activity in left somatosensory, parieto-occipital and temporo-occipital cortex and bilaterally in superior parietal cortex. In another condition where the angle of the stimulus was larger (90-150°), thereby inducing a greater requirement for mental rotation, no additional activation was found.

In a second experiment, uppercase letters were presented upside-down to avoid processing of linguistic symbols. An experimenter manually applied the stimuli, enabling presentation of a larger number of trials during the 90 s scan acquisition than in the first experiment. When mirror-image discrimination was contrasted between a large stimulus angle (120° or 150°) and an angle of 0°, an active focus was found in left superior parietal cortex. This is attributable to a specific effect of mental rotation that was absent in the first experiment, where the stimulus angles were not as widely separated between conditions. Compared to a task requiring detection of a gap in a bar, mental rotation recruited foci in left superior parietal and bilateral parieto-occipital cortex. Simple discrimination between two forms activated right temporo-occipital cortex, relative to a condition involving discrimination of bar orientation.

Thus, recruitment of visual cortical processing during tactile perception is not limited to grating orientation discrimination, but occurs generally during a variety of tactile tasks involving form perception as well. Moreover, areas in both dorsal and ventral visual pathways are recruited in a task-dependent manner. Spatial tasks engage dorsal areas, whereas form tasks engage ventral areas in the left or right hemisphere depending on whether recognition of linguistic symbols is involved or not. Specifically, mental rotation and discrimination of grating orientation activate similar foci in parieto-occipital cortex, suggesting not only a common basis for visual cortical processing in both cases (and perhaps other tactile tasks), but also that the common basis might be mental imagery.

VISUAL-VESTIBULAR AND VISUOVISUAL CORTICAL INTERACTION: NEW INSIGHTS FROM FMRI AND PET

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PET ad fMRI studies have revealed that excitation of the vestibular system by caloric or galvanic stimulation not only activates the parieto-insular vestibular cortex but also bilaterally deactivates the occipital visual cortex. Likewise, visual motion stimulation not only activates the visual cortex but also deactivates the parieto-insular vestibular cortex. These findings are functionally consistent with the hypothesis of an inhibitory reciprocal visual-vestibular interaction for spatial orientation and motion perception. Transcallosal visuovisual interaction between the two hemispheres was found by using half-field visual motion stimulation: activation of motion-sensitive areas hMT/V5 and deactivations of the primary visual cortex contralateral to the stimulated hemisphere. The functional significance of these inter- and intrasensory interactions could be that they (A) allow a shift of the sensorial weight between two incongruent sensory inputs and (B) ensure a correspondence of the two hemispheres during evaluation of contradictory motion stimulation of the right and left hemifields. In terms of mathematical modeling, these findings may reflect the concepts of a sensory conflict mechanism or a mismatch between expected and actual sensory input.

PERCEPTUAL INTEGRATION OF DYNAMIC INFORMATION ACROSS SENSORY MODALITIES

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Keywords: *Motion perception; Apparent motion; Multisensory conflict*

Multisensory integration is often demonstrated through the behavioral consequences of intersensory conflict. For example, in the classical ventriloquist illusion, the perceived location of a sound is often heard as coming from near the position of a concurrent visual event, even if they originated from different locations. Here, we study the phenomenon of crossmodal dynamic capture, by which the perceived direction of a moving sound source can be reversed when concurrent visual motion is seen in the opposite direction. As has been the case in the ventriloquism literature until recently, the contribution of perceptual and higher level (cognitive) factors to the dynamic capture illusion has not been determined. In the present study, we addressed the perceptual nature of crossmodal dynamic capture using the method of psychophysical staircases. The results indicate that crossmodal dynamic capture is a perceptual phenomenon that depends critically on the experience of motion, and in which auditory motion is biased as a function of visual information but not vice versa.

THE VENTRILOQUIST EFFECT:
A CASE OF CROSSMODAL PERCEPTUAL GROUPING

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The ventriloquist effect is one of the best-known cases of crossmodal interaction. It consists in the fact that subjects who are asked to localize target sounds that are accompanied by visual distracters presented synchronously in a slightly different location tend to displace these target sounds toward the visual distracters. It has generally been assumed that the phenomenon reflects some interaction of auditory and visual perceptual processes, but its usual demonstrations do not rule out alternative non-perceptual explanations through factors such as response biases, attentional setting or even voluntary strategies. Using a new paradigm based on psychophysical staircases, we have shown that the apparent location of sounds can be biased toward synchronized visual distracters even when the subject is not aware of the auditory-visual discrepancy. Hence, the effect cannot reduce to voluntary corrections. Other experiments have shown it does not depend on whether visual attention is focused on the visual distracter, through either endogenous or exogenous orientation. Such results suggest that ventriloquism reflects a phenomenon of automatic crossmodal pairing, i.e. formation of a crossmodal perceptual unit which takes place at a pre-conscious, pre-attentional processing stage and must be clearly distinguished from conscious perceptual fusion. Whether other cases of crossmodal interaction - like audiovisual speech recognition, multimodal event identification or audiovisual affect perception - present similar profiles is a matter for future research.

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TOOL USE-INDUCED PLASTICITY OF VISUO-SOMATOSENSORY INTEGRATION IN THE MONKEY PARIETAL CORTEX

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Keywords: *monkey, parietal cortex, body-image, tool-use*

Bimodal (visual and somatosensory) neurons in the monkey intraparietal cortex code the image of the self-body, which is subject to intentional modification: When trained to use a tool, it becomes an extension of the hand both physically and perceptually, resulting in alteration of the body image in accordance with the characteristics of the tool at hand. In above bimodal neurons, use-dependent expansion of the receptive field occurred only when the monkeys held a tool and intended to use it as an extension of their hand. These findings may constitute the neural correlate for modification of the body schema as a basis of assimilation of the tool into our own body. Also, we found that these neurons can also code the body-image projected onto the video monitor, perhaps corresponding to its "iconic" representation. During the course of training, behavioral analyses suggested that a novel mode of somatosensory-visual integration seemed to develop in order to organize adequate bodily movement to manipulate the tool, possibly subserved by reformation of the neural circuitry in which molecular genetic processes in the cortical area described above are involved. When these representations were further advanced, it would become totally free from physical constraints of the actual world to become a (pre-)symbolic one to represent evolutionary precursors of higher cognitive functions, and might eventually lead to evolution of human language or to the metaphysical thoughts. We are now extending these studies (by combining behavioral, electrophysiological, neuroanatomical, molecular biological, and positron emission tomography imaging techniques) to examine cortical mechanisms subserving tool use-induced on-going plasticity and maintenance of the mode of visuo-somatosensory integration in the parietal cortex.

CROSS-MODAL RECOGNITION OF SHAPE FROM HAND TO EYES IN HUMAN NEWBORNS

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The hypothesis that the ability to coordinate information between visual and tactual modalities is present at the start of life and dependent on perceptual inherent structures was tested with human newborns. Using an intersensory paired-preference procedure, we show that newborns can visually recognize the shape of an object that they have previously manipulated with their right hand, out of sight. This is the first experimental evidence that newborns can extract shape information in a tactual format and can transform it in a visual format before they have had the opportunity to learn from the pairings of visual and tactile experience and contrary to a host of theories and models of perceptual learning, both traditional (empiricist philosophers) and modern (connectionist).

DIRECTIONAL REMAPPING OF SOUND LOCATION AFTER SACCADES

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Keywords: auditory space perception, saccades, multisensory illusion

Although sound position is initially coded in head-centred coordinates, neurophysiological and behavioural evidence suggests that differences in static eye-position can modulate auditory responses and sound localisation. Here we provide the first behavioural evidence for directional remapping of sound location following a dynamic change in eye-position. Two experiments studied the effect of saccades on human sound localisation performance, with auditory inputs to the ears held constant by preventing head movements. Participants judged the relative position (same/different) of two sequential sounds, presented from a horizontal array of speakers. Visual fixation was either static throughout the trial (to the left or right of the loudspeaker array), or shifted to the opposite far side during the interval between the two sounds. Speakers were visible in Exp.1 and occluded in Exp.2. Results showed that intervening saccades clearly reduced participants' ability to detect a change in sound position. This impairment was most pronounced when the second sound shifted in the direction opposite to the intervening saccade. This result is compatible with a directional remapping of the first sound location following the saccade. This effect was present when speakers were occluded (Exp. 2), but reduced with respect to the visible condition (Exp.1). Thus, even without visual input and in a purely auditory task, changes in eye-position play a role in auditory spatial perception.

MECHANISMS OF MULTISENSORY FUSION DERIVED FROM DYNAMIC CHARACTERISTICS OF HUMAN SPATIAL ORIENTATION

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The ability to select and reweight alternative orientation references adaptively is considered one of the most critical factors for postural control in patient and elderly populations with balance problems. Despite the importance of multisensory reweighting for balance control, little is known about how it is achieved. Multisensory reweighting is a crucial component of the process of estimation, in which sensory information from multiple sources is combined to give continuously-updated estimates of the body's position and velocity (i.e., dynamics). The complement of estimation is the process of control, which sends commands to the musculature to maintain the center of mass upright, based upon the current estimates of body dynamics.

We have identified dynamic characteristics of body sway with time series models that have led to measures that distinguish estimation from control. Using these measures to then develop models that hypothesize underlying mechanisms has resulted in two important findings. First, most of the variability observed in body sway can be linked to the process of estimating the center of mass from multisensory information. Standard control theory algorithms cannot account for how multisensory information is fused for center of mass estimation without a process we refer to as "noisy computation". Computation noise may represent a major distinction between the control of engineered systems and the neural processes involved in human spatial orientation. Second, we have provided evidence for one potential mechanism of multisensory fusion: a nonlinear process which we refer to as "inverse gain" reweighting. Such reweighting clearly indicates that the sensory modalities are not separable streams of information and provides a strong constraint as to how the nervous system processes multisensory information.

A COMPUTATIONAL MODEL OF THE DEVELOPMENT OF THE CORTICO-TECTAL PATHWAYS MEDIATING MULTISENSORY ENHANCENENT

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Keywords: *multisensory integration, development, computational modeling*

Neurons in the deep layers of the superior colliculus (SC) detect targets in the environment by integrating input from multiple sensory systems. Some deep SC neurons receive input of only one sensory modality (unimodal) while others receive input of multiple modalities. Multimodal deep SC neurons exhibit multisensory enhancement, in which the response to input of one modality is augmented by input of another modality. The phenomenon of enhancement is consistent with the hypothesis that deep SC neurons use sensory input to compute the probability that a target has appeared. Multisensory enhancement can be simulated using a model in which sensory inputs are random variables and target probability is computed using Bayes' rule. Informational analysis of the model indicates that input of another modality can indeed increase the amount of target information received by a multimodal neuron, but only if the input is ambiguous. Simple neural models can implement the processing required for computing Bayes' rule. Depending on input distributions, target probability can be computed exactly by single-neuron models or accurately estimated using feed-forward neural networks. The models suggest that multisensory enhancement is a natural consequence of neural computation and could arise from ascending sensory input alone. Interestingly, neurophysiological findings show that both ascending and cortical descending inputs are required for multisensory enhancement (Jiang, Wallace, Jiang, Vaughn, and Stein, *J Neurophysiol* 85: 506-522, 2001). We have constructed a two-stage model of the development of multisensory enhancement in the deep SC that includes ascending and cortical descending inputs. Both stages of the model are unsupervised and rely only on local, neurobiologically plausible mechanisms of synaptic plasticity. The first stage involves an algorithm that increases information transmission from stochastic ascending inputs to deep SC neurons. Multimodal and unimodal units emerge at this stage, and their ratio increases as the ambiguity of the input increases, as expected from informational analysis of the Bayes' rule model. The second stage involves a novel algorithm based on correlation between the activities of deep SC and cortical neurons, and on anti-correlation between cortical neurons and ascending inputs, which alters the amount by which cortical descending influences pre-synaptically facilitate ascending synapses. The fully trained model reproduces the experimental finding that cortical inactivation drastically reduces multisensory enhancement but has little effect on the modality-specific responses of deep SC neurons.

HUMAN INFANTS' PERCEPTION OF AUDIOVISUAL TEMPORAL STRUCTURE

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A number of recent studies have shown that human infants are sensitive to the statistical distributional properties of auditory and visual input. Underlying this sensitivity is an ability to perceive the temporal distribution of sensory input and there is no doubt that this ability is a fundamental precursor to the development of higher-level perceptual and cognitive skills related to the development of action sequencing, social interaction skills, and language abilities. In my laboratory we have been studying the developmental precursors to these skills by investigating infants' perception of bimodally specified temporal structure. In this talk, I report the results from a series of studies addressing this issue. First, I review the results from our studies in which we asked whether infants can perceive audiovisual temporal structure specified by rhythmic patterns and whether intersensory temporal synchrony is important for the perception of such patterns. I show that regardless of whether a bimodal rhythm is instantiated by a bimodally specified sequence of syllables spoken in a rhythmical manner or whether it is instantiated by a moving/sounding object bouncing in a rhythmical manner, infants can easily perceive its rhythmical character. Second, I show that infants' sensitivity to the synchrony between the auditory and visual components making up bimodal rhythmic patterns is subordinate to their sensitivity to the rhythmic pattern cues. Third, I show that infants' ability to perceive bimodal rhythmic patterns is limited in that they are unable to perceive the constancy of a given rhythmic pattern in the face of variations in its overall temporal rate. Finally, I discuss the results of studies on infants' perception of bimodally specified temporal serial order and show that infants can encode serial order information but that selective attention to audio-visual synchrony relations can actually interfere with its perception. When considered together, the results show that infants possess some impressive multimodal temporal perception skills and provide interesting insights into how the audible and visible components of temporally structured information interact with one another.

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Graduate Students Symposium
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REFERENCE FRAMES OF SOMATOSENSORY AND VISUAL SPACE REPRESENTATIONS IN VENTRAL INTRAPARIETAL (VIP) AREA OF MONKEYS

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Keywords: *Posterior parietal cortex, eye position, macaque*

The ventral intraparietal (VIP) area receives converging inputs from different sensory modalities, raising the question of a common reference frame for encoding stimulus location. By mapping visual receptive fields (vRF) for different eye positions, Duhamel et al. (1997) have already shown that, in VIP, visual space is encoded either in retinotopic, head-centered, or intermediate coordinates.

Single-cell activity was recorded extracellularly in VIP of one monkey. Tactile receptive fields (tRF) were estimated by using trains of air puffs delivered through needles arranged in an orderly manner on a mask fitting the monkey's face; this procedure was performed while the monkey fixated a spot of light located either centrally, or at 18 deg. left or right on a tangent screen. vRF were also determined for the same three eye positions by using a moving bar of light. Fifteen out of 26 neurons were bimodal and their visual and tactile receptive fields were found roughly aligned. Changes in eye position did not shift the location of tRF on the body surface, i.e. the tRFs remained anchored to a body-centered reference frame. However, in half of the cells, eye position modulated the amplitude of the response to air puff, and defined a "gain field". The reference frame of the matching vRF of these bimodal cells was not exclusively head-centered; it could also be retinotopic or intermediate. Therefore, evidence for the use of a common reference frame for the visual and tactile RF was found only in a subset of VIP bimodal cells (n=6/15). This results stand in contrast with observations made in other brain regions, such as the superior colliculus or the ventral premotor cortex, where multisensory stimuli are systematically encoded in eye and body-centered reference frames, respectively. We therefore suggest that area VIP may represent an intermediate stage in multisensory coordinate transformations.

VISUO-TACTILE BINDING SITES ARE MODULATED BY SPATIAL COHERENCE, ATTENDED MODALITY AND TASK: AN FMRI STUDY

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Keywords: fMRI, vision, touch, multisensory, integration

Introduction: Recent human neuroimaging studies have suggested that the inferior parietal lobe may play an important role in the binding of visual and tactile co-ordinate information[1]. The following study aimed to firstly identify sites of visuo-tactile integration using statistical interaction techniques and then test whether manipulating attention to either the visual or tactile modality or the nature of the task (simple detection vs. intensity discrimination) would modulate these binding sites.

Method: A mixed block/event-related design was used in order to present unpredictable sequences of unimodal (visual **or** tactile) and bimodal (visual **and** tactile) single events within blocks where attention could be directed to either the visual or tactile modality. In addition, bimodal events could either be together in space (congruent) or apart (incongruent). Reaction times were simultaneously collected for comparison with imaging results.

Results: Sites of visuo-tactile integration were first identified by looking for bimodal responses that were greater than the algebraic sum of the two unimodal conditions - "multisensory integration"[2]. This strategy identified a core network of regions putatively involved in the crossmodal binding of visual and tactile co-ordinate information including the caudate nucleus, intraparietal sulcus, superior parietal lobule and posterior cingulate gyrus. When bimodal inputs were spatially congruent activation was identified exclusively in the caudate nucleus, parahippocampal gyrus and posterior cingulate gyrus. When attention was directed to vision activation occurred preferentially in the intraparietal sulcus whereas attention to touch activated the caudate nucleus. Finally, discrimination but not detection activated frontal cortex, which is consistent with previous studies implicating this region in crossmodal object binding[3].

Conclusion: An interaction analysis identified a network of regions putatively involved in the binding of visual and tactile co-ordinate information. Further, this network could be modulated by explicitly changing the spatial, attentional and task-related parameters and the relation to task performance. This alludes to a more 'context-related' recruitment of visuo-tactile binding sites than previously suggested.

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MULTISENSORY VISUAL-AUDITORY OBJECT RECOGNITION IN HUMANS: A HIGH-DENSITY ELECTRICAL MAPPING STUDY

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Keywords: *Multisensory, visual, auditory, high density ERPs, object recognition*

An object can often be identified based on information from several sensory modalities. Clearly, the sight of a common animal immediately reveals its identity. Similarly, with one's eyes closed, most animals are readily identified by their vocalizations and this would also be the case should one feel the animal for a few moments. Yet the joint influence of information from multiple senses on object recognition has not been extensively examined. The present study tested the effect of visual and auditory information on object recognition. High density evoked potentials (from 128 scalp electrodes) were recorded while subjects performed an object recognition task in which they pressed a key to the occurrence of a target animal. On each trial one of four stimulus types was presented: animal pictures alone; animal sounds alone; paired pictures and sounds of the same animal (congruent pairs); and paired pictures of one animal and sounds of another (incongruent pairs). Five types of targets were derived from the four stimulus types: auditory-alone targets, visual-alone targets, auditory incongruent targets, visual incongruent targets, and congruent targets. There were 8 animals, and each served as the target for two runs. Reaction times to the congruent targets were significantly faster than reaction times to any of the other target conditions. Miller's test of the race model was violated over the early portion of the RT distribution, providing evidence for the contribution of the interaction of the multisensory target information to RT facilitation. The evoked potentials elicited by the targets showed a significantly larger and extended visual N1 to congruent pairs compared to the incongruent pairs, suggesting that auditory information influences early visual object recognition processes.

DECONSTRUCTING TEMPORAL VENTRILOQUISM: HOW DO SOUNDS CAPTURE THE PERCEIVED OCCURENCE OF LIGHTS?

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Keywords: *Temporal perception, audition dominance, appropriateness hypothesis*

Several experiments examined how the temporal positioning of irrelevant sounds influenced performance in a visual temporal order judgement (TOJ) task. The first two experiments established the finding that sounds occurring before and after two successive lights improved visual TOJ performance compared to when sounds appeared simultaneously with the lights. Additional experiments examined the role of the first and second sounds independently, revealing that the effect was due to the second sound lagging after the second light. In a final experiment it was found that the second sound improved performance to the greatest extent when the first sound was present. This suggests that the integration of lights and sounds depends on the overall context. These experiments illustrate a temporal ventriloquism whereby the perceived temporal occurrence of lights is biased by the timing of sounds.

CONVERGENCE OF AFFECTIVE INFORMATION IN MULTIMODAL REGIONS OF THE HUMAN BRAIN

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Keywords: *Multisensory, affect, PET, middle temporal gyrus*

A PET study investigated whether convergence brain regions were activated during the perception of affective audio-visual events. Happy or fearful stimuli were presented to eight subjects in three conditions (visual only, auditory only and audio-visual). A convergence region situated in the left lateral temporal cortex (-52x, -30y, -12x) was selectively more activated by affective bimodal stimuli than affective unimodal stimuli (whether visual or auditory). Distinguishing positive and negative emotions, supplementary convergence areas situated mainly anteriorly in the left hemisphere for happiness and in the right hemisphere for fear were activated. Right amygdala activation was observed equally for visual fearful and audio-visual fearful stimulations. These results are consistent with previous fMRI data (Dolan, Morris & de Gelder, 2001) suggesting that facial expression and auditory fragment are concurrently processed in convergence regions rather than in modality-specific cortex.

Dolan, R.J., Morris, J.S., & de Gelder, B. (2001). Crossmodal binding of fear in voice and face. *Proc Natl Acad Sci USA* **98:** 10006-10.

THE CEREBRAL REORGANIZATION OF LANGUAGE FUNCTIONS IN LATE BLIND ADULTS AS AN EXAMPLE OF CROSS-MODAL PLASTICITY IN ADULTHOOD

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Keywords: *language, fMRI, late blindness, plasticity*

It has been shown that the nature and timing of language input significantly influence the neuro-anatomical implementation of language functions. For example, a recruitment of right hemispheric areas for language has been observed in users of American Sign Language (ASL). However, an activation of the right homologous perisylvian areas was less pronounced and only partly in late learners of ASL. Similarly, a bilateral rather than strongly left-lateralized brain activation during speech processing has been observed in congenitally blind adults both with event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI). Moreover, evidence for a language-related activation of visual cortex in the blind was reported. It is not known yet, if the more efficient processing of speech and / or the altered neural representation of language in the blind are linked to 'critical' or 'sensitive' periods during development or if similar changes occur when visual deprivation starts after puberty. These questions were addressed using fMRI. Nine late blind adults listened to meaningful or pseudo-word sentences which had an easy or difficult syntactic structure. Task of the participants was to detect rare sentences with an incorrect word order. The data showed a left-lateralized activation of perisylvian brain regions in the sighted controls but a bilateral activation pattern in the late blind participants. Furthermore, the language related activation extended into visual cortex areas in the late blind but in none of the sighted controls. The observed changes of language functions in the late blind group are similar to those observed for congenitally blind adults although they were partly not as pronounced after late than early onset of blindness. The present study demonstrates cross-modal plasticity of auditory language functions in adulthood.

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DYNAMIC PROPERTIES OF VISUAL PERIPERSONAL SPACE

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Neurophysiological and neuropsychological evidence converge in showing that peripersonal space is represented through the integrated processing of multiple sensory inputs. In close analogy with neurophysiological findings in monkeys, neuropsychological studies have shown that the human brain constructs visual maps of space surrounding different body parts. In right brain damaged patients with tactile extinction, the multisensory coding of visual peripersonal space has been revealed by showing that cross-modal visual-tactile extinction is mainly segregated in the space near the hand. That is, tactile stimuli on the contralesional hand are more consistently extinguished by visual stimuli presented near the ipsilesional hand than far from it. Here, it will be discussed whether such cross-modal links between touch and vision in the peripersonal space can still be evoked in the case of conflicting information, provided by vision and proprioception, about hand position in space. Neuropsychological evidence will be presented supporting the idea that multisensory processing systems can be deceived by "seeing" a rubber replica of the hand, instead of a real hand. Finally, it will be shown that visual peripersonal space extension can vary: it can be expanded and contracted depending upon tool use.

A MOVING IMAGE OF PHANTOM LIMBS. VISUAL-KINESTHETIC INTEGRATION IN TWO PERSONS BORN WITHOUT HANDS

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keywords: *body schema; congenital amputation; phantom sensations; visual-somesthetic integration*

Perceived apparent motion trajectories may be modified by “obstacles” placed in between the two alternating stimulus positions suggesting a top-down regulation of lower level visual functions. Crossmodal sensory integration can be observed if the visual stimuli involve pictures of body parts and the visual impression corresponds, for instance, to the rotation of a limb around a joint. In this case, apparent motion paths are subject to biomechanical constraints imposed on the visual system. This begs the question of whether sensorimotor experience with a limb is mandatory for the occurrence of such crossmodal, visual-kinesthetic integration, or whether there is an innate representation of basic functional properties of joints.

We studied the perception of apparent motion using pictures of hands and arms in two persons born without these body parts. One person, AZ, is a 44-year-old university-educated woman with intact shoulder articulations and short upper arms (no joints). AZ reports vivid phantom experiences of all missing body parts, crucially involving movements of fingers, hands and lower arms. For the most part, the experienced trajectories of these phantom movements correspond to the natural trajectories of real limbs. The other person, CL, is a 40-year-old man born without arms (no shoulder articulations) who, in contrast to AZ, has never experienced any phantom sensations of his missing body parts. Six additional observers, matched to the experimental subjects with respect to age and educational background but with an intact body, were tested as well. Stimuli were pairs of photographs depicting a hand/an arm held in two different postures. Rapid flashing the two pictures in each a pair induced apparent motion percepts in all subjects. Control subjects and AZ perceived paths that followed the shortest distance at high flash rates but corresponded to the longer, anatomically possible trajectories at low flash rates. Independent of flash rate, CL perceived only the short, anatomically impossible paths, indicating that his visual system was not constrained by kinesthetic information. We conclude that (1) physically executed limb movements do not appear to be a necessary prerequisite for visual-kinesthetic integration to occur, whereas (2) the phenomenal experience of limb movements may be a more decisive factor.

THE ANATOMY OF AUTOSCOPIC EXPERIENCE

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Keywords: *body schema, neurology, cortical stimulation, visual, vestibular, somatosensory*

Among the disorders of body cognition or somatognosia, the experiences involving an illusory reduplication of one's own body (IRB) are among the most intriguing. They are generally characterized by the experience of seeing or feeling one's own body in the near extrapersonal space. IRB have been reported mostly in epileptic and psychotic patients, but also in healthy subjects. The most common forms of IRB are autoscopy, heautoscopy and out-of-body experience. Whereas autoscopy is phenomenologically a purely visual manifestation, heautoscopy and out-of-body experiences are believed to be multisensory IRBs including visual and somatosensory symptoms. Yet, apart from phenomenological descriptions of the affected individuals, little is known about the cognitive and anatomical characteristics of these strange and often frightening somatognosic disorders.

Here we report about IRBs in five epileptic patients. Detailed case histories were taken with respect to visual, auditory, somatosensory, and vestibular symptomatology. This was combined with MRI, multichannel EEG and PET in order to localize brain damage and/or the epileptic seizure onset zone with high spatial resolution. In addition, in one patient an IRB could be induced artificially by electrical cortical stimulation during invasive presurgical epilepsy evaluation. The visual phenomenology allowed us to classify the different forms of IRBs to the categories of autoscopy, heautoscopy and out-of-body experience. However, this analysis also revealed that next to visual sensations all patients experienced vestibular sensations characterized by feelings of levitation, lightness, and floating or flying in the air. Auditory and somatosensory sensations were less frequently encountered. Lesion and epileptic focus localization found the angular gyrus and the posterior part of the superior temporal gyrus to be implicated in all cases. The present phenomenological results suggest that IRBs may reflect a failure to integrate visual and vestibular information in body-related cognition. Anatomically, this integration seems to be mediated by the angular and superior temporal gyri, which is in close proximity to the core region of the human vestibular cortex.

AN EXCEPTIONAL GENERALIZATION AND TRANSFER OF PRISM ADAPTATION IN UNILATERAL NEGLECT

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Keywords: prism adaptation, neurology, rehabilitation

Prism adaptation in healthy subjects can be restricted to the exposed arm, to a specific gesture or to movement speed during exposure. But adaptation to base-left wedge prisms in patients has been found to produce strong effects on unexposed tasks performed with the exposed arm, such as line bisection, copy of line drawing or drawing from memory (Rossetti et al. 2001). Motor tasks performed with unexposed effectors such as postural control or wheel-chair driving, have been also shown to be strongly altered following one short prism adaptation session (Rossetti et al. 1999, Tilikete et al. 2001). In addition, visual tasks involving no arm movement, such as word reading or object naming, were also improved after adaptation, and by the same amount as visuo-motor tasks (Farnè et al. 2001). Even visual imagery, which can be amputated from the left half in patients with unilateral neglect, is markedly improved following adaptation (Rode et al. 1998, 2001. Furthermore, tasks performed within another sensory modality, such as dichotic listening (Jacquin et al. 2001), haptic circle centering (McIntosh et al. 2001) of haptic object recognition (Toutounji et al. 2001) were also strongly affected by prism adaptation. It is also striking that the effects of a 5 minute exposure to a prismatic shift of vision to the right may last from several hours to 24 h or even several days (Pisella et al. 2001, Farnè et al. 2001).
These results strongly suggest that a lesion of the right hemisphere can be responsible for super-adaptation to a conflict between visual and proprioceptive information.

TOOL-USE CHANGES VISUAL-TACTILE SPATIAL INTERACTIONS IN THE NORMAL AND DAMAGED BRAIN

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Keywords: *Vision, Touch, Tool, Attention, Space processing, Brain damage*

INTRODUCTION

When we wield a long tool, we extend our possible reaching space. We can touch distant objects with the tool, so that tactile information felt at the hand can now relate to visual information from distant objects. Moreover, a hand located on, say, the right side of space may contact visual objects in the left visual field with the tool, or vice-versa, given that tools can be wielded in innumerable different postures. This means that the spatial mapping between tactile stimulation at the hand, and any related visual information near the end of the tool, alters as a tool is used. A wielded tool may become incorporated into the 'body schema', such that the end of the tool effectively becomes an extension of the effecter wielding it. Here we examined whether experience in actively wielding a long tool can modulate automatic aspects of visual-tactile spatial integration for normal human subjects and a right brain damaged patient with left crossmodal extinction (i.e. unawareness of left touch with simultaneous right visual stimulation).

METHODS

In a visual-tactile interference paradigm, subjects judged whether tactile vibrations arose on a finger or thumb (upper vs. lower locations), while ignoring distant visual distracter lights, fixed in vertical pairs (again in upper or lower locations) at the far end of each of two “tools” grasped with each hand. Previous work using visual distracters located on the hands showed that judgements of such tactile stimuli are slower and/or less accurate when the concurrent visual distracter is incongruent (i.e. upper vibration with lower light, or vice versa). Importantly, this crossmodal interference has repeatedly been found to be stronger when visual and tactile stimuli appear on the same side of space (e.g. right visual field stimulation paired with vibration on the right hand). Here we tested whether actively wielding a long tool can alter this crossmodal mapping plastically, such that when the tools are held crossed (connecting the right hand to the left visual field, and vice-versa), crossmodal interference might now become larger from visual distractors in the opposite visual field to the tactually stimulated hand.

RESULTS

We show that actively wielding tools can change this pattern of crossmodal interference. When such tools were held in crossed positions (connecting the left hand to the right visual field, and vice-versa), the spatial constraints on crossmodal interference reversed, so that visual distracters in the other visual field now disrupted tactile judgements most for a particular hand. This phenomenon depended on active tool use, developing with increased experience in using the tool.

A logically related result was found in a right brain damaged patient showing extinction of left touch by right visual stimulation. The patient was trained to reach for object in the right visual field, using the rake with the left hand. After the training, the same right visual stimulus which produced strong left tactile extinction before training, now produced significantly less extinction.

CONCLUSIONS

We discuss these results in terms of change of the hand representation in the body schema, which can effectively modulate crossmodal spatial attention in the normal and damaged brain.

BRAIN OSCILLATORY RESPONSES DURING AN AUDIOVISUAL MEMORY TASK – AN MEG STUDY

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***Keywords*: brain, oscillations, audiovisual, MEG, memory**

Brain oscillatory responses during an audiovisual memory task were studied in twelve adult subjects (six males) by means of the magnetoencephalography (MEG) using graphically (letters), visually (articulating face), acoustically (voice) and audiovisually (articulating face and voice) presented vowels as stimuli. ERD/ERS (event-related desynchronization/synchronization) responses were calculated for the 1-45 Hz MEG frequencies during memory encoding and retrieval for all stimuli. The encoding and retrieval of material presented in different modalities evoked distinct patterns of brain oscillatory responses. Both encoding and retrieval of letters were accompanied by ERD (i.e., relative power decrease) in the theta and alpha frequencies. In contrast, the encoding of acoustic information was accompanied by theta, alpha and beta rhythm ERS (i.e., power increase) responses, the encoding of visual information by a "narrow band" alpha ERS whereas audiovisual encoding was accompanied theta and alpha ERS. During retrieval of acoustic, visual and audiovisual material, initial theta, alpha and beta rhythm ERS responses were evoked which were followed by alpha and beta rhythm ERD responses. We summarize our findings as follows: First, the brain oscillatory responses evoked by the encoding and retrieval of letters differed considerably from the responses obtained during the encoding and retrieval of acoustic, visual and audiovisual material. Second, the ERD/ERS responses obtained during the encoding of visual material (articulating face) resembled more those obtained during the encoding of acoustic information than those observed during the encoding of letters. Third, the encoding of acoustic information was accompanied by a broad frequency alpha ERS, the encoding of audiovisual material was accompanied by a narrower frequency alpha ERS and the encoding of visual material was accompanied by the narrowest frequency alpha ERS. Fourth, the ERD/ERS responses during the presentation of audiovisual material were not merely the sum or average of the acoustic and visual ERD/ERS responses.

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AUDITORY AND CROSS-MODAL (AUDIO-VISUAL) VERSIONS OF THE 'VISUAL' FLASH-LAG EFFECT

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Keywords: *psychophysics, vision, audition, cross-modal, illusions*

Introduction

In vision, a briefly flashed stimulus presented in physical alignment with a moving stimulus appears to lag behind the moving one. This spatial error is the 'flash-lag effect'. Several theories have tried to explain the effect but none is undisputed. Here, we broaden the enquiry by investigating the flash-lag effect in audition.

Methods

A translating sound source (low-pass noise, <2kHz; speed=50°/s; duration=0.64s) was paired with an auditory 'flash' (1kHz tone; 20ms). The point of subjective alignment of the sound burst and the moving sound source was measured. A visual condition, with the sound sources replaced by Gaussian luminance profiles (same duration & trajectory), was also tested. In cross-modal conditions, visual flashes and auditory movement (V_f/A_m) were paired, or auditory flashes with visual movement (A_f/V_m). Finally, the effect was tested using spectral (instead of spatial) motion. Movement was a pure tone sweeping upwards or downwards in frequency, paired with a brief pure tone.

Results

In all conditions, the brief stimulus lagged behind the moving stimulus (the flash-lag effect). Expressing errors in temporal terms, the auditory effects were much larger (spatial+=170ms; spectral=155ms) than the visual effect (13ms). Cross-modal effects were intermediate (V_f/A_m = 73ms, and A_f/V_m = 119ms).

Conclusions

Theories of the flash-lag effect based on motion extrapolation or on differential latencies for sustained and transient stimuli between eye and cortex, cannot explain the data. Our results suggest differential neural integration times for sustained and transient stimuli underlie the flash-lag effect. The cross-modal data indicate that latency and integration delays are linearly combined across modalities at a perceptual level. To fully account for the cross-modal data, a temporal component due to the much shorter latencies in audition must be considered. We used a reaction-time study to estimate latency differences between modalities for static and moving stimuli.

ENDOGENOUS VISUAL SPATIAL ATTENTION AFFECTS AUDIOVISUAL SPEECH PERCEPTION

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Keywords: *Attention, Audiovisual, Speech*

The goal of this study was to examine how endogenous spatial attention interacts with audiovisual speech perception.

Visual speech was either bilateral, with faces on both sides of a central fixation point, or unilateral. In the bilateral condition, one face was uttering /eme/ and the other /ene/. A cueing arrow indicated which face to attend. In the unilateral condition, the face was uttering either /eme/ or /ene/. Auditory speech was /eme/ or /ene/.

The main finding was that, in the bilateral conditions, the attended face largely determined the auditory percept. When the congruent face was attended, correct identification was facilitated in comparison with unimodal auditory conditions, but when the incongruent face was attended it gave rise to a McGurk illusion of hearing what the attended face was uttering. It was also more pronounced in the unilateral condition, indicating that the unattended face also influenced perception.

The decreased effect of the attended face in the bilateral condition could be due to an attenuation of visual influence in general, or the imposing of the competing face upon perception. In order to elucidate this effect, we performed another experiment.
Now, auditory speech was always /epe/ and visual speech was either /eke/ or /ete/. We used articulations of /eke/ and /ete/ that were visually distinguishable. We thus hoped to be able to better distinguish influences from the unattended face and auditory speech, which were now never the same.

In the bilateral condition, there were substantially more auditory responses indicating that visual influence was weaker than in the previous experiment. Subjects gave more /eke/ responses when attending /eke/ than when attending /ete/. Similarly, they gave more /ete/ responses when attending /ete/ than when attending /eke/. Again, the speech percept was shifted toward the utterance of the attended face, but the effect did not increase significantly in the unilateral condition. Therefore, we were not able to determine whether the substitute for lost influence from the attended face was the competing face or auditory speech.

INTERSENSORY FACILITATION IN EYE AND ARM MOVEMENTS

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The question whether eye movements (saccades) and arm movements (pointing and reaching) share common processing stages or are programmed separately in parallel is still under debate. Recent physiological findings have provided new evidence for combined representation of eye and arm movements in several brain areas. These shared brain areas could either be involved in common control processes for both movements or in the coordination between eye and arm movements.

Here a new approach is introduced to investigate this issue. We analyse the characteristics of multisensory, visual-auditory integration in eye movements compared to arm movements in order to gain further insight in the underlying processes. If eye and arm movements share processes based on the same multimodal representation of sensory stimuli, then experimental manipulations of the bimodal stimulus arrangement should reveal analogous effects for both movements.

In the experiments discussed here we employed a focussed attention paradigm. Subjects were asked to respond to a visual target stimulus with a saccadic eye movement, a goal directed hand movement or both and to ignore an accessory auditory stimulus. Latencies were used as measure of visual-auditory interaction.

In a first experiment the temporal and spatial relationship between target and accessory stimulus were varied. This led to similar overall patterns for eye and arm movements. However, hand movement latencies showed a markedly stronger dependence on spatio-temporal stimulus variation. This suggests a stronger influence of the auditory stimulus on manual latencies.

The variation of the intensity of the accessory stimulus in a second experiment showed that latencies for both types of movement decreased with increasing auditory intensity in a similar manner. There was no evidence of a stronger effect of auditory intensity on arm movements.

The apparent contradiction may be due to the fact that manual latencies are longer (by about 100 ms) than saccadic latencies. This might allow for a longer processing of the auditory signal resulting in different spatio-temporal effects. To investigate this problem we are varying the temporal stimulus arrangement over a wide range (300 ms) in a third experiment. The results of this experiment will be presented and discussed.

THE VIRTUAL BODY EFFECT ACROSS SPACE

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Keywords: *visual-tactile interactions, apparent vs real limb position, spatial distance effects, limb visibility*

Humans often receive tactile information in one location while concurrently receiving visual information in another (e.g., typing on a keyboard while viewing a computer screen). What factors influence the perception of tactile location? Pavani, Spence and Driver (2000) demonstrated that tactile perception was influenced by the location of non-informative visual distractors, especially when a pair of false hands were visible and aligned with observer's own hands. We examined this virtual body effect when distractors were in the same horizontal location as targets, or separated by 15-30 cm. We also manipulated the visibility of the observer's hand and the false hand. Results show reductions in visual distractor influence on tactile perception when there is either a spatial separation or when no hand is visible. This suggests that the false hand is used to link the tactile and visual locations in the mental representation of space.

REFERENCE FRAMES OF SOMATOSENSORY AND VISUAL SPACE REPRESENTATIONS IN VENTRAL INTRAPARIETAL (VIP) AREA OF MONKEYS

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Keywords : ***posterior parietal cortex, eye position, macaque***

The ventral intraparietal (VIP) area receives converging inputs from different sensory modalities, raising the question of a common reference frame for encoding stimulus location. By mapping visual receptive fields (vRF) for different eye positions, Duhamel et al. (1997) have already shown that, in VIP, visual space is encoded either in retinotopic, head-centered, or intermediate coordinates.

Single-cell activity was recorded extracellularly in VIP of one monkey. Tactile receptive fields (tRF) were estimated by using trains of air puffs delivered through needles arranged in an orderly manner on a mask fitting the monkey's face; this procedure was performed while the monkey fixated a spot of light located either centrally, or at 18 deg. left or right on a tangent screen. vRF were also determined for the same three eye positions by using a moving bar of light. Fifteen out of 26 neurons were bimodal and their visual and tactile receptive fields were found roughly aligned. Changes in eye position did not shift the location of tRF on the body surface, i.e. the tRFs remained anchored to a body-centered reference frame. However, in half of the cells, eye position modulated the amplitude of the response to air puff, and defined a "gain field". The reference frame of the matching vRF of these bimodal cells was not exclusively head-centered; it could also be retinotopic or intermediate. Therefore, evidence for the use of a common reference frame for the visual and tactile RF was found only in a subset of VIP bimodal cells (n=6/15).

This results stand in contrast with observations made in other brain regions, such as the superior colliculus or the ventral premotor cortex, where multisensory stimuli are systematically encoded in eye and body-centered reference frames, respectively. We therefore suggest that area VIP may represent an intermediate stage in multisensory coordinate transformations.

UNIMODAL AND CROSSMODAL EFFECTS OF ENDOGENOUS ATTENTION TO VISUAL AND AUDITORY MOTION

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Keywords: auditory motion, visual motion, crossmodal attention

Many studies have demonstrated that spatial attention facilitates stimulus discrimination at the attended location both for the attended and less relevant modality. In contrast, effects of attention to motion (another supramodal dorsal feature) has not yet received as much consideration, neither within a single nor across modalities.

Goal of the present study was to test if attending endogenously to a particular direction of visual and auditory motion facilitates visual and auditory stimulus processing, respectively, and to find out whether or not a crossmodal facilitation exists.

Task of the participants was to discriminate the speed (slow versus fast) of moving sounds and moving random dot patterns. Endogenous attention was manipulated by presenting stimuli of one modality and of one direction with a probability of 0.7 while all other stimulus conditions (same modality but different direction; different modality and either same or different direction) were equally probable ($p = 0.1$).

In conditions when visual stimuli were more likely, speed discrimination was faster when visual stimuli moved in the attended (i.e., more probable) direction than when they moved in the unattended (i.e., less probable) direction. Similarly, when auditory stimuli were more likely, response times to sounds were faster when moving in the more frequent direction as compared to the less likely direction. The reaction time gain was of equivalent size for the visual and auditory modality. Moreover, there was a tendency towards shorter speed discrimination times for visual stimuli moving in the same direction as the attended auditory stimuli.

The present study demonstrates behavioral effects of endogenous attention to visual and auditory motion. If auditory motion in fact affects visual motion processing is currently investigated with event-related potentials, a more sensitive measure for crossmodal effects.

THE VENTRILOQUIST EFFECT:
A CASE OF CROSSMODAL PERCEPTUAL GROUPING

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The ventriloquist effect is one of the best-known cases of crossmodal interaction. It consists in the fact that subjects who are asked to localize target sounds that are accompanied by visual distracters presented synchronously in a slightly different location tend to displace these target sounds toward the visual distracters. It has generally been assumed that the phenomenon reflects some interaction of auditory and visual perceptual processes, but its usual demonstrations do not rule out alternative non-perceptual explanations through factors such as response biases, attentional setting or even voluntary strategies. Using a new paradigm based on psychophysical staircases, we have shown that the apparent location of sounds can be biased toward synchronized visual distracters even when the subject is not aware of the auditory-visual discrepancy. Hence, the effect cannot reduce to voluntary corrections. Other experiments have shown it does not depend on whether visual attention is focused on the visual distracter, through either endogenous or exogenous orientation. Such results suggest that ventriloquism reflects a phenomenon of automatic crossmodal pairing, i.e. formation of a crossmodal perceptual unit which takes place at a pre-conscious, pre-attentional processing stage and must be clearly distinguished from conscious perceptual fusion. Whether other cases of crossmodal interaction - like audiovisual speech recognition, multimodal event identification or audiovisual affect perception - present similar profiles is a matter for future research.

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THE ANATOMY OF AUTOSCOPIC EXPERIENCE

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Keywords: *body schema, neurology, cortical stimulation, visual, vestibular, somatosensory*

Among the disorders of body cognition or somatognosia, the experiences involving an illusory reduplication of one's own body (IRB) are among the most intriguing. They are generally characterized by the experience of seeing or feeling one's own body in the near extrapersonal space. IRB have been reported mostly in epileptic and psychotic patients, but also in healthy subjects. The most common forms of IRB are autoscopy, heautoscopy and out-of-body experience. Whereas autoscopy is phenomenologically a purely visual manifestation, heautoscopy and out-of-body experiences are believed to be multisensory IRBs including visual and somatosensory symptoms. Yet, apart from phenomenological descriptions of the affected individuals, little is known about the cognitive and anatomical characteristics of these strange and often frightening somatognosic disorders.

Here we report about IRBs in five epileptic patients. Detailed case histories were taken with respect to visual, auditory, somatosensory, and vestibular symptomatology. This was combined with MRI, multichannel EEG and PET in order to localize brain damage and/or the epileptic seizure onset zone with high spatial resolution. In addition, in one patient an IRB could be induced artificially by electrical cortical stimulation during invasive presurgical epilepsy evaluation. The visual phenomenology allowed us to classify the different forms of IRBs to the categories of autoscopy, heautoscopy and out-of-body experience. However, this analysis also revealed that next to visual sensations all patients experienced vestibular sensations characterized by feelings of levitation, lightness, and floating or flying in the air. Auditory and somatosensory sensations were less frequently encountered. Lesion and epileptic focus localization found the angular gyrus and the posterior part of the superior temporal gyrus to be implicated in all cases. The present phenomenological results suggest that IRBs may reflect a failure to integrate visual and vestibular information in body-related cognition. Anatomically, this integration seems to be mediated by the angular and superior temporal gyri, which is in close proximity to the core region of the human vestibular cortex.

POLYMODAL SPACE REPRESENTATION IN PRIMATE AREA VIP

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Keywords: *Monkey; Human; Intraparietal; Craniocentric; Self-motion*

The neural circuits underlying normal spatial vision and attentive sensorimotor behavior of primates have been most intensively studied in macaque monkeys. Both electrophysiological and anatomical studies have highlighted the importance of the posterior parietal cortex for the integration of neural signals from different sensory modalities and its use for guiding and controlling action in space. In the monkey, a highly modular structural and functional specialization has been demonstrated within this part of the brain. One such functionally specialized area is the ventral intraparietal area (VIP) located in the fundus of the intraparietal sulcus (IPS). I will review recent studies demonstrating that area VIP contains many neurons which show polymodal directionally selective discharges. A considerable proportion of these neurons encode this polymodal information in a common, probably head-centered, frame of reference. Furthermore, direct anatomical connections between area VIP and an area within the ventral premotor cortex (PMv), which subserves head movements, have been reported recently. Although many specific human behaviors necessitate the convergence and integration of information conveyed through anatomically distinct sensory pathways, to date little is known about polymodal motion information processing and integration in humans. To test for equivalencies between macaque and human polymodal motion processing, we used functional MRI in normals while presenting moving visual, tactile, or auditory stimuli. Increased neural activity evoked by all three stimulus modalities was found in the depth of the intraparietal sulcus (IPS), ventral premotor, and lateral inferior post-central cortex. The observed activations strongly suggest that polymodal motion processing in humans and monkeys is supported by equivalent areas. The activations in the depth of IPS imply that this area constitutes the human equivalent of macaque area VIP.

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PARALLEL PATHWAYS IN HUMAN VISION AND AUDITION

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The human visual and auditory cortex presents several characteristics that are compatible with parallel and hierarchical processing. Chemoarchitectonic and tracing studies revealed that the primary sensory areas are surrounded by several other areas, both in the visual (Clarke and Miklossy 1990; Clarke 1994) and auditory modality (Rivier and Clarke 1997) with a putatively hierarchical organisation (Mesulam and Geula 1994; Hustler and Gazzaniga 1996; Rivier and Clarke 1997). In the primary visual cortex intraareal compartments were identified anatomically in non-human primates (Horton and Hubel 1981) and in man (e. g. Clarke 1994). In the auditory domain, human, but not non-human primate primary area was shown to contain intraareal compartments which can be visualised with cytochrome oxidase histochemistry (Clarke and Rivier 1998). Furthermore, patterns of human cortico-cortical connectivity strongly support parallel processing (Di Virgilio and Clarke 1997; Tardif and Clarke 2001).

Parallel processing is generally believed to play a major role in vision but not in audition. Our recent evidence suggests otherwise.

A sound in natural setting conveys information about the identity of the sound source and about its location. Activation studies with fMRI in normal subjects suggest that the two aspects are processed independently within anatomically distinct pathways (Maeder et al. 2001). Lesions of either of these networks were shown to result in selective deficits of sound recognition or sound localisation (Clarke et al. 2000). Attending to meaningful auditory events in natural setting involves several aptitudes, including auditory spatial attention. Auditory hemineglect, most often concerning left hemispace following right hemispheric lesions, is most commonly diagnosed by the failure to report stimuli presented to the left ear in tasks of dichotic listening. Our recent observations indicate that there are two behaviourally and anatomically distinct types of auditory neglect: i) a deficit in allocation of auditory spatial attention following lesions centred on basal ganglia; and ii) distortion of auditory spatial representation following fronto-temporo-parietal lesions (Bellmann et al. 2001).

MULTIPLE SENSORY REPRESENTATIONS IN FERRET CEREBRAL CORTEX

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keywords: neuroanatomy, somatosensory, vision

While the ferret is increasingly being used as a model for neural development and plasticity, very little is known regarding the organization of its extraprimary sensory cortices. Neuroanatomical and electrophysiological methods were used to assess the location and distribution of non-primary visual and somatosensory representations.

Injections (Biotinylated Dextran Amine, n=3) made into V1 cortex labeled axon processes and terminals along the syprasylvian sulcus, as well as within the posterior portion of the pseuosylvian sulcus. BDA injections (n=4) into SI cortex produced terminal label within the anterior suprasylvian sulcus. Single and multi-unit electrophysiological recordings found visually-responsive neurons within the mid- and rostral suprasylvian sulcus, as well as within the pseuosylvian sulcus. Somatosensory-responsive neurons were identified within the suprasylvian sulcus and gyrus, and their receptive fields, although somatotopically organized, showed a clear differentiation from those in the more dorsally positioned SI. Bimodal, multisensory neurons were encountered in both suprasylvian and pseudosylvian sulci, although not in large numbers.

These data indicate the presence of a visual area within the pseudosylvian sulcus. Given the intermingling of auditory, visual, and multisensory responses in this region, it seems that this outlying visual area may represent the homologue of the ectosylvian visual area in the cat. In addition, the somatosensory area within the suprasylvian sulcus/gyrus that receives projections from SI, but has a different receptive field organization, might be considered the second (SII) somatosensory representation in this animal model. Supported by NIH Grant NS39460.

A MAXIMUM-LIKELIHOOD MODEL OF MULTISENSORY ENHANCEMENT IN THE SUPERIOR COLLICULUS

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Keywords: *maximum likelihood, multisensory enhancement, superior colliculus, inverse effectiveness*

The deep layers of the superior colliculus (DLSC) integrate multisensory input and initiate an orienting response toward the source of stimulation. *Multisensory response enhancement* (MRE) is the augmentation of a neural response of a DLSC neuron to sensory input from one modality by input from another modality. The maximum likelihood (ML) model presented here extends the *Bayesian model* for MRE by Anastasio *et al.* (2000) by incorporating a decision strategy to maximize the number of correct decisions. It operates at the level of a single DLSC neuron. The neuron`s behavior is solely based on the a-priori probability of a target and the likelihood function for the different sensory inputs. Like the Bayesian model, it accounts for the *inverse effectiveness* observed in neurophysiological recording data. Moreover, the model allows to derive a measure of the neuron`s ability to discriminate between targets and non-targets. It makes specific predictions how uni- and bimodal discriminability measures (signal-to-noise ratio) are related and, thereby, opens up further avenues for testing the model assumptions.

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COMPENSATORY PERFORMANCE CHANGES IN AUDITORY WORD RECOGNITION IN CONGENITALLY BLIND ADULTS

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keywords: *Language, blindness, compensatory plasticity*

It has repeatedly been reported that blind children do not only show delayed language acquisition but also several deviations from its normal time course. However, in adults there is evidence for superior speech comprehension skills in the blind as compared to sighted controls. Goal of the present study was to find out which aspects of language processing contribute to compensatory speech comprehension skills in the blind.

A semantic and morpho-syntactic priming paradigm was used: First an adjective was presented that was or was not semantically associated with the consecutively presented target noun and that was either correctly or incorrectly inflected for gender with respect to the following noun. In half of the trials a pseudo-word was presented as target and task of the congenitally blind and sighted participants (matched for age, gender and with respect to education) was to decide whether or not the last word of a trial was a legal German noun. Nouns that were primed semantically and morpho-syntactically had shorter lexical decision times than those primed only semantically or only morpho-syntactically and decision times for the latter two conditions were shorter than in a condition without a semantically or morpho-syntactically congruent context. Semantic and syntactic priming effects did not differ between groups. The blind, however, showed shorter decision times than the sighted for pseudo-words, and overall decision times for words tended to be shorter in the blind as well.

It is concluded that cross-modal compensatory speech comprehension skills of blind adults most likely arise from a more efficient perceptual analysis of the speech input rather than from a more extended use of semantic or morpho-syntactic context information.

MODELING THE TIME COURSE OF VISUAL-TACTILE SPATIAL INTERACTION

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Keywords: visual-somatosensory interaction, saccadic reaction time, two-stage model

Presenting an auditory stimulus in close spatio-temporal relation to a visual target stimulus has been shown to influence saccadic reaction time (SRT) to a visual target even if participants are instructed to ignore the auditory accessory (focused-attention task). Here we investigate whether a tactile stimulus has a similar bisensory interaction effect. A visual target (LED) and a tactile accessory stimulus (vibrator applied to palm) were presented at 20° or 70° eccentricity ipsi- and contralaterally at different stimulus onset asynchronies (tactile stimulus 100 ms, 50 ms, 0 ms before visual, or 50 ms after visual stimulus). Average visual-tactile SRT was up to 80 ms shorter than unimodal (visual) SRT. Specifically, average bimodal SRT was shorter for ipsi- than for contralateral presentation, and shorter for 20° than for 70° eccentricity. SRT facilitation decreased with SOA: response to the visual target was faster the earlier the accessory was presented.

The two-stage model for multisensory interaction (Colonius & Arndt, 2001) distinguishes a peripheral parallel processing stage from a more central decision stage where interaction occurs. Probability of interaction depends on the outcome of the first stage contingent upon unisensory stimulus properties only, while the amount and direction of interaction (facilitation/inhibition) is a function of the spatial configuration of stimuli. A parametric version of the two-stage model gave a satisfactory fit for individual data from 6 subjects. We conclude (1) that presentation of a tactile accessory stimulus has a facilitating effect on SRT to a visual target depending both on the spatial and temporal configuration, and (2) that these effects can be described by the two-stage model.

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CORTICAL MOTION DEAFNESS

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keywords: *auditory system, motion perception, motion deafness, human, electrical stimulation, intracranial AEPs*

Introduction

Recent findings have revealed a partially segregated pathway in the processing of moving and stationary sound sources, suggestive of the existence of an auditory analog to area MT+/V5 in the visual domain. In order to test for this hypothesis, behavioral measures, electrical stimulation as well as intracranial auditory evoked potentials (AEPs) were combined in one patient undergoing invasive presurgical evaluation and operation for right temporal lobe epilepsy.

Methods

Patient : 43 year-old right-handed woman with normal audition.

Stimuli : Auditory moving and stationary sounds created by varying interaural time differences; (earphones; blocked design).

Tasks : Behavioral pre- and post- operative tasks, consisting of 40 stimuli per condition (motion, location) to be judge by the patient with respect to their position or direction, respectively. For control purpose, a visual motion discrimination task was also given.

Behavioral tests were complemented during presurgical epilepsy evaluation by electrical stimulation and the recordings of AEPs to auditory location and motion (100 stimuli/condition; blocked design) from the 84 surgically implanted electrodes in the temporo-parieto-frontal region.

Results

Pre-operative behavioral tests revealed a high percentage of correct answers in both auditory conditions and a normal ability to discriminate different directions of visual moving targets.

Electrical stimulation of three electrodes, situated in a region surrounding the primary auditory cortex, induced a strong sensation of auditory movement coming towards the patient. Intracranial AEPs revealed that two of these three electrodes were responsive to moving but not to stationary sounds.

Post-operative behavioral tests showed that following right temporal lobectomy and cortectomy of the posterior part of the superior temporal gyrus, the patient was able to localize different stationary sounds and to detect different directions of visual moving targets, but was severely deficient in discriminating different directions of moving sounds.

Conclusion

These behavioral as well as intracranial electrophysiological data suggest the existence, in the right superior temporal gyrus, of a module specialized in auditory motion processing.

DYNAMIC PROPERTIES OF VISUAL PERIPERSONAL SPACE

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Neurophysiological and neuropsychological evidence converge in showing that peripersonal space is represented through the integrated processing of multiple sensory inputs. In close analogy with neurophysiological findings in monkeys, neuropsychological studies have shown that the human brain constructs visual maps of space surrounding different body parts. In right brain damaged patients with tactile extinction, the multisensory coding of visual peripersonal space has been revealed by showing that cross-modal visual-tactile extinction is mainly segregated in the space near the hand. That is, tactile stimuli on the contralesional hand are more consistently extinguished by visual stimuli presented near the ipsilesional hand than far from it. Here, it will be discussed whether such cross-modal links between touch and vision in the peripersonal space can still be evoked in the case of conflicting information, provided by vision and proprioception, about hand position in space. Neuropsychological evidence will be presented supporting the idea that multisensory processing systems can be deceived by "seeing" a rubber replica of the hand, instead of a real hand. Finally, it will be shown that visual peripersonal space extension can vary: it can be expanded and contracted depending upon tool use.

SPATIAL INTEGRATION OF AUDIO-VISUAL STIMULATION IN RETINOTOPIC AREAS MEASURED WITH FMRI

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Keywords: *audio-visual, spatial representation, crossmodal localization, visual cortex, retinotopic mapping*

We studied the effects of spatially congruent and incongruent audio-visual stimulation on the activity in human visual cortex using functional magnetic resonance imaging (fMRI). Auditory stimulation that fitted one of four locations in space was jointly presented with either a relevant matching visual cue (congruent), a spatially matching but semantically inconsistent visual cue (low incongruity), or a spatially non-matching visual cue (high incongruity). A control experiment with equally relevant visual cues at each of the four spatial locations was designed in order to investigate the direct effect of the auditory stimulation on activity in visual cortex. Data were obtained from seven subjects. Each subject performed two runs for retinotopic mapping (polar angle, eccentricity) and three experiments with audio-visual stimulation. Subjects were instructed to decide about the spatial congruity of the auditory (barking) and visual (barking dog) stimulus by pressing a button. Cortex based fMRI analysis was performed using BrainVoyager 4.6.

Careful positioning of stimuli allowed us to analyze the cortical response to each position separately. Retinotopic mapping of early visual areas confirmed that activity was found for each visual stimulus along the cortical representations of the horizontal meridian in V1 and at the borders of V2/V3. For each cortical representation of a stimulus, the change of MR-signal was analyzed. We were not able to find a direct effect of auditory stimulation on the activity in visual cortex (control experiment). We found higher activity for the incongruent conditions compared to the congruent conditions.

To explain our data we postulate a recurrent feedback process that signals mismatch. According to this model, the feed-forward process of perception is interrupted at multisensory stages of the brain as soon as spatial (or semantic) incongruity is detected between the modalities. This may lead to a redirection of spatial attention to relevant locations in space. In cases of low incongruity, auditory cues are attributed to the spatially congruent visual distractor instead of the semantically better matching, but spatially displaced visual stimulus.

CROSSMODAL INTEGRATION DURING ACTIVE OR PASSIVE PROCESSING OF AUDIO-VISUAL STIMULI

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keywords: attention, auditory, visual, humans, ERP

Cross-modal integration is an essential feature of sensory perception. Animal data and more recently human recordings have shown that the integrative processes are mediated by multiple and highly flexible neural operations.

In two previous electrophysiological (ERP) studies, we have examined the neural correlates of multisensory integration when subjects had to actively process (identify or detect) bimodal stimuli. We found that the networks of crossmodal interaction partly depend on the nature of the task and on the sensory dominance of the subject for that task.

Here, we examined whether these integrative networks may be engaged automatically, and if so, whether they differ of those induced in active processing. ERPs were recorded from 35 scalp electrodes in 17 subjects during two forced-choice categorization conditions using the same stimuli. These consisted in two bimodal objects (A and B) defined either by unimodal (auditory or visual) features alone, or by the combination of their two features. The objects were delivered randomly in either form and between each presentation, a letter or a question mark was displayed on the screen. In the first (no-attention) condition, subjects had to ignore the objects and to report whether the series of letters between two question marks formed a word or not. In the second (attention) condition, they had to identify the objects (A or B) and to ignore the letters. In both conditions, cross-modal interactions were measured, before 200 msec, as the differences between the ERPs to bimodal objects and the sum of ERPs to unimodal objects. The results showed significant interaction patterns in both conditions that however differed quantitatively and qualitatively between the two conditions, suggesting that partly different integrative mechanisms were involved in automatic and in attentional processing. In addition, as in previous studies, the effects again depended on the sensory dominance of the subjects.

A SOUND IMPROVES VISUAL DETECTION IN NEGLECT PATIENTS: INTERACTION AMONG SPATIALLY AND TEMPORALLY COINCIDENT AUDIO-VISUAL INPUTS

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keywords: crossmodal integration, visual neglect, and audio-visual interaction

Neurophysiological studies have shown in animals that a sudden sound enhanced perceptual processing of subsequent visual stimuli (Stein & Meredith, 1993). In the present study, we explored the possibility that such enhancement exists also in humans and can be explained with crossmodal integration effects, whereby the interaction occurs at level of bimodal neurons. To this purpose, neglect patients were required to detect brief flash of light presented in one of eight spatial position, either in a unimodal condition (i.e., only visual stimuli were presented) or in a cross modal condition (i.e., a sound was presented simultaneously to the visual target, either at the same spatial position, or at one of the remaining seven possible positions). Moreover, in order to determine the effect of the temporal proximity on auditory-visual interaction, the acoustic and the visual stimuli were presented simultaneously (Experiment 1) or the acoustic stimulus preceded the visual stimulus by 500 ms (Experiment 2).

The results showed an improvement of visual detection when visual and auditory stimuli were originating from the same position in space, or at close spatial disparity (16 degrees). In contrast, no improvement was found when the spatial separation of visual and auditory stimuli was superior to 16 degrees. Moreover, the spatially specific effects were found only when the stimuli in the two different modalities were presented simultaneously (Experiment 1); at an interval of 500 ms, no response enhancement was found. Finally, the improvement was larger for visual positions that were more affected by the spatial impairment, i.e., the most peripheral positions in the left visual field.

In conclusion, the results of the present study showed an increased visual detection under condition of spatially and temporally specific combination of auditory and visual stimuli, according with the spatial and temporal principles underlying crossmodal integration at neuronal level.

RECALIBRATION OF AUDITORY-VISUAL SPACE: SPATIAL EXTENSION

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keywords: ventriloquism, adaptation, generalization, spatial extension

Introduction

The ventriloquism aftereffect is a shift in the apparent location of a sound source consequent on exposure to synchronous, but spatially disparate audio-visual stimulus pairs[1]. It indicates that the perceptual system has recalibrated its mapping between auditory and visual space. But how are these two spaces related? We investigated this by testing whether adaptation to an audio-visual stimulus pair presented at only one location in space, affected other locations as well. If mapping between auditory and visual space is based on simple local associations, one expects that single-site adaptation should have little or no impact on other locations. Alternatively, mapping between auditory and visual space might be constraint by some general transformation rule. Thus, any local transformation is automatically applied to all other locations.

Method

The experiments used a variation to the pretest-adaptation-posttest paradigm. The pretest consisted of a series of 98 sound localization trials on seven speaker locations (±27°, ±18°, ±9°, and 0° azimuth). The exposure phase and posttest were combined. Subjects were first adapted, for one minute, to an auditory-visual spatial discrepancy of 9°. Critically, the stimulus pair was presented from one location only, either in the median plane (Exp. 1), or in a lateral location (Exps. 2 and 3). Immediately following the exposure phase, sound localization was retested. The seven speaker locations were probed twice. This combination of exposure phase and sound localization was repeated seven times.

Results

In all three experiments the shift was largest at the original position of exposure and showed a linear decrease with distance.

Conclusion

It is clear that the shift was not rigidly applied to all locations, ruling out a general transformation explanation[3]. However, the shift was not exclusively restricted to the original location either. The results support a model of generalization with "semilocal representation"[2].

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CROSS-MODAL RECOGNITION OF SHAPE FROM HAND TO EYES IN HUMAN NEWBORNS

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The hypothesis that the ability to coordinate information between visual and tactual modalities is present at the start of life and dependent on perceptual inherent structures was tested with human newborns. Using an intersensory paired-preference procedure, we show that newborns can visually recognize the shape of an object that they have previously manipulated with their right hand, out of sight. This is the first experimental evidence that newborns can extract shape information in a tactual format and can transform it in a visual format before they have had the opportunity to learn from the pairings of visual and tactile experience and contrary to a host of theories and models of perceptual learning, both traditional (empiricist philosophers) and modern (connectionist).

BEHAVIOR AND ERP CORRELATES OF REDUNDANT VISUAL-AUDITORY STIMULUS PROCESSING

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keywords: ***multisensory facilitation, multisensory regions***

When subjects are required to detect simultaneously stimuli of different modalities (divided attention), shorter reaction times are observed for bimodal as compared to unimodal stimuli. It has been suggested that this “redundant target effect” (RTE) results from a coactivation at some sensory processing stages. Goal of the present study was to determine if pairings with task-irrelevant stimuli cause similar reductions of reaction times, and if the RTE is dependent of the spatial relationship between the two stimuli.

A stimulus discrimination paradigm was used. Auditory and visual stimuli were presented from two loudspeakers with embedded LEDs, located 20° to the left and to the right of the participants. Standard stimuli (70%, with no response relevance) were simple noise bursts or LED flashes from left or right, or bimodal combinations (same side or opposite). Target stimuli (30%) were double flashes or double noise bursts, presented alone, or in combination with a standard (standard-target) or a target stimulus (target-target) of the other modality. Subjects were asked to respond as quickly as possible with a foot pedal when they had detected any target stimulus.

Subjects reacted slowest to simple targets, faster to bimodal standard-target combinations, and even faster to target-target combinations. For all bimodal conditions (standard-target and target-target), subjects gained from spatial congruent presentations. Pooled comparison of the opposite with the same-side bimodal stimulus ERPs revealed a posterior parietal spatial congruency effect, lasting from 170 to 190 ms post stimulus.

The study demonstrated that additional task irrelevant stimuli can also accelerate target detection. Moreover, our results suggest that spatial congruency matters, and that this effect is mediated by multimodal posterior parietal brain regions.

SPATIAL AND TEMPORAL ASPECTS OF VISUO MOTOR INTEGRATION STUDIED WITH DISTRIBUTED INVERSE SOLUTIONS

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Keywords: Linear inverse solutions (LAURA), Poffenberger task, visuo-motor integration, time frequency analysis, neuroelectromagnetic inverse problem

A more comprehensive neuroimaging is essentially linked to the analysis of the fine temporal information available only in electrophysiological techniques (EEG, MEG, ERP). However, these techniques describe neurophysiological processes at the scalp level and possess limited localization value. Here, we present tomographic images of the functioning human brain obtained by solving the electromagnetic inverse problem combining linear distributed models and biophysical constraints. This solution (LAURA, Grave de Peralta et al., 2001) raises the number of sources that can be retrieved with zero localization error without any assumptions about their number and positions (up to 50% from previous 22%). The achieved spatial and temporal resolution permits the dynamic exploration of sensory and cognitive processes. In contrast to hemodynamic techniques, electrically reconstructed tomographic images are directly linked to neuronal processes. Because of their high temporal resolution, these images allow the extraction of information about the short-lived neuronal networks functioning on specific frequency bands and subserving cognitive and sensory events.

Here we present the results of a study aimed at characterizing the spectral and temporal features of visuo-motor integration in a set of normal subjects performing the Poffenberger task. The analysis is performed on the individuals' single trials so as to view spectral features over all frequency bands that might otherwise be obscured by classical averaging procedures. The analysis applies the inverse solution (LAURA) to the single trials and the subsequent analysis of the estimated waveshapes at nodes selected as belonging to specific regions of interest according to the Tailairach atlas. A time-frequency decomposition (complex wavelet) is applied to the estimates at such nodes and the temporal evolution of the energy at the classical frequency bands is obtained, permitting statistical comparisons across conditions and subjects. Such analysis allows us to shed light on the role played by brain oscillations in multisensory interactions. A consistent result over subjects is the presence of statistically significant differences in the alpha and gamma band energy between slower and faster reaction times at the motor area contralateral to hand response execution. An earlier gamma peak at the motor area generally coincident with a gamma burst at the responding visual area is characteristic of the fastest responses. In general, a gamma bursting increase is accompanied by alpha bursting reduction in both scalp and estimated intracranial signals, contradicting the hypothesis that gamma band oscillations are simply harmonics of alpha band.

CROSSMODAL ASSOCIATIVE LEARNING MODULATES FUSIFORM FACE AREA'S RESPONSES TO SOUND

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keywords: FFA, audiovisual associative learning, cortical modulation

Introduction

A traditional perspective is that visual and auditory cortices are tuned to selectively respond to visual and auditory input, respectively (1, 2). However, the brain may also exhibit a high degree of experience-dependent plasticity. Furthermore, it has been observed that cells in primary visual cortex of a normally developed cat brain can be activated by nonvisual stimuli (3, 4). In this experiment we aimed to investigate whether human visual cortex is capable of responding to sounds after learning sound-picture association which render a sound predictive of a picture. More specifically, we hypothesised that not only would visual cortex respond to auditory stimuli, but that if the association was between a tone and a face, with learning the associated tone alone would evoke activation in the fusiform face area.

Methods

For this purpose 12 healthy subjects were scanned while performing an incidental task involving presentation of sounds (pure tones) and pictures (faces or a moving pattern), either associated (sound-picture) or alone. MRI data were acquired in a 1.5T Siemens scanner. Data analysis was performed using spm99. Scans were realigned, slice-timing corrected, normalised and smoothed with an 8mm kernel. Subsequently, the data were statistically analysed using a random effects model.

Results

Comparing time by condition interactions for a tone that was paired to a face half of the time versus a tone that was always presented alone and masking this by the main effect of face alone, we found that activation in right fusiform gyrus ($x=21$, $y=-75$, $z=-6$; $Z=2.63$; $p<0.05$ uncorrected) increased exponentially over time relatively more than the unassociated tone. However, it was also observed that right dorsolateral prefrontal cortex ($x=57$, $y=21$, $z=21$; $Z=5.21$; $p<0.05$ corrected) decreased exponentially in activation over time.

Conclusion

These results show that visual cortex can respond to auditory stimuli and more specifically functionally specialised visual areas, such as the fusiform face area, can respond to sounds which, through associative learning, become predictive of a face. The activation in this area increases over time as a function of learning. Furthermore, a region of the right dorsolateral prefrontal cortex seems to be involved in the early stages of associative learning and decreases in activation when the material becomes familiar.

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ROUGHNESS INTEGRATION IN VISUOTACTILE PERCEPTION OF TEXTURE

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Keywords: Roughness texture vision touch integration

Three varieties of forced-choice task were used to investigate the multisensory integration of textile-roughness ('pilling') information between vision and touch. In a first experiment, visual, tactile and bimodal roughness discriminations were made between pairs of stimuli, using a 2-interval forced-choice method. Visuotactile discriminations were typically performed with sensitivity somewhere between that seen for the unimodal presentations. In the second experiment, a similar design was used except that during the stimulus presentation, one interval contained a unimodal (vision or touch) stimulus, the other interval a bimodal presentation. Bias toward the bimodal interval would indicate roughness additivity for such presentations. This type of bias was not seen. In Experiment 3, participants were required to make bimodal discriminations, determining whether a rough stimulus was presented to touch, to vision, to both modalities, or to neither modality. Performance in this experiment (still in progress) will allow the interaction between vision and touch to be further quantified, determining whether the 'averaging' pattern of performance reported in the earlier experiments is due to trial-wise attentional shifting or some other pattern of integration between the senses for multisensory roughness perception.

MULTISENSORY CONVERGENCE IN MACAQUE AUDITORY CORTEX & ITS RELATIONSHIP TO THE ANATOMICAL ORGANIZATION & BEHAVIORAL FUNCTIONS OF THE AUDITORY SYSTEM

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keywords: *Auditory, Somatosensory, Primate, Bimodal, Sensory, Cortex*

Current models of auditory cortical organization in primates include a central core region of two to three areas with characteristics of primary cortex, surrounded by belt and parabelt regions containing multiple nonprimary areas. The core, belt, and parabelt regions represent successive hierarchical stages of processing, while subdivisions of each region appear to process at least some inputs in parallel (Hackett et al., 1998). The caudal belt and parabelt areas are preferentially connected with areas in lateral intraparietal and prefrontal cortex associated with the processing of spatial related information, whereas the rostral belt and parabelt areas have stronger connections with ventral and orbital prefrontal domains associated with the processing of nonspatial information. Compared to neurons in the rostral belt areas, neurons in the caudal belt fields have greater spatial selectivity for complex sounds, including species-specific vocalizations. By comparison, neurons in the rostral belt areas exhibit reduced spatial selectivity and are more selective for the type of call (Tian et al., 2001). These findings support the hypothesis that cortical processing of spatial and nonspatial auditory information is performed in specialized streams (Rauschecker & Tian, 2000). The propensity for spatial processing in caudal superior temporal cortex is consistent with growing evidence of auditory and somatic sensory convergence in the temporoparietal region of the primate brain. In addition to connections with caudal belt and parabelt areas of auditory cortex, the temporoparietal area (Tpt) has connections with the superior temporal sulcus, lateral intraparietal cortex, caudal prefrontal cortex, and thalamic nuclei with multimodal inputs (e.g., suprageniculate, limitans, and pulvinar nuclei). Neurons responsive to auditory and somatic or visual inputs were found in Tpt by Leinonen et al (1980), but the multimodal properties of this region had not been explored further until recently. Schroeder et al (2001) sampled multi-unit and current source density profiles in the core area, AI, and a caudal belt area adjacent to AI, known as CM (caudomedial area). Only sites in CM were found to be responsive to both auditory and somesthetic stimulation. In a subsequent study (Fu et al, 2002) single- and multi-unit recordings from AI and CM revealed that single neurons in CM were responsive to both auditory and cutaneous stimulation. These neurons were responsive to pure tone acoustic stimuli, but more broadly tuned than neurons in AI. Cutaneous receptive fields were also broad, often bilateral, and included areas on dorsal hand surfaces, but appeared biased toward a representation of the face, head and neck. CM is known to receive auditory cortical inputs from the core region, especially AI, and is considered to lie in the second tier of the auditory processing hierarchy. Subcortical auditory inputs primarily arise from the dorsal (nonprimary) divisions of the medial geniculate complex. Other inputs to CM include LIP of the posterior parietal cortex (Lewis & Van Essen, 2000) and the magnocellular division of the medial geniculate complex, both of which may be sources of somatic sensory input to CM. The somatic representation in CM is unexpected, given its position at an early stage of auditory cortical processing, but the bias of the somatic input toward the head and neck is consistent with its integration into the proposed stimulus localization (spatial) functions of the caudal auditory cortices. The demonstration of multisensory convergence in CM challenges the view that such processing occurs only in “higher-order” cortical domains.

AUDIO-TACTILE LINKS IN SUSTAINED SPATIAL ATTENTION: AN ERP STUDY

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keywords: *spatial attention, tactile, auditory, crossmodal*

There is an increasing number of studies, both in animals and humans, suggesting that spatial representations in the brain are shared by different sensory systems.

The goal of the present study was to test, if crossmodal links between audition and touch exist and at which processing stage spatial attention in audition may influence the processing of tactile stimuli and vice versa.

Event-related brain potentials (ERPs) were recorded while tactile (pins at the index fingers) and auditory stimuli were presented at the left or right side with respect to the participant's body midline. Task of the participants was to attend to one, either the auditory or tactile modality, and to respond to double-stimuli of either the left or right side.

Results showed that spatial attention modulated both early and late auditory and somatosensory ERPs when audition and touch were relevant, respectively. Moreover, early auditory (N1) and somatosensory (N80, N150) potentials (but not later deflections) were affected by spatial attention as well when they were irrelevant, demonstrating bi-directional crossmodal links between audition and touch. ERPs were generally more pronounced to stimuli when they belonged to the attended vs. non-attended modality suggesting additional intermodal selection mechanisms.

The present results provide evidence for the existence of both spatial and intermodal selection mechanisms that influence early processing stages in parallel.

TOOL USE-INDUCED PLASTICITY OF VISUO-SOMATOSENSORY INTEGRATION IN THE MONKEY PARIETAL CORTEX

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Keywords: *monkey, parietal cortex, body-image, tool-use*

Bimodal (visual and somatosensory) neurons in the monkey intraparietal cortex code the image of the self-body, which is subject to intentional modification: When trained to use a tool, it becomes an extension of the hand both physically and perceptually, resulting in alteration of the body image in accordance with the characteristics of the tool at hand. In above bimodal neurons, use-dependent expansion of the receptive field occurred only when the monkeys held a tool and intended to use it as an extension of their hand. These findings may constitute the neural correlate for modification of the body schema as a basis of assimilation of the tool into our own body. Also, we found that these neurons can also code the body-image projected onto the video monitor, perhaps corresponding to its "iconic" representation. During the course of training, behavioral analyses suggested that a novel mode of somatosensory-visual integration seemed to develop in order to organize adequate bodily movement to manipulate the tool, possibly subserved by reformation of the neural circuitry in which molecular genetic processes in the cortical area described above are involved. When these representations were further advanced, it would become totally free from physical constraints of the actual world to become a (pre-)symbolic one to represent evolutionary precursors of higher cognitive functions, and might eventually lead to evolution of human language or to the metaphysical thoughts. We are now extending these studies (by combining behavioral, electrophysiological, neuroanatomical, molecular biological, and positron emission tomography imaging techniques) to examine cortical mechanisms subserving tool use-induced on-going plasticity and maintenance of the mode of visuo-somatosensory integration in the parietal cortex.

MONOLOGUE, DIALOGUE OR DISCUSSION FORUM WITH THE OTOLITHS: A SINGLE MULTISENSORY SYSTEM

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Keywords: *vestibular system, otoliths, spatial orientation, human.*

In order to understand the role played by the otoliths of the vestibular system during self-motion perception and estimation, I have long tried to let them speak alone. Alone means that subjects were passively transported along linear paths in complete darkness. But alone, when studying self-motion, means together with the somatosensory system which cannot be separated from the vestibular one, on earth. And alone means that all the movement parameters (distance, velocity, acceleration) were measured by the otolith-somatosensory system.

And the otoliths didn't speak, just enough to tell that they are necessary to estimate a passively travelled distance in the dark.

But during self-driven reproduction of passively travelled linear distances in the dark, the otoliths did not bother to compute the distances length, and disregarded distances duration.

When we presented a visual target before linear motion, the otoliths whispered that the estimation of visual distance was also involved, so that they were not responsible for the errors that the subjects produced during the self-travelled distance.

When we added specific training to facilitate visual distance estimation, the otoliths shouted that movement duration is critical; furthermore they suggested that different types of distance or space do exist.

During triangular 2D motion, the otoliths argued that passive linear distances in light are longer than in the dark.

During circular 2D motion in the dark, the otoliths claimed that they need to chatter with the semi-circular canals to know self-motion orientation.

Future experiments include: distance estimation of self-driven transport, velocity perception with stabilizing a laser-pointer during 2D self-motion, interaction of distance and time estimation....

It could be thought that the perception and estimation of self-motion is crucial for orientation and navigation in space. As the otoliths are the only sensory organs dedicated to linear self-motion (and tilt) in human, and since linear motion is the most common self-displacement that we use (by walking, swimming, driving...), it could be thought that the otoliths do represent our navigation sense.

However, spatial orientation must be allocentric (spatiotopic) to be efficient: it must be multisensory. The fact that the otoliths are themselves both dependent upon, and greatly influenced by other sensory systems, suggests that they are indeed considered by the brain as our navigation system: their fragility is intended to ensure multisensoriality of navigation in space. The large idiosyncrasy encountered in vestibular navigation tasks points at their hidden multisensoriality.

TWO CORTICAL AREAS FACILITATE MULTISENSORY INTEGRATION IN SUPERIOR COLLICULUS (SC) NEURONS AND SC-MEDIATED BEHAVIORS

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***Keywords**: physiology, behavior, cross-modal, cortical deactivation.*

The current study examined the role of two corticotectal regions (the anterior ectosylvian sulcus [AES] and the rostral lateral suprasylvian sulcus [rLS]) in multisensory integration. Physiological experiments examined the multisensory properties of 70 SC cross-modal integrative neurons in cats with cryogenic deactivation probes chronically implanted within AES and rLS. Nearly all (93%) of the SC neurons studied lost their capacity for multisensory enhancement when these cortices were deactivated, and often did so without substantially altering their modality-specific responses. In many (49%) of the SC neurons studied, multisensory integration depended on only one of these cortical areas (37% AES, 4% rLS), but many (52%) depended on the integrity of both areas. Behavioral experiments then examined the impact of cortical deactivation on orientation to sensory cues. Cats were trained in a perimetry device to approach near-threshold visual (LED) and ignore an auditory (white noise) stimulus. These modality-specific stimuli were then presented at various locations either (a) alone, (b) in combination at the same location (spatially coincident), or (c) separated by 45° (spatially disparate). In control conditions, the animals showed enhanced success rate (96% ± 9%) to spatially-coincident visual-auditory stimuli, and degraded success to spatially-disparate stimuli (18±15%, centrally disparate) as compared to the visual target alone (40%±18%). However, enhanced performance to spatially coincident stimulus pairs was lost during AES or rLS deactivation, and the normally degraded performance to spatially disparate stimulus pairs was significantly ameliorated, despite the fact that responses to modality-specific stimuli were unchanged. The similarity of the effects of cortical deactivation on single SC neurons and presumptive SC-mediated behaviors supports the postulate that corticotectal influences from AES and rLS are essential for SC neurons to synthesize cross-modal cues, and that compromising this capability in a substantial proportion of SC neurons disrupts overt multisensory orientation behavior. Supported by NIH grants NS 22543 and NS 36916.

VISUAL-AUDITORY INTERSTIMULUS CONTINGENCIES IN AURALLY GUIDED SACCADES

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keywords: multisensory facilitation, saccadic reaction times, aurally guided saccades

It is now a well-established fact that spatial and temporal proximity of a visual and an auditory stimulus can modulate manual as well as saccadic reaction time (Colonius & Arndt, 2001). However, it is less clear whether these effects can still be enhanced by the use of interstimulus contingencies (Lambert et al., 2000).

This question was addressed in a new experimental procedure (Kirchner, 2001) in which the probability of presenting an auditory target stimulus at a certain location was varied in dependency of the occurrence of a visual accessory stimulus at the same or at the opposite location. The auditory stimulus was presented via a virtual display either right or left of fixation. The conditional probability that the auditory target occurred in the same hemisphere as the visual stimulus was 20%, 50% or 80%, in different blocks of trials. Saccadic reaction times to the unimodal visual or auditory stimuli were measured in separate blocks at the end of the sessions.

The results in the bimodal trials showed facilitation in the 80% contingency and inhibition in the 20% contingency compared to the control condition (50%), but only in those trials in which the stimuli were presented in opposite hemispheres (invalid). Latencies in the trials in which the stimuli were presented at the same location (valid) were significantly shorter than in the invalid trials. Furthermore, saccadic latencies in the valid bimodal trials showed intersensory facilitation (bimodal, auditory shorter than visual). Latencies in the invalid bimodal trials, on the other hand, showed intersensory inhibition (bimodal longer than visual, auditory).

These results suggest that the processing of visual-auditory stimuli can be modulated by a top-down control in the form of interstimulus contingencies. However, this effect only emerges if subjects have to choose between saccade directions (invalid trials). The observed multisensory facilitation (resp. inhibition) effects further support this conclusion: In invalid trials, subjects first have to inhibit an automatic orienting response to the visual stimulus before they can voluntarily program a saccade in the direction of the auditory target, thereby using the predictive context of the contingencies.

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ADAPTATION TO VISUAL MOTION-IN-DEPTH PRODUCES AN AUDITORY AFTEREFFECT

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Keywords: *cross-modal aftereffect, adaptation, auditory, visual, motion-in-depth*

It has been implicitly assumed that motion aftereffects reflect fairly low-level neural processing and that they do not occur across sensory modalities. In this study, we report that an auditory aftereffect occurs from adaptation to visual motion in depth. After a few minutes of viewing a square moving in depth (size-changing or retinal-disparity-changing), a steady sound was perceived as changing loudness in the opposite direction. Adaptation to a combination of auditory and visual stimuli changing in a compatible direction increased the aftereffect and the effect of visual adaptation almost disappeared when the directions were opposite. On the other hand, listening to a sound changing in intensity did not affect the visual changing-size aftereffect. The visual effect on the auditory aftereffect was also observed when the test sound was presented to left ear only. However, when the adapting sound was also presented to left ear only, the visual effect disappeared. The results provide psychophysical evidence that, for processing of motion in depth, the auditory system responds to both auditory and visual motion in depth.

BRAIN OSCILLATORY RESPONSES DURING AN AUDIOVISUAL MEMORY TASK – AN MEG STUDY

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Keywords: *brain, oscillations, audiovisual, MEG, memory*

Brain oscillatory responses during an audiovisual memory task were studied in twelve adult subjects (six males) by means of the magnetoencephalography (MEG) using graphically (letters), visually (articulating face), acoustically (voice) and audiovisually (articulating face and voice) presented vowels as stimuli. ERD/ERS (event-related desynchronization/synchronization) responses were calculated for the 1-45 Hz MEG frequencies during memory encoding and retrieval for all stimuli. The encoding and retrieval of material presented in different modalities evoked distinct patterns of brain oscillatory responses. Both encoding and retrieval of letters were accompanied by ERD (i.e., relative power decrease) in the theta and alpha frequencies. In contrast, the encoding of acoustic information was accompanied by theta, alpha and beta rhythm ERS (i.e., power increase) responses, the encoding of visual information by a "narrow band" alpha ERS whereas audiovisual encoding was accompanied theta and alpha ERS. During retrieval of acoustic, visual and audiovisual material, initial theta, alpha and beta rhythm ERS responses were evoked which were followed by alpha and beta rhythm ERD responses. We summarize our findings as follows: First, the brain oscillatory responses evoked by the encoding and retrieval of letters differed considerably from the responses obtained during the encoding and retrieval of acoustic, visual and audiovisual material. Second, the ERD/ERS responses obtained during the encoding of visual material (articulating face) resembled more those obtained during the encoding of acoustic information than those observed during the encoding of letters. Third, the encoding of acoustic information was accompanied by a broad frequency alpha ERS, the encoding of audiovisual material was accompanied by a narrower frequency alpha ERS and the encoding of visual material was accompanied by the narrowest frequency alpha ERS. Fourth, the ERD/ERS responses during the presentation of audiovisual material were not merely the sum or average of the acoustic and visual ERD/ERS responses.

IDIOSYNCRATIC USE OF CONFLICTING VISUAL AND NON-VISUAL INFORMATION FOR THE MEMORIZATION OF A PATH TRAVELED IN VIRTUAL REALITY

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keywords: spatial memory, sensory conflict, virtual reality, human, multisensory interaction

Studies of sensory interactions in self-motion perception suggest that prolonged exposure to sensory conflicts induces a modification of the relation between sensory modalities. Within most models conflicts are solved by a weighting process. However, the inter-individual variability of such a process remains to be clarified. The present study focused on the effect of mismatched visual and non-visual information on the reproduction of actively performed turns. Standing subjects viewed a virtual corridor in which forward movements were simulated at a constant linear velocity, and rotations were actually performed. They were asked to learn the trajectory and then to reproduce it from memory in total darkness. In the baseline condition, the relative amplitudes of visual and non-visual information for the performed rotations were the same, but were systematically manipulated in six "sensory conflict" conditions. The subjects carried out these seven conditions ten times (10 sessions), with a delay of at least two days between each session.

The data allowed us to distinguish between three groups of subjects according to their use of visual and non-visual information. Out of ten subjects, five reproduced rotations on the basis of visual information during active blindfolded movements, while three subjects rather relied on non-visual information. Finally two subjects seemed to switch from visual to non-visual information across the conditions. These two subjects also differed from the others by 1) their feeling of difficulty of the task and 2) their relative inaccuracy in reproducing essential features of the trajectories. According to the results, the relative weight of conflicting cues for spatial memory of routes would be subject-dependent. Furthermore, it seems that the instability of the perceptual decision (i.e. selection of either visual or non-visual information) is associated with lower performance and weaker self-confidence in performing the task.

ATTENDING POINTS IN TIME

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<u>*keywords:*</u> *time processing, cross-modal binding, event-related potentials, attention*

Input of different sensory systems is most likely integrated on the basis of stimulus properties common to all modalities. The most often investigated supramodal feature is the location of an event in space. However, of similar importance is the point in time when an event happens. Input from different sensory channels is more likely attributed to the same object if it is perceived to emerge at the same than at different points in time.

The goal of the present study was to test if attention can be allocated flexibly in time as it has been observed for space and if so, which processing stages are modulated by allocating attention to different points in time.

Empty intervals of 600 and 1200 ms duration, defined by auditory on- and offset markers, were used. Participants were instructed to attend to the ending of one interval and to detect rare deviant offset markers of that interval, only. Event-related potentials (ERPs) were averaged for the more frequent "standard" offset markers (which were not associated with any response) separately for the attend-short and attend-long intervals. Results show that early auditory ERP deflections (in particular the N1) were modulated by attending a point in time. This implies that perceptual processing stages are affected by the allocation of attention in time. Slow negative shifts that developed after the presentation of the onset markers showed a differential preparation as a function of which interval was relevant in a run, indicating a flexible control of attention along the time dimension.

The present study suggests that attention can be flexibly controlled in time and moreover modulates early perceptual processing stages. The moment when an event arises, therefore, most likely serves as an important supramodal feature to bind input of different sensory systems together.

HUMAN INFANTS' PERCEPTION OF AUDIOVISUAL TEMPORAL STRUCTURE

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A number of recent studies have shown that human infants are sensitive to the statistical distributional properties of auditory and visual input. Underlying this sensitivity is an ability to perceive the temporal distribution of sensory input and there is no doubt that this ability is a fundamental precursor to the development of higher-level perceptual and cognitive skills related to the development of action sequencing, social interaction skills, and language abilities. In my laboratory we have been studying the developmental precursors to these skills by investigating infants' perception of bimodally specified temporal structure. In this talk, I report the results from a series of studies addressing this issue. First, I review the results from our studies in which we asked whether infants can perceive audiovisual temporal structure specified by rhythmic patterns and whether intersensory temporal synchrony is important for the perception of such patterns. I show that regardless of whether a bimodal rhythm is instantiated by a bimodally specified sequence of syllables spoken in a rhythmical manner or whether it is instantiated by a moving/sounding object bouncing in a rhythmical manner, infants can easily perceive its rhythmical character. Second, I show that infants' sensitivity to the synchrony between the auditory and visual components making up bimodal rhythmic patterns is subordinate to their sensitivity to the rhythmic pattern cues. Third, I show that infants' ability to perceive bimodal rhythmic patterns is limited in that they are unable to perceive the constancy of a given rhythmic pattern in the face of variations in its overall temporal rate. Finally, I discuss the results of studies on infants' perception of bimodally specified temporal serial order and show that infants can encode serial order information but that selective attention to audio-visual synchrony relations can actually interfere with its perception. When considered together, the results show that infants possess some impressive multimodal temporal perception skills and provide interesting insights into how the audible and visible components of temporally structured information interact with one another.

INTERSENSORY REDUNDANCY FACILITATES PERCPETUAL DISCRIMINATION, LEARNING, AND MEMORY IN INFANCY

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Keywords: infancy; intersensory perception; development of multimodal responsiveness

Despite the fact that the infant's world is inherently multimodal and that virtually all perception, learning, memory, and social development emerge in this multimodal context, the majority of research in developmental psychology has focused on the development of skills in only a single sensory modality at a time. Further, research findings from human and animal infant studies of intersensory functioning have rarely informed the other. Our research program integrates studies of human and animal infants to address the role of multimodal stimulation in guiding and constraining the development of early perception, learning, and memory. We have proposed an intersensory redundancy hypothesis to describe how information presented redundantly and in temporal synchrony to two or more sense modalities recruits infants' attention and facilitates learning of bimodally specified properties (amodal information). Consistent with research from neural studies demonstrating hightened neural responsiveness to redundant multimodal stimulation, our labs have shown that embryos and young infants demonstrate enhanced perceptual discrimination, learning, and memory as a result of congruent multimodal stimulation as compared with unimodal stimulation. For example, research has demonstrated that human infants discriminate the amodal properties of rhythm and tempo when presented in two sense modalities (auditory-visual), but not when presented to one sense modality alone (auditory or visual). Similar facilitating effects of redundant bimodal stimulation on learning and memory for a maternal call have been found in quail embryos and hatchlings. Embryos receiving redundant visual stimulation with a maternal call learned the call four times faster and remembered the familiar call four times longer than embryos receiving no redundant visual stimulation. These converging findings across human and animal infants highlight the importance of intersensory redundancy in facilitating perceptual discrimination, learning, and memory during early development. The salience of intersensory redundancy gives an initial advantage to the perceptual processing of stimulus properties that are bimodally specified (synchrony, rhythm, tempo, intensity) as opposed to other stimulus properties (modality-specific) in a given episode of exploration, thereby guiding and constraining infants' selective attention.

VISUO-TACTILE BINDING SITES ARE MODULATED BY SPATIAL COHERENCE, ATTENDED MODALITY AND TASK: AN FMRI STUDY

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keywords: ***fMRI, vision, touch, multisensory, integration***

Introduction

Recent human neuroimaging studies have suggested that the inferior parietal lobe may play an important role in the binding of visual and tactile co-ordinate information[1]. The following study aimed to firstly identify sites of visuo-tactile integration using statistical interaction techniques and then test whether manipulating attention to either the visual or tactile modality or the nature of the task (simple detection vs. intensity discrimination) would modulate these binding sites.

Method

A mixed block/event-related design was used in order to present unpredictable sequences of unimodal (visual **or** tactile) and bimodal (visual **and** tactile) single events within blocks where attention could be directed to either the visual or tactile modality. In addition, bimodal events could either be together in space (congruent) or apart (incongruent). Reaction times were simultaneously collected for comparison with imaging results.

Results

Sites of visuo-tactile integration were first identified by looking for bimodal responses that were greater than the algebraic sum of the two unimodal conditions - "multisensory integration"[2]. This strategy identified a core network of regions putatively involved in the crossmodal binding of visual and tactile co-ordinate information including the caudate nucleus, intraparietal sulcus, superior parietal lobule and posterior cingulate gyrus. When bimodal inputs were spatially congruent activation was identified exclusively in the caudate nucleus, parahippocampal gyrus and posterior cingulate gyrus. When attention was directed to vision activation occurred preferentially in the intraparietal sulcus whereas attention to touch activated the caudate nucleus. Finally, discrimination but not detection activated frontal cortex, which is consistent with previous studies implicating this region in crossmodal object binding[3].

Conclusion

An interaction analysis identified a network of regions putatively involved in the binding of visual and tactile co-ordinate information. Further, this network could be modulated by explicitly changing the spatial, attentional and task-related parameters and the relation to task performance. This alludes to a more 'context-related' recruitment of visuo-tactile binding sites than previously suggested.

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REFERENCE FRAMES AND PERCEPTION OF ORIENTATIONS: BODY AND HEAD TILT EFFECTS ON THE HAPTIC AND VISUAL OBLIQUE EFFECT

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keywords: reference frames, oblique effect, perception of orientations, subjective vertical

The "oblique effect" reflects the more accurate processing of vertical and horizontal orientations relative to oblique orientations. The aim of this research was to examine the effect of whole body tilts on the haptic and visual reproduction of orientations ("Class 2" oblique effect in the Essock's 1980 terminology). Two series of experiments were carried out, respectively, on visual and haptic perceptivo-motor systems. Body or head tilts lead to a mismatch between egocentric (trunk/head and retinotopic axes) and gravitational axes and indicate whether the oblique effect is defined in an egocentric or a gravitational reference frame. The ability to reproduce gravitational (vertical and horizontal) and oblique orientations was studied in upright and tilted postures. Moreover, by controlling the deviation of the visual and haptic subjective vertical provoked by body tilt, the possible role of a subjective gravitational reference frame was tested. Results showed that both the haptic and visual reproduction of orientations were strongly affected by the position of the body. In particular, the classical oblique effect observed in upright posture disappeared in tilted conditions, mainly because of a decrease in the precision of the vertical and horizontal settings. The subjective vertical appeared to be the orientation reproduced the most precisely. These results suggest that the oblique effect is not purely gravitationally or egocentrically defined but, rather, could depend on a subjective gravitational reference frame which is tilted in the same direction that the body tilts in visual modality and in opposite direction on haptic modality. Then, the strong effect of the modality used to reproduce the orientations questions the central origin of this frame of reference.

TOOL-USE CHANGES VISUAL-TACTILE SPATIAL INTERACTIONS IN THE NORMAL AND DAMAGED BRAIN

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Keywords: *Vision, Touch, Tool, Attention, Space processing, Brain damage*

Introduction

When we wield a long tool, we extend our possible reaching space. We can touch distant objects with the tool, so that tactile information felt at the hand can now relate to visual information from distant objects. Moreover, a hand located on, say, the right side of space may contact visual objects in the left visual field with the tool, or vice-versa, given that tools can be wielded in innumerable different postures. This means that the spatial mapping between tactile stimulation at the hand, and any related visual information near the end of the tool, alters as a tool is used. A wielded tool may become incorporated into the 'body schema', such that the end of the tool effectively becomes an extension of the effecter wielding it. Here we examined whether experience in actively wielding a long tool can modulate automatic aspects of visual-tactile spatial integration for normal human subjects and a right brain damaged patient with left crossmodal extinction (i.e. unawareness of left touch with simultaneous right visual stimulation).

Methods

In a visual-tactile interference paradigm, subjects judged whether tactile vibrations arose on a finger or thumb (upper vs. lower locations), while ignoring distant visual distracter lights, fixed in vertical pairs (again in upper or lower locations) at the far end of each of two “tools” grasped with each hand. Previous work using visual distracters located on the hands showed that judgements of such tactile stimuli are slower and/or less accurate when the concurrent visual distracter is incongruent (i.e. upper vibration with lower light, or vice versa). Importantly, this crossmodal interference has repeatedly been found to be stronger when visual and tactile stimuli appear on the same side of space (e.g. right visual field stimulation paired with vibration on the right hand). Here we tested whether actively wielding a long tool can alter this crossmodal mapping plastically, such that when the tools are held crossed (connecting the right hand to the left visual field, and vice-versa), crossmodal interference might now become larger from visual distractors in the opposite visual field to the tactually stimulated hand.

Results

We show that actively wielding tools can change this pattern of crossmodal interference. When such tools were held in crossed positions (connecting the left hand to the right visual field, and vice-versa), the spatial constraints on crossmodal interference reversed, so that visual distracters in the other visual field now disrupted tactile judgements most for a particular hand. This phenomenon depended on active tool use, developing with increased experience in using the tool.

A logically related result was found in a right brain damaged patient showing extinction of left touch by right visual stimulation. The patient was trained to reach for object in the right visual field, using the rake with the left hand. After the training, the same right visual stimulus which produced strong left tactile extinction before training, now produced significantly less extinction.

Conclusions

We discuss these results in terms of change of the hand representation in the body schema, which can effectively modulate crossmodal spatial attention in the normal and damaged brain.

AUDITORY-SOMATOSENSORY MULTISENSORY PROCESSING IN AUDITORY ASSOCIATION CORTEX: AN FMRI STUDY

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Using high-field (3 Tesla) functional magnetic resonance imaging (fMRI), we demonstrate that auditory and somatosensory inputs converge in a sbregion of human auditory cortex along the superior temporal gyrus. Further, simultaneous stimulation in both sensory modalities resulted in activity exceeding that predicted by summing the responses to the unisensory inputs, thereby showing multisensory integration in this convergence region. Recently, intracranial recordings in macaque monkeys have shown similar auditory-somatosensory convergence in a subregion of auditory cortex directly caudomedial to primary auditory cortex (area CM). The multisensory region identified in the present investigation may be the human homologue of CM. Our finding of auditory-somatosensory convergence in early auditory cortices contributes to mounting evidence for multisensory integration early in the cortical processing hierarchy, in brain regions that were previously assumed to be unisensory.

HIGH TEMPORAL RESOLUTION FMRI IN A VISUAL-MOTOR TASK: DELAYS IN BOLD RESPONSES

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Keywords: *brain connectivity, fMRI, visual, motor*

Purposes

During a complex task, some of the different regions of the brain involved in the process may be activated sequentially. Delays can be observed in the BOLD signals between the activations of these areas and may be related to the transfer of the information. Estimated delays could reflect the activation order across brain regions. We propose a method to evaluate these delays using an Event-Related fMRI experiment.

Methods

The paradigm was a visual-motor task. During continuous MR acquisition, a checkerboard was randomly presented about every 16s in either the right or in the left hemifield (lateralized 9.5°; 100ms duration; randomized across trials). Each time the subject saw the checkerboard, he had to press a sequence of keys on a pad with one hand.

Functional images were obtained using a single shot gradient-echo EPI sequence (TR = 2s, TE = 60ms, FoV = 240mm, matrix size 64x64), at 1.5T. Each volume was made of 16 images parallel to the bicommissural plane covering the entire brain (slice thickness 5mm, gap 1mm). The Inter Stimulus Interval varied randomly from 14.125 to 17.875s by steps of 125ms. This allowed the sampling of the BOLD signal with a time frame of 125ms. The checkerboard appeared 32 times for each visual hemifield, to achieve a signal averaging of 2. Each session was made of 512 sets of images. Ten right-handed subjects were been studied during two sessions. They were asked to respond with the right hand during the first session and with the left one during the second. Reaction times were recorded. Data analysis was carried out using SPM99. Data were spatially and temporarily realigned, normalized and smoothed (FWHM = 9mm), and analyzed to detect the regions activated during the task. Finally, the time series from interesting activated clusters were extracted from the preprocessed images. The BOLD signals were reconstructed using the averaging technique, and time delays were analyzed.

Results

Activations were detected in the striate and extrastriate visual cortex, predominantly on the side contralateral to the stimulus. V5 was activated bilaterally. In the motor area the activations were mainly located in the SMA and in the M1 region corresponding to the hand motion. Measurements of time delays of the BOLD signal showed sequential activations of V5/MT, V1 and SMA (almost at the same time) and finally M1. The delay of the activation of M1 was correlated to the mean reaction time, while there was no correlation for V1. These results are in favor of a correlation between BOLD time course and the underlying neuronal activity.

Conclusions

The ER-fMRI protocol developed in this study, allowed the study of BOLD responses with high temporal resolution during complex tasks. This opens the door to a new approach to brain connectivity. Also these data can be compared to the ones obtained by ERP-EEG techniques under similar tasks.

MULTISENSORY INTEGRATION AT PREATTENTIVE AUDITORY PROCESSING: EFFECTS OF GAZE, VISUAL AND TACTILE STIMULI ON MISMATCH FIELDS

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Keywords: *auditory cortex, whole-head magnetoencephalography, mismatch negativity, gaze direction, visual-tactile gating*

In non-human primates, multisensory neurons were found in secondary auditory cortex. In humans, whole-head magnetoencephalography (MEG) allows studying non-invasively the left and right acoustic areas seperately. Mismatch negativity (MMN) or fields (MMNm) are measures of preattentive change detection.

The present study thought to investigate the interaction of multisensory spatial information as reflected by MMNm. Responses to spatially separated sounds (dichotic noise bursts) were tested during asymmetric presentation in other modalities. We modified

a) gaze direction
b) motion field direction
c) unilateral visual input
d) tactile stimulation during the randomised occurrence of duration deviants at either ear.

In all cases of lateralized co-stimulation (a, c, and d), change detection, i.e. MMNm amplitude, increased at the same acoustic hemi-space as compared to the other side. Horizontal motion fields (b) did not yield this effect. The interaction of the deviant side with the eye position was the strongest. Conceivably, in humans as in other primates, eye position induces lateralized gating at the brainstem reflected at cortical neuronal activations. Simple visual and tactile stimuli affect preattentive processing and, thus, suggest early functional connectivity between the sensory areas. Due to the behavioural relevance of attention modulating processes, multisensory stimuli have to be taken into account for human information processing.

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MIRRORS AND MIRROR CELLS IN MULTISENSORY PERCEPTION: VISUO-TACTILE AND VISUO-MOTOR INTERACTION AND INTEGRATION

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Keywords: *Visuo-tactile facilitation, learning, mirrors*

Vision of a body site, without proprioceptive orienting of eye and head to that body site, can facilitate tactile perception, when that body site viewed is the hand (which can be seen directly under normal viewing conditions) (Tipper et al., 1998). Subsequent research has shown (i) that vision similarly affects tactile perception at body sites that cannot normally be viewed directly, such as the face or neck (ii) prior experience e.g., with mirrors, influences such visuo-tactile links, and (iii) there is a temporal window within which such visual information can affect tactile target detection.

One explanation for the visuo-tactile effect observed is that a form of visuo-tactile spatial transfer occurs, whereby the subject perceives themselves within the spatial frame of reference of the observed individual. The discovery of mirror neurons (Rizzolatti et al., 1996), cells that respond both during performance of an action and during passive observation of another performing that same action, may support this interpretation. Since their discovery, their function has been speculated to include learning, motor control and empathy to theory of mind and language. The potential importance of the action-observation system in visuo-motor and visuo-tactile transfer will be discussed in the context of this work.

CORTICAL CONNECTIVITY UNDERLYING INHIBITORY CROSS-MODAL CONVERGENCE

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For multisensory behavioral and perceptual effects to occur, information from the different sensory modalities must converge onto individual neurons. The most obvious and well known form of multisensory neuron is one which receives excitatory inputs from more than one sensory modality. These neurons respond with excitation to either modality input alone, (usually) integrate the resultant activity when the two modalities are combined, and have been well documented throughout the neuroaxis and across phylogeny. However, recent studies in this laboratory suggest that multisensory convergence may occur in other, fundamentally different forms.

Tract tracing methods identified that projections occur between the auditory field in the Anterior Ectosylvian sulcus (FAES) and the fourth somatosensory (SIV) representation in the cat cortex. Standard electrophysiological recordings in SIV, however, failed to reveal the expected bimodal neurons, suggesting that the auditory inputs from FAES to SIV must either be subthreshold, or inhibitory. These alternatives were tested in chronically prepared, anesthetized cats. Extracellular recordings were made from SIV neurons in response to electrical stimulation of FAES through indwelling electrodes. Orthodromic activation from FAES was not observed in any SIV neuron. Next, repeatable tactile stimulation (modified Ling vibrator) within the somatosensory receptive field and electrical stimulation of auditory FAES were presented alone and in combination in an interleaved fashion. Of the SIV neurons tested, approximately 70% showed a significant reduction in response to a tactile cue when FAES was stimulated, while only 6% showed an increased discharge. Stimulation using control electrodes located in the adjacent auditory area AI yielded no significant SIV response changes; neurons in the adjacent second somatosensory area (SII) were unaffected by FAES stimulation. Furthermore, the suppressive effect of FAES stimulation on SIV neurons was blocked by the application of the GABA-A antagonist, bicuculline methiodide (100 uM).

These data indicate that the cross-modal projection from auditory FAES to somatosensory SIV corresponds to a feedback-type projection. The lack of orthodromic (excitatory) input from FAES to SIV, the suppressive effect of FAES stimulation on a large proportion of SIV responses to tactile stimulation, and the sensitivity of the effect to bicuculline are consistent with the idea that the functional connection between the two regions is inhibitory results in suppression. Thus, multisensory convergence not only occurs in the well known excitatory-excitatory arrangement that leads to integration, but also in an excitatory-inhibitory format that may underlie more subtle forms of cross-modal modulation. Supported by NIH NS 39460 and by the Human Frontiers Science Program.

THE SPATIO-TEMPORAL DYNAMICS OF AN AUDITORILY DRIVEN VISUAL ILLUSION: A HIGH-DENSITY ELECTRICAL MAPPING STUDY

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Keywords: *multisensory; visual; auditory; ERPs; illusion*

It has been shown that the presence of sound can induce dramatic effects upon perception of an ambiguous visual event. When two identical and aligned moving stimuli meet in the center of a computer screen, they at times appear to pass through each other and continue along the same trajectory as before they met, and at other times to bounce off each other. In contrast, presentation of a tone at the moment the visual stimuli meet causes the two visual stimuli to consistently appear to bounce off each other. Here, we examined the neurophysiology underlying this auditory induced visual illusion, with the use of high-density electrical mapping (128 scalp electrodes). We compared the event-related potentials between a condition in which the squares bounced due to the presence of a tone, and a control condition in which they instead passed through each other because they were slightly misaligned. This revealed a significant modulation of electrical activity over scalp regions associated with visual motion processing areas (MT+), 200-300 ms following the moment of "impact". We interpret this modulation over MT+ as evidence that auditory inputs can strongly influence processing in visual motion areas.

MULTISENSORY VISUAL-AUDITORY OBJECT RECOGNITION IN HUMANS: A HIGH-DENSITY ELECTRICAL MAPPING STUDY

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keywords: Multisensory, visual, auditory, high density ERPs, object recognition

An object can often be identified based on information from several sensory modalities. Clearly, the sight of a common animal immediately reveals its identity. Similarly, with one's eyes closed, most animals are readily identified by their vocalizations and this would also be the case should one feel the animal for a few moments. Yet the joint influence of information from multiple senses on object recognition has not been extensively examined. The present study tested the effect of visual and auditory information on object recognition. High density evoked potentials (from 128 scalp electrodes) were recorded while subjects performed an object recognition task in which they pressed a key to the occurrence of a target animal. On each trial one of four stimulus types was presented: animal pictures alone; animal sounds alone; paired pictures and sounds of the same animal (congruent pairs); and paired pictures of one animal and sounds of another (incongruent pairs). Five types of targets were derived from the four stimulus types: auditory-alone targets, visual-alone targets, auditory incongruent targets, visual incongruent targets, and congruent targets. There were 8 animals, and each served as the target for two runs. Reaction times to the congruent targets were significantly faster than reaction times to any of the other target conditions. Miller's test of the race model was violated over the early portion of the RT distribution, providing evidence for the contribution of the interaction of the multisensory target information to RT facilitation. The evoked potentials elicited by the targets showed a significantly larger and extended visual N1 to congruent pairs compared to the incongruent pairs, suggesting that auditory information influences early visual object recognition processes.

DECONSTRUCTING TEMPORAL VENTRILOQUISM: HOW DO SOUNDS CAPTURE THE PERCEIVED OCCURENCE OF LIGHTS?

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keywords: Temporal perception, audition dominance, appropriateness hypothesis

Several experiments examined how the temporal positioning of irrelevant sounds influenced performance in a visual temporal order judgment (TOJ) task. The first two experiments established the finding that sounds occurring before and after two successive lights improved visual TOJ performance compared to when sounds appeared simultaneously with the lights. Additional experiments examined the role of the first and second sounds independently, revealing that the effect was due to the second sound lagging after the second light. In a final experiment it was found that the second sound improved performance to the greatest extent when the first sound was present. This suggests that the integration of lights and sounds depends on the overall context. These experiments illustrate a temporal ventriloquism whereby the perceived temporal occurrence of lights is biased by the timing of sounds.

FMRI-STUDIES OF AUDIO-VISUAL OBJECT PERCEPTION - SEMANTIC CONSISTENCY

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Keywords: *audio-visual, fMRI, object perception, semantic consistency*

We used functional magnetic resonance imaging (fMRI) to identify the human cortical network involved in audio-visual perception of natural objects such as cars, tools, animals, and humans. As the consistency between visual and auditory stimuli plays an important role for crossmodal binding, we varied semantic consistency in our study to investigate multisensory properties of higher sensory areas.

Ten subjects were instructed to passively view and/or listen to five different stimulus types: sounds of objects (s), sounds played backwards (s_bw), gray-scaled pictures of objects (p), consistent combination of s and p (c), and inconsistent combination of s and p (but p and s belong to the same category of objects, e.g. animals) (i).

Early sensory areas revealed highest activity for the preferred sensory input (sounds in auditory areas, pictures in visual areas), a reduced activity for the non-preferred sensory input (pictures in auditory areas, sounds in visual areas) and intermediate activity for combined audio-visual stimulation. Early and most of the higher sensory areas showed no difference between consistent and inconsistent audio-visual stimulation.

The only regions showing differences between consistent and inconsistent stimulation were distinct parts of the intra-parietal sulcus (IPS), superior temporal sulcus (STS), inferior temporal gyrus (ITG), and superior temporal gyrus (STG). Interestingly, activity in IPS and STS was higher during the inconsistent compared to the consistent stimulation. Activity in ITG and STG of the left hemisphere was lower during inconsistent stimulation.

While early sensory areas show strong inter-modal interference their activity seems not to reflect multisensory integrative properties. Regions with integrative properties respond either differentially to inconsistent and consistent stimuli or stronger to bimodal than unimodal stimulation. We found four distinct regions with these properties. We suppose that the IPS and STS sites are involved in the detection of crossmodal semantic inconsistency and in the initiation of further processing or attention shifting in order to resolve the perceived inconsistency.

FMRI-STUDIES OF CATEGORY-SPECIFIC AUDIO-VISUAL PROCESSING – AUDITORY CORTEX

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Keywords: *auditory cortex, fMRI, audio-visual, object perception*

We investigated human auditory cortex in response to sounds or pictures of natural objects such as cars, tools, animals, and humans using functional magnetic resonance imaging (fMRI).

We conducted three experiments. Each of them included the direct comparison of two object categories (e.g. tools and animals). Ten subjects were instructed to passively view or listen to five different stimulus types per category: sounds of objects (s), sounds played backwards (s_bw), gray-scaled pictures of objects (p), consistent combination of s and p (c), and inconsistent combination of s and p (i). Stimulation periods alternated with a baseline fixation condition of equal length (16 s) in a classical block design.

First we searched for regions that showed selective signal increases for the various sound categories. We could locate four spatially separated regions (in the posterior part of medial temporal gyrus, MTG) that showed specificity for sounds of either tools, or humans, or animals, or cars. Interestingly, the cortical patches that preferred sounds of animals and tools also showed a clear preference for the respective object category during consistent audio-visual (c) and purely visual stimulation (p), but not during inconsistent stimulation (i) or backward played sounds (s_bw).

The cortical sound processing network is therefore not restricted to the processing of unimodal auditory stimuli. Rather it seems to utilize crossmodal information for the identification and categorization of objects.

FMRI-STUDIES OF CATEGORY-SPECIFIC AUDIO-VISUAL PROCESSING – VISUAL CORTEX

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Keywords: *visual cortex, fMRI, audio-visual, object perception*

We investigated human visual cortex in response to natural sounds of cars, tools, animals, and humans using functional magnetic resonance imaging (fMRI).

We conducted three experiments. Each of them included the direct comparison of two object categories (e.g. tools and animals). Ten subjects were instructed to passively view or listen to five different stimulus types per category: sounds of objects (s), sounds played backwards (s_bw), gray-scaled pictures of objects (p), consistent combination of s and p (c), and inconsistent combination of s and p (i). Stimulation periods alternated with a baseline fixation condition of equal length (16 s).

First we searched for regions that showed selective signal increases for the various visually presented object categories. We could locate five spatially separated regions showing specificity for pictures of either tools (in intra-parietal sulcus, IPS; and inferior temporal sulcus, ITS), or humans (inferior temporal gyrus, ITG), or animals (anterior ITG), or cars (fusiform gyrus, FG), respectively. Then we used sounds only to identify regions exhibiting preferences for the various sound categories. Using the same thresholds none of the areas exhibited specificity for sound categories. However, after lowering the threshold we located five spatially separated regions (in close proximity to the previously found regions) that showed specificity for sounds of either tools (IPS; medial temporal gyrus, MTG), or humans (MTG), or animals (ITS), or cars (ITG/FG), respectively. Interestingly, the two cortical patches activated preferentially by a particular object category (sounds only and pictures only) were located next to each other partially overlapping. Thus, the human ventral stream does not seem to be restricted to the processing of unimodal visual stimuli but appears to utilize crossmodal signals for the identification of objects (what pathway) and their categorization.

TOUCHED BY SOUND: EVIDENCE OF CROSS-MODAL ALLOESTHESIA

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Keywords: *extinction, alloesthesia, auditory, tactile, body schema, peripersonal space.*

Alloesthesia is a rare clinical condition characterized by the mislocalization of contralesional stimuli to the ipsilesional space. A more frequently observed clinical condition is extinction, which is defined as the inability to detect a contralesional stimulus when presented simultaneously with an ipsilesional stimulus despite a preserved detection of single stimuli. Both condition follow right hemispheric brain damage. Whereas it has been demonstrated that extinction may occur across modalities (crossmodal extinction), crossmodal effects are not unequivocally demonstrated for alloesthesia.

Here we report a patient with crossmodal, auditory-tactile, alloesthesia subsequent to very circumscribed right frontal and parietal brain damages. A tactile stimulus delivered on the ipsilesional (right) side induced crossmodal alloesthesia: a mislocalization of the contralesional (left) auditory stimulus to the ipsilesional (right) body side. However, this was only found for ipsilesional tactile stimuli applied on the face and hand, but not on the foot. In comparison, a tactile stimulus delivered on the contralesional side, simultaneously with an ipsilesional auditory stimulus, systematically led to crossmodal alloesthesia for all tested body parts (face, hand, foot).

We draw the following conclusions. First, alloesthesia might be detected more easily by the simultaneous application of stimuli from different modalities. Second, alloesthesia - as previously reported for extinction - seems to be systematically influenced by a body gradient. Given previous work on tactile auditory interaction and peripersonal tactile-auditory space, it might be argued that a tactile stimulus falling outside the "near auditory space" (foot stimulation) only weakly interferes with the auditory representation, whereas tactile stimuli on the hand and face (inside near auditory space) have a strong influence. This influence might lead to the here-described phenomenon of crossmodal alloesthesia.

MULTISENSORY RESPONSE ENHANCEMENT AND SEITZ'S LAW OF HETEROGENEOUS SUMMATION

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keywords: *multisensory communication; behavior; visual and vocal playbacks; additive and multiplicative models*

In the early 1940's, A. Seitz proposed an additive model for how information from multiple sources is combined. His "Law of Heterogeneous Summation" stated that input from disparate stimuli will cause a behavioral response equal to the sum of the responses to each stimulus on its own. This model has been tested by various researchers, their results discussed here. Comparisons will be made to the neural responses of multisensory neurons. Particular attention will be paid to the current various uses of the terms "response enhancement" and "response depression." The differences in usage may stem from what is chosen as the baseline for comparison: should the response to a multimodal stimulus be compared to the responses to the unimodal stimuli independently, or should it be compared to the sum of the unimodal stimuli? This distinction becomes important when we decide on a level of significance for what we consider to be "integration" of multiple stimuli. In addition, if a mulitmodal stimulus causes a greater response than either of the unimodal stimuli, but less than the sum of the parts, shall we consider this an "enhanced" response (above the level of the unimodal responses), or a "depressed" response (below the level of the sum of the parts)? These questions will be discussed, and preliminary data from a study of Carneaux pigeon (Columba livia) responses to natural auditory and visual stimuli of conspecifics will be presented in an effort to test Seitz's Law.

DIRECTIONAL REMAPPING OF SOUND LOCATION AFTER SACCADES

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Keywords: auditory space perception, saccades, multisensory illusion

Although sound position is initially coded in head-centred coordinates, neurophysiological and behavioural evidence suggests that differences in static eye-position can modulate auditory responses and sound localisation. Here we provide the first behavioural evidence for directional remapping of sound location following a dynamic change in eye-position. Two experiments studied the effect of saccades on human sound localisation performance, with auditory inputs to the ears held constant by preventing head movements. Participants judged the relative position (same/different) of two sequential sounds, presented from a horizontal array of speakers. Visual fixation was either static throughout the trial (to the left or right of the loudspeaker array), or shifted to the opposite far side during the interval between the two sounds. Speakers were visible in Exp.1 and occluded in Exp.2. Results showed that intervening saccades clearly reduced participants' ability to detect a change in sound position. This impairment was most pronounced when the second sound shifted in the direction opposite to the intervening saccade. This result is compatible with a directional remapping of the first sound location following the saccade. This effect was present when speakers were occluded (Exp. 2), but reduced with respect to the visible condition (Exp.1). Thus, even without visual input and in a purely auditory task, changes in eye-position play a role in auditory spatial perception.

CONVERGENCE OF AFFECTIVE INFORMATION IN MULTIMODAL REGIONS OF THE HUMAN BRAIN

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keywords: Multisensory, affect, PET, middle temporal gyrus.

A PET study investigated whether convergence brain regions were activated during the perception of affective audio-visual events. Happy or fearful stimuli were presented to eight subjects in three conditions (visual only, auditory only and audio-visual). A convergence region situated in the left lateral temporal cortex (-52x, -30y, -12x) was selectively more activated by affective bimodal stimuli than affective unimodal stimuli (whether visual or auditory). Distinguishing positive and negative emotions, supplementary convergence areas situated mainly anteriorly in the left hemisphere for happiness and in the right hemisphere for fear were activated. Right amygdala activation was observed equally for visual fearful and audio-visual fearful stimulations. These results are consistent with previous fMRI data (Dolan, Morris & de Gelder, 2001) suggesting that facial expression and auditory fragment are concurrently processed in convergence regions rather than in modality-specific cortex.

Dolan, R.J., Morris, J.S., & de Gelder, B. (2001). Crossmodal binding of fear in voice and face. *Proc Natl Acad Sci USA* **98**, 10006-10.

A MODEL FOR BINDING MULTISENSORY STIMULI

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keywords: multisensory, neural networks, model

Recent neuroimaging studies show the importance of a multisensory convergence zone (Calvert et al, 2001) for identifying multimodal inputs. The role of unimodal cortices has also been highlighted by different researches, using various methods. These studies show that activity is enhanced in unimodal cortices when integrating multimodal stimuli. Hypotheses have been made that enhancement is due to feedback connections from a multisensory convergence zone to unimodal areas.

Here we propose a model of this idea, using modular neural networks, i.e. neural networks dedicated to different tasks that cooperate in a common framework. Neural classifiers process each sensory stream. Sensory representations are then dynamically integrated into a unified picture of the object, by a bi-directional propagation of activity into a recurrent network. Each of the representations to be integrated can influence the other over time, via a central convergence zone and feedback connections. The task of the model is to identify an object, when fed with multiple sensory inputs. We tested this model with pixel-based images of vowels, in conjunction with their oral form, and with images and sounds of animals.

Since the model works like a hetero-associative memory that stores associations between unimodal experiences, stimulation of a single modality can lead to a “sensory image” in another associated modality.

We plan to add to our model a module dedicated to detecting temporal correlation between inputs, as it is a key for assuming that they come from the same object, in the same vein as the idea of an “event-detection center” proposed by de Gelder (de Gelder, 2000).

SYNESTHETIC DESIGN. THE LABORATORY OF BASIC DESIGN AS PLACE OF EXPERIMENTATION ON THE INTERSENSORY CORRESPONDENCES

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Keywords: *Basic design, Synesthesia, Intersensory correspondence, multimodal communication*

This text deals about the theme of intersensory correspondences and synesthesia applied to the communication design. In our daily contact with objects and messages we involves the globality of senses, but we must consider also that our multisensorial behaviour and use of objects is often in opposition to a monosensorial projectuality, which gives an exclusive importance to the visual register only. The introduction of specific technologies (for example artificial materials with their sensorial qualities, or informatic technologies with a pluri-registic features) it defines a new role for the designer, as a *synesthetic orchestrator*; we can see him as a new project figure who is able to place different informations in different sensory registers, to obtain specific perceptive congruences and to avoid possible negative interferences in a multisensory project.

These main factors generated the idea to create a fundamental course of design based on the comprehension and control of interactive sensorial dynamics. Actually we are conducting a didactic and research activity (into the Design Faculty at Politecnico di Milano, Italy), with the main purpose to find the right combination between different factors (as shapes, colours, sounds, rhythms, timbres, etc.) in an audio-visual communication that integrate them, giving to the project new intersubjective values. This first experience will continue with the creation of a web site which is completely oriented to synesthesia – as a perceptive phenomenon, figure of speech or artistic representation where you can find a specific relation between different registers (Riccò, 1999) – that in its final definition will become a sperimental laboratory about intersensory correspondences. You can see the site at: www.sinestesie.it (already active but under construction).

LOOK BUT NO TOUCH:
VISUAL EXPERIENCE OF TOUCH ENHANCES TACTILE PERCEPTION

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Vision and touch, like all of our sensory modalities, provide us with valuable information about our environments. However, it has long been argued that the visual modality dominates over our other sensory systems. Here we show that visual experience of touch can alter tactile sensitivity when there is inconsistent information conveyed between vision and touch. While observers viewed a mirror reflection of their right hand, which was positioned such that it gave the visual impression of viewing their left hand, a series of brush strokes were delivered to only the right hand. This situation provided a conflict between vision of the "left hand" appearing to be stroked and touch of the left and not feeling the brush strokes. After exposure to this conflict situation, tactile sensitivity was altered such that the detection rate of a near threshold stimulus was consistently increased for the left, untouched hand. These results provide strong evidence for visual dominance and demonstrate that such influences can have lasting effects.

MULTIMODAL CONVERGENCE IN CALCARINE VISUAL AREAS IN MACAQUE MONKEY

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keywords: *Area V1, Area V2, Layer 1, Peripheral vision*

Multimodal convergent inputs and interactions are well-documented in association cortical areas, such as parts of the cingulate cortex, parahippocampal gyrus, or superior temporal sulcus in monkeys. Recently, however, we have found evidence for direct connections to areas V1 and V2 from auditory (Rockland and Ojima, SFN 2001) and parietal (Rockland, SFN 2000) related areas. Connections were demonstrated by injections of anterograde tracer in auditory belt areas (n=3), or in different parts of areas 5, 7a, and 7b (n=5). The auditory injections resulted in projections to V1, in the upper bank of the calcarine fissure (peripheral lower visual field representation). These were primarily in the anteriormost 3.0mm. The parietal projections were widely distributed, with less of a bias for the upper bank. Terminations were in layers 1 and/or 6, and were very divergent (1.0-4.0mm), although sparse. These could be considered "feedback" connections, but other interpretations are possible. Both auditory and parietal areas also projected to dorsal area V2 in the calcarine fissure (peripheral lower visual field). Projections to V2 were denser than those to V1, but less divergent. They were mainly in layer 1, but extended through other layers as well. Retrogradely labeled neurons occurred in layers 3 and 5 of V2, but were not observed in V1. Possible functional roles include vestibular, spatial, or attentional processes. Also relevant is psychophysical evidence for illusory visual motion induced by sound (Shams et al., SFN 2001).

CROSS-MODAL COMPENSATION OF AUDITORY LONG-TERM MEMORY AFTER EARLY AND LATE BLINDNESS

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Keywords: *developmental plasticity, cross-modal compensation, long-term auditory memory, visual deprivation*

Cross-modal plasticity after early visual deprivation has mainly been investigated for perceptual functions. In a first study, we had reported enhanced memory for auditorily presented words in a group of congenitally blind adults which was most likely due to a more efficient encoding leading to more successful retrieval.

The goal of the present study was to test how material specific the initially observed superiority of the blind was, if they show particular advantages for physical encoding strategies and if cross-modal compensation of auditory long-term memory functions is linked to critical periods.

A group of congenitally and late blind and sighted adults listened to environmental sounds. Half of the participants of each group named the sounds (semantic encoding) and the other half judged them as hard or soft (physical encoding). In the retrieval phase previously encountered stimuli were presented intermixed with new sounds. Some of the new sounds represented the same concept as old sounds but they were physically distinct from the latter (false memory items). Task of the participants was to judge whether or not they had heard the environmental sound during study.

Semantic encoding led to higher memory than physical encoding irrespectively of visual status. The congenitally blind adults showed overall higher recognition than the sighted and, moreover, they had lower false memory rates after physical encoding. The late blind displayed similar memory scores as the congenitally blind when matched for absolute age (rather than for duration of blindness).

The present findings demonstrate compensatory capacities of long-term memory functions after visual deprivation and suggest that these cross-modal adaptations are even possibly in adulthood.

THE EXPLOITATION OF INTERSENSORY REDUNDANCY BY AUDITORY-VISUAL INTEGRATION MECHANISMS

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***Keywords*: discrimination threshold, neural summation, interaction models**

In a natural environment there exist many situations in which the effects of a single event or a single object lead not only to simultaneous stimulation of several senses, but even to a systematic covariation of the input signals to these sensory channels. Especially relative movements between an object and an observer cause such covariations in the sensory stimulation. Since it is known from unimodal sensory research that neural systems make use of the natural input statistics, we ask here whether the perceptual system as a whole is capable of exploiting such intermodal statistical redundancies. An efficient exploitation would require the ability for a true integration of multimodal information and our study thus aims at the provision of evidence for such a multisensory processing scheme. The experiment was additionally designed for a possible differentiation between conditions with ecological relevance, i.e. stimulus configurations which are statistically typical for the behaviour in a natural environment, as opposed to combinations which are much less common under natural conditions.

We investigated the perceptual performance for basic auditory-visual stimulus configurations: In a temporal forced choice design we measured various two-dimensional discrimination thresholds for compound stimuli, which consisted of a 1kHz tone, which we varied in intensity, combined with a lightspot, which we varied in intensity or size. The subjects' task was to detect any change in this bimodal stimulus configuration, irrespective of modality.

The resulting two-dimensional jnd-curves cannot be explained by an independent, modality-specific processing. The sensitivity for the combined stimulus changes in the two modalities was higher than to be expected from the usual psychophysical summation exponents. In particular the difference thresholds for the ecologically relevant quadrants (joint increments or decrements for both tone and light) showed a significant increase in sensitivity. This points to a selective neural summation of only the ecologically valid combinations, instead of an undifferentiated probability summation, which would pool any type of change information from the two modalities. It thus seems that the intermodal neural information processing is optimally adapted to the typical statistics of the multisensory covariations, which result from dynamic behaviour in a natural environment.

AN EXCEPTIONAL GENERALIZATION AND TRANSFER OF PRISM ADAPTATION IN UNILATERAL NEGLECT

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Keywords: *prism adaptation, neurology, rehabilitation*

Prism adaptation in healthy subjects can be restricted to the exposed arm, to a specific gesture or to movement speed during exposure. But adaptation to base-left wedge prisms in patients has been found to produce strong effects on unexposed tasks performed with the exposed arm, such as line bisection, copy of line drawing or drawing from memory (Rossetti et al. 2001). Motor tasks performed with unexposed effectors such as postural control or wheel-chair driving, have been also shown to be strongly altered following one short prism adaptation session (Rossetti et al. 1999, Tilikete et al. 2001). In addition, visual tasks involving no arm movement, such as word reading or object naming, were also improved after adaptation, and by the same amount as visuo-motor tasks (Farnè et al. 2001). Even visual imagery, which can be amputated from the left half in patients with unilateral neglect, is markedly improved following adaptation (Rode et al. 1998, 2001. Furthermore, tasks performed within another sensory modality, such as dichotic listening (Jacquin et al. 2001), haptic circle centering (McIntosh et al. 2001) of haptic object recognition (Toutounji et al. 2001) were also strongly affected by prism adaptation. It is also striking that the effects of a 5 minute exposure to a prismatic shift of vision to the right may last from several hours to 24 h or even several days (Pisella et al. 2001, Farnè et al. 2001).
These results strongly suggest that a lesion of the right hemisphere can be responsible for super-adaptation to a conflict between visual and proprioceptive information.

VISUAL CORTICAL ACTIVATION DURING TACTILE FORM PERCEPTION

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Keywords: *Mental imagery, visual cortex, tactile perception*

In a previous positron emission tomographic (PET) study in normal humans, we found that an area of extrastriate visual cortex near the parieto-occipital fissure is active during tactile discrimination of grating orientation (NeuroReport 8:3877-3881, 1997). Further, we showed that interfering with the function of this cortical area using transcranial magnetic stimulation (TMS) selectively disrupted this ability (Nature 401:587-590, 1999). Thus, visual cortical processing is necessary for optimal performance of this tactile task in normally sighted people. Whether it occurs on a top-down basis, due to visual imagery, or on a bottom-up basis, reflecting multimodal inputs, is not clear.

In the present study, we investigated whether visual cortical processing also accompanies tactile form perception. One task we used, requiring mental rotation of tactile stimuli, is a classic mental imagery task. We reasoned that finding activity in similar visual cortical regions during this and other tactile tasks would support the idea that mental imagery underlies visual cortical processing in tactile perception. We used PET scanning with $H_2^{15}O$ while stimuli were applied to the immobilized right index fingerpad. Activations were corrected for multiple comparisons within an *a priori* mask comprising all of occipital and parietal cortex. Two experiments were performed with separate groups of normal subjects.

In the first experiment, uppercase Js were applied using an electromechanical device. Subjects reported whether the J was in a normal or mirror-reversed configuration. In one condition, the angular deviation of the J from the long axis of the finger was either 0° or 30°. Compared to a control condition without tactile stimulation, this condition evoked activity in left somatosensory, parieto-occipital and temporo-occipital cortex and bilaterally in superior parietal cortex. In another condition where the angle of the stimulus was larger (90-150°), thereby inducing a greater requirement for mental rotation, no additional activation was found.

In a second experiment, uppercase letters were presented upside-down to avoid processing of linguistic symbols. An experimenter manually applied the stimuli, enabling presentation of a larger number of trials during the 90 s scan acquisition than in the first experiment. When mirror-image discrimination was contrasted between a large stimulus angle (120° or 150°) and an angle of 0°, an active focus was found in left superior parietal cortex. This is attributable to a specific effect of mental rotation that was absent in the first experiment, where the stimulus angles were not as widely separated between conditions. Compared to a task requiring detection of a gap in a bar, mental rotation recruited foci in left superior parietal and bilateral parieto-occipital cortex. Simple discrimination between two forms activated right temporo-occipital cortex, relative to a condition involving discrimination of bar orientation.

Thus, recruitment of visual cortical processing during tactile perception is not limited to grating orientation discrimination, but occurs generally during a variety of tactile tasks involving form perception as well. Moreover, areas in both dorsal and ventral visual pathways are recruited in a task-dependent manner. Spatial tasks engage dorsal areas, whereas form tasks engage ventral areas in the left or right hemisphere depending on whether recognition of linguistic symbols is involved or not. Specifically, mental rotation and discrimination of grating orientation activate similar foci in parieto-occipital cortex, suggesting not only a common basis for visual cortical processing in both cases (and perhaps other tactile tasks), but also that the common basis might be mental imagery.

INFLUENCE OF VISUAL INFORMATION ON THE DISPLACEMENT OF THE AUDITORY MEDIAN PLANE OF THE HEAD (SAMP)

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keywords: *head position, posture, auditory localization, visual deprivation*

Spatial information obtained through different modalities is initially encoded in modality specific coordinates. Since receptors of the different modalities are not fixed in relation to each other, the posture of eyes, limbs, the head and the body must be taken into account in order to combine input of different modalities into a common reference frame. These transformations seem to be partly subject to systematic errors. For example, it has been reported that with eccentric head position the perception of the subjective auditory median plane of the head (SAMP) is displaced towards the side to which the head is turned.

The present experiment investigated the role of visual input for the SAMP displacement due to head position. A group of congenitally blind and two groups of sighted adults – one with eyes open (employing a fixation point), one with eyes closed - adjusted the location of a tone presented through headphones in such a way that they perceived it to originate at their SAMP. Head position was altered between straight ahead and turned 60° to the right.

When sighted subjects turned their heads to the right, their SAMP, as indicated by their tone adjustments, was displaced to the right as compared to when they held their head straight irrespectively if they performed the task with eyes open or eyes closed. In contrast, the blind did not show a SAMP displacement when turning their head.

It could be speculated that the SAMP displacement observed in sighted subjects is due to visually induced biases in multimodal coordinate transformation processes. In the blind, such a bias does not exist. Furthermore, it may be speculated that the more precise integration of proprioceptive input due to the lack of visual information contributes to superior auditory localization skills repeatedly reported for the blind.

VISUAL CORTEX AS A SITE OF CROSS-MODAL INTEGRATION

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Keywords: *cross-modal illusion, auditory-visual perception, multi-modal brain areas*

It has been shown that visual perception can be strongly affected by auditory stimuli. It is unclear, however, what the brain circuitry subserving these inter-actions may be. We used the sound-induced illusory flash effect (a single flash accompanied by two auditory beeps is perceived as two flashes) as a tool to investigate this question. This illusion is much stronger in the periphery than fovea. In a previous study using event-related brain potentials, we had investigated whether this illusion is due to modulation of activity in the visual pathway or a higher perceptual area, such as associative cortex. We compared the visual evoked potentials (VEPs) in the presence and absence of sound. Activity was modulated significantly already prior to 200 ms poststimulus in the illusion trials (periphery) but not in trials where no illusion occurred (fovea). In addition, the VEP associated with the illusory second flash was qualitatively very similar to the VEP associated with a physical second flash, suggesting that similar representations underlie the percept of the illusory and a physical flash. These results suggested that the observed modulation of activity by sound occurs within the visual cortex. In the present study we tried to localize the brain regions involved in the perception of the illusory flash more directly and more accurately using event-related fMRI. We collected the functional images of 3 participants in the following conditions. Unimodal conditions Vp and Vf consisted of visual stimulation: a small disk flashed once in the periphery or fovea, respectively. Bimodal conditions AVp and AVf consisted of auditory-visual stimulation: combination of 2 beeps with visual stimuli Vp and Vf, respectively. In another unimodal condition, Vp2, a physical double flash was presented in the periphery. Trials were randomized. Contrasting the (illusion) condition AVp against Vp resulted in activity in Brodmann's areas 17, 18, and 19. Contrasting (no-illusion) condition AVf versus Vf, however, did not show any activity in the occipital lobe ruling out the possible role of attention in the aforementioned enhanced visual activity. Considering that the visual stimulus was identical in AVp and Vp , the enhanced activity of early visual areas in AVp can only be attributed to the perception of the illusory flash caused by sound. Similar brain areas were indicated when contrasting Vp2 against Vp. The common brain areas involved in these two contrasts confirm our previous ERP results suggesting similar mechanism underlying the percept of a physical and an illusory flash. These results altogether indicate that the activity in the early visual cortical areas is modulated by sound.

EFFECTS OF ACOUSTIC VIBRATIONAL MUSIC STIMULATION ON PHANTOM PAIN USING THE MUSICA MEDICA METHOD

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Keywords: music, auditory & somatosensory stimulation, phantom pain

Background

A common experience among amputee patients is the sensation of pain at as if it were emanating from the amputated body part – the phantom limb. The pain is described by these patients as severe and often interferes with their daily lives. Here we describe the use of the Musica Medica method in treating the phantom limb pain of such patients. This method works in the following way. The music generated through the Musica Medica device is delivered as an auditory-somatosensory multisensory stimulus, such that the patients feel through two transducers what they hear through headphones. These somatosensory transducers are placed on selected body regions.

Methods

We report here on three patients (aged 20-25yrs) following lower limb amputation. All three suffered from severe phantom pain. The treatment entailed sessions of Musica Medica over a 3-month period (3 sessions per week) that totalled ~13sessions per month. The duration of each session was 15 minutes for the first two months and was increased to 45 minutes for the third month. The transducers were usually held against the amputated stump where the phantom pain was perceived. For those wearing prosthetics, they were positioned on the sternum or held in the hands. Patients were asked to rate their pain on a scale of 1 to 4, where 1 = severe pain and 4 = no pain.

Results

By the end of the 3-month treatment, pain at the phantom limb had completely disappeared. Likewise, as the therapy was progressing, the patients reported a reduction of the pain's intensity, an increased sense of well-being, and an assessment of their individual life situation that included making plans for the future.

Conclusions

These results suggest that there may be neuroplasticity of some phantom pain that is ameliorated by auditory-somatosensory stimulation.

PERCEPTUAL INTEGRATION OF DYNAMIC INFORMATION ACROSS SENSORY MODALITIES

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Charles Spence, University of Oxford, England
Alan Kingstone, University of British Columbia, Canada

Keywords: Motion perception; Apparent motion; Multisensory conflict

Multisensory integration is often demonstrated through the behavioral consequences of intersensory conflict. For example, in the classical ventriloquist illusion, the perceived location of a sound is often heard as coming from near the position of a concurrent visual event, even if they originated from different locations. Here, we study the phenomenon of crossmodal dynamic capture, by which the perceived direction of a moving sound source can be reversed when concurrent visual motion is seen in the opposite direction. As has been the case in the ventriloquism literature until recently, the contribution of perceptual and higher level (cognitive) factors to the dynamic capture illusion has not been determined. In the present study, we addressed the perceptual nature of crossmodal dynamic capture using the method of psychophysical staircases. The results indicate that crossmodal dynamic capture is a perceptual phenomenon that depends critically on the experience of motion, and in which auditory motion is biased as a function of visual information but not vice versa.

THE CEREBRAL REORGANIZATION OF LANGUAGE FUNCTIONS IN LATE BLIND ADULTS AS AN EXAMPLE OF CROSS-MODAL PLASTICITY IN ADULTHOOD

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<u>keywords</u>: language, fMRI, late blindness, plasticity

It has been shown that the nature and timing of language input significantly influence the neuro-anatomical implementation of language functions. For example, a recruitment of right hemispheric areas for language has been observed in users of American sign language (ASL). However, an activation of the right homologous perisylvian areas was less pronounced and only partly in late learners of ASL. Similarly, a bilateral rather than strongly left-lateralized brain activation during speech processing has been observed in congenitally blind adults both with event-related brain potentials (ERPs) and functional magnetic resonance imaging (fMRI).

Moreover, evidence for a language-related activation of visual cortex in the blind was reported. It is not known yet, if the more efficient processing of speech and / or the altered neural representation of language in the blind are linked to 'critical' or 'sensitive' periods during development or if similar changes occur when visual deprivation starts after puberty. These questions were addressed using fMRI.

Nine late blind adults listened to meaningful or pseudo-word sentences which had an easy or difficult syntactic structure. Task of the participants was to detect rare sentences with an incorrect word order.

The data showed a left-lateralized activation of perisylvian brain regions in the sighted controls but a bilateral activation pattern in the late blind participants. Furthermore, the language related activation extended into visual cortex areas in the late blind but in none of the sighted controls.

The observed changes of language functions in the late blind group are similar to those observed for congenitally blind adults although they were partly not as pronounced after late than early onset of blindness.

The present study demonstrates cross-modal plasticity of auditory language functions in adulthood.

ILLUSORY FLASHES ARE INDUCED BY BEEPS, BUT ARE ILLUSORY BEEPS INDUCED BY FLASHES?

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keywords: ***Audiovisual, illusion, conflicting information***

We studied a visual illusion induced by sound, discovered by Shams, Kamitani and Shimojo (Nature, 408:788, 2000), in which multiple beeps presented together with a single flash of light result in the perception of multiple flashes. They also found that a single beep did not cause two flashes to fuse, and on this basis hypothesized that the modality in which stimulation is discontinuous will have a greater effect on perception. This can be contrasted with the appropriateness hypothesis that states that the modality most appropriate for the perceptual task at hand will have a greater impact. In order to test these hypotheses, we replicated the experiment and furthermore investigated whether a converse illusion exists, that is, whether the perception of beeps is affected by concurrent flashes. The visual stimuli were 1 to 4 flashes with a diameter of 2 deg and 17 ms duration. The auditory stimuli were 1 to 4 beeps at 3.5 kHz and 7 ms duration. Stimulus onset asynchrony was 67 ms for both beeps and flashes. Unimodal and audiovisual stimuli were presented in an extended factorial design to ten subjects in two conditions: visual and auditory. In the visual condition, subjects counted the number of flashes. They reported seeing several flashes when a single flash was accompanied by multiple beeps, confirming the finding of Shams et al. However, when multiple flashes were accompanied by a single beep, subjects reported fewer flashes – an effect which was absent in the study of Shams et al. and which disfavors the notion that discontinuous stimuli should dominate bimodal perception. In the auditory condition, subjects counted the number of beeps. Now there was no illusion. Instead, a single beep was consistently reported as one, independent of the number of accompanying flashes. These findings support the appropriateness hypothesis, given that subjects were better at counting unimodal beeps than unimodal flashes. In conclusion, we can confirm the existence of illusory flashes caused by concurrent beeps, but the illusion does not work the other way around. We propose that the appropriateness hypothesis is better suited to account for these results.

TEMPORAL DYNAMICS OF LATERALISED ERP COMPONENTS ELICITED DURING ENDOGENOUS ATTENTIONAL SHIFTS TO RELEVANT TACTILE EVENTS

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Keywords: *Tactile-spatial attention, Attentional control, Event-related brain potentials*

To investigate the temporal dynamics of lateralised event-related brain potential (ERP) components elicited during covert shifts of spatial attention, ERPs were recorded in a task where central symbolic cues instructed participants to direct attention to their left or right hand in order to detect infrequent tactile targets presented to that hand, and to ignore tactile stimuli resented to the other hand, as well as all randomly intermingled peripheral visual stimuli. In different blocks, the stimulus onset asynchrony (SOA) between cue and target was 300 ms, 700 ms, or 1100 ms. Anterior and posterior ERP modulations sensitive to the direction of an attentional shift were time-locked to the attentional cue, rather than to the anticipated arrival of a task-relevant stimulus. These components thus appear to reflect central attentional control rather than the anticipatory preparation of sensory areas. In addition, attentional modulations of ERPs to task-irrelevant visual stimuli were found, providing further evidence for crossmodal links in spatial attention between touch and vision.

VISUAL MOTION AFFECTS THE CONTINGENT MOTION AFTEREFFECT IN THE AUDITORY SYSTEM

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Keywords: ***contingent aftereffect, auditory-visual illusion, motion***

Pairs of stimulus attributes, such as color and orientation, that are normally uncorrelated in the real world, are generally perceived independently in the sense that perception of orientation is not affected by color and vice versa. Yet, this independence can be altered by relatively brief exposure to arbitrarily paired stimuli, as has been shown for vision[1]. Recently, an analogous contingent aftereffect has been reported in the auditory modality[2]. After about ten minutes of adaptation, during which subjects listened to a spatially rightward moving sound with a falling pitch alternated with a spatially leftward-moving sound with a rising pitch, a spatially stationary sound with a falling pitch was perceived as moving leftward, whereas a spatially stationary sound with a rising pitch was perceived as moving rightward.

In our experiments, we show that this auditory contingent motion aftereffect is strongly affected by a visual stimulus that moves in the same or in the opposite direction of the sound. Subjects listened to a spatially rightward moving sound with a falling pitch alternated with a spatially leftward-moving sound with a rising pitch (or vice versa). When during adaptation a visual stimulus (a bright square against a dark background) moved in spatial congruence with the sound, aftereffects (i.e., a shift in the psychometric functions for unimodal auditory motion) were bigger than when the adapter sound was presented unimodally. Moreover, when the visual stimulus moved in the opposite direction of the sound, aftereffects tended to be negative. Contingent aftereffects are thus not specific to vision or to audition per se, but they reflect general properties of crossmodal stimulus processing.

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2. Dong, C-J., Swindale, N. V., & Cynader, M. S. Nature Neurosci. **2** 863-865 (1999).

THE BARKING CHICKEN AND THE CROWING BELL: MODULATION OF VISUAL OBJECT EXTINCTION BY SEMANTICALLY-RELATED AUDITORY SOUNDS IN PATIENTS WITH SPATIAL NEGLECT

Patrik Vuilleumier[1,2], Sophie Schwartz[1], Karen Clarke, Masud Husain[1,3], Jon Driver[1]

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Keywords: visual extinction, spatial neglect, inter-sensory facilitation, attention.

Visual extinction after right parietal damage is characterized by a deficit of attention towards contralesional space, with a loss of awareness for stimuli on the left side when presented with concurrent stimuli on the right side, even though isolated left stimuli may still be perceived. We tested whether the extent of extinction for contralesional visual stimuli would be influenced by presenting them together with matching or non-matching auditory sounds. Pictures of common objects or animals were briefly shown in the right, left, or both fields, paired with a meaningful sound (heard in both ears through headphones). On the critical presentation of bilateral visual stimuli, the heard sound could match the identity of either the left or right visual stimulus, or instead corresponded to another non-presented item. Visual extinction was reduced when a stimulus in the contralesional left visual field (e.g. chicken) was paired with a matching (e.g. crowing) versus a non-matching (e.g. barking) auditory sound. This suggests that a rapid intermodal integration of visual information from the left field with concurrent auditory information can enhance detection of stimuli in unattended contralesional space despite right parietal damage.

A CHANGE IN FLICKER RATE SOMETIMES DRIVES PERCEIVED AUDITORY FLUTTER RATE: CROSS-MODAL ASSYMMETRICAL EFFECTS IN TEMPORAL PERCERTION

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Key words: *cross-modal asymmetrical effect, temporal perception, information reliability hypothesis, apparent movement*

A change in the flutter rate of a clicking sound induces a simultaneous change in the apparent flicker rate of a flashing light. This phenomenon is regarded as evidence for the auditory dominance over vision in temporal perception. Contrary to this, however, it seems that there is an opposite phenomenon, that is, visual dominance over audition under some conditions. In this study, we examined whether the reverse effect would be observed in temporal perception. In Experiment I, each of 12 participants was asked to judge not only the direction of change in the flicker rate of a flashing disk but also, in separate sessions, the direction of change in the flutter rate of auditory stimuli. We changed the rates of frequency of stimuli exposure in focal modality: acceleration, constant, and deceleration, and those of background modality: acceleration constant, deceleration, and no-background stimuli. A total of 360 trials (2 focal modalities x 12 stimulus conditions x 15 repetitions) were administered to each participant. We measured the degree of influence of background stimuli on judgment for each focal modality. The results demonstrated not only a traditional phenomenon but also a new phenomenon: the changes of visual flicker rate induced perceived change of auditory flutter rate under the condition impoverished cue where auditory stimuli exposed in constant frequency. In Experiment II, we employed visual stimuli that caused apparent motion in place of the flashing disk used in Experiment I. Each of 12 participants judged the direction of change in the velocity of apparent motion and that in the auditory flutter rate. The results showed the cross-modal interaction similar to that observed in Experiment I. It can be concluded that cross-modal asymmetrical effects are determined by the reliability of the visual and auditory information rather than by modality appropriateness.

ANTICIPATORY DEPLOYMENT OF ATTENTION BETWEEN SENSORY MODALITIES

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Brain activity associated with directing attention to one of two possible sensory modalities was examined using high-density mapping of human event-related potentials. The deployment of selective attention was based on auditorily presented symbolic cues instructing subjects on a trial-by-trial basis, which sensory modality to attend. When subjects are pre-cued to selectively deploy attention during voluntary (endogenous) attentional tasks, these mechanisms can be set up in advance of actual stimulus processing - the brain can be placed in a biased attentional state. We measured the spatio-temporal pattern of activation in the approximately 1 second period between the cue-instruction and a subsequent compound auditory-visual imperative stimulus. This allowed us to assess the brain regions involved in deploying and sustaining intermodal selective attention, prior to the actual selective processing of the compound stimulus itself. Activity over frontal and parietal areas showed modality specific increases in activation during the anticipatory period, likely representing the activation of fronto-parietal attentional deployment systems for top-down control of attention. In the later period preceding the arrival of the "to-be-attended" stimulus, sustained differential activity was seen over fronto-central regions and parieto-occipital regions, suggesting the maintenance of modality specific biased attentional states that would allow for subsequent selective processing. These late sensory specific biasing effects were accompanied by sustained activations over frontal cortices that also showed modality specific activation patterns, suggesting that maintenance of the biased state includes top-down inputs from modality-specific frontal control areas. These data support extensive interactions between sensory, parietal and frontal regions during processing of cue information, deployment of attention, and maintenance of the focus of attention in anticipation of impending attentionally relevant input.

AUDIOVISUAL TEMPORAL ORDER JUDGMENTS

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keywords: temporal perception, audiovisual, TOJs, synchrony

Previous studies in which people were required to judge which of two stimuli were presented first have resulted in widely differing estimates of the temporal precision with which people can make multisensory temporal order judgments (TOJs). Such variation suggests the existence of one or more methodological confounds in previous research. We assessed whether people use spatial cues when making crossmodal TOJs regarding which modality is presented first. Auditory and visual stimuli were presented from either the left and/or right of fixation at varying stimulus onset asynchronies (SOAs). Participants were required to make an unspeeded TOJ regarding either 'which modality was presented first' or else 'which side was presented first'. The same paradigm was used on simultaneous / successive judgment tasks to address questions such as whether or not the various tasks provide consistent measures of multisensory temporal perception.

Observers were more precise in crossmodal TOJs when stimuli came from different locations rather than from the same location, thus highlighting one important methodological confound present in previous research. Also, observers were more precise when making a modality judgment than when making a spatial judgment—this may also account for some of the variation reported in previous studies. Finally, observers were more likely to judge pairs of auditory and visual stimuli as being synchronous if they come from the same, rather than from different, positions supporting the important status of space in multimodal binding.

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International Multisensory Research Forum
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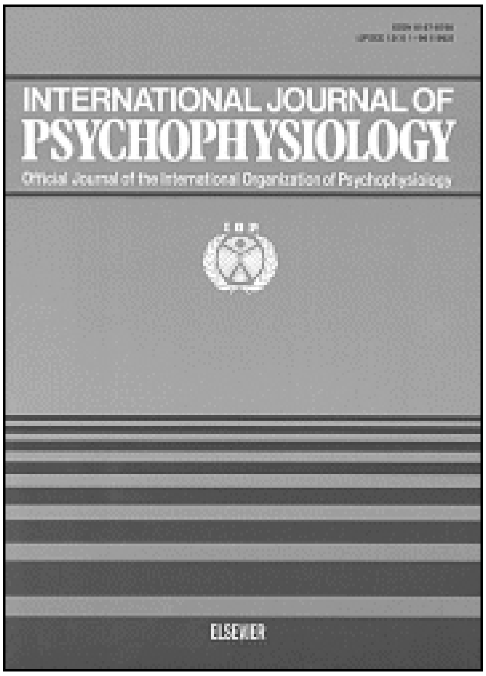

A selection of the most original studies presented at the 3rd Annual Meeting will be invited to submit to a special issue of the journal, *International Journal of Psychophysiology* (www.elsevier.com/locate/issn/01678760), which will report on the proceeding's of this year's meeting. Please contact one of the guest editors with any questions you might have.

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Contact: David Shore (dshore@mcmaster.ca)

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5th Annual Meeting, Oxford University, Oxford, England
Contact: Charles Spence (charles.spence@psy.ox.ac.uk)

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