Editorial

Dear Readers,

Welcome to the first issue of the Nijmegen CNS, the Proceedings of the Cognitive Neuroscience Master of the Radboud University. Run entirely by students, Nijmegen CNS strives to be a scientific journal reflecting the research carried out within the Masters´ programme. The journal is an integral part of the Master degree in Cognitive Science offered by the Radboud University. One the one hand, Nijmegen CNS offers an in-depth perspective on the research carried out by the students of the programme. Scientific problems as well as the approaches the students choose to tackle them are documented in an accessible manner. On the other hand, Nijmegen CNS is a proving ground for all students of the programme, offering the possibility to hone their skills in editing and writing in a real environment.

Nijmegen CNS will be published in two versions: online and as a hardcopy. The online version is located at www.cns.ru.nl/nijmegencns and features an archive of all printed journals as well as a complete archive of all thesis published as part of the Master programme. Additionally, the webpage contains all information necessary to contact the editorial board. We look forward to your feedback and responses!

All students of the Master programme are encouraged to submit their thesis work to the journal. Papers undergo an editing process supervised by the editors of the journal and guided by input from students as well as senior supervisors. Nijmegen CNS features the final versions of this editorial process on its webpage. The hardcopy contains a selection of several articles. The editorial board will base the selection on quality and significance of the written work. In this way, the journal aims to be the voice of the students of the neuroscience community in Nijmegen.

Although students run the journal, it relies heavily on the support by the Radboud University: the Faculty of Social Sciences, Faculty of Science, the University Medical Center, the Nijmegen Institute for Cognition and Information, the Max-Planck-Institute for Psycholinguistics and the F.C Donders Centre for Cognitive Neuroimaging are integral in their support of our publication. Finally, without the support of certain people, the journal would have not been possible. The board of editors would specifically like to thank Peter Desain for backing, developing and guiding our efforts from the beginning with limitless patience and enthusiasm, Eric Roubos for help in the initial stages of the journal, Robin Kayser for the support of the cooperation with Stanford University and Yvonne Schouten for her help in organization and administration.

It has been our pleasure to see our initial ideas develop into a first issue that contains the best of our students work in the rapidly developing field of Cognitive Neuroscience. We think you'll be as excited reading it as we were in creating it!

Best regards,

Jochen Hempleman
Editor-in-chief

From the Programme Director

It is a pleasure to see the publication of the first issue of Nijmegen CNS, the Proceedings of the Cognitive Neuroscience Master of the Radboud University. This journal for students and by students is set up to provide an overview of the research activities of the Master students and to train students in the reviewing process of scientific manuscripts.

The Research Master in Cognitive Neuroscience selects the best students in the field and provides a multi-disciplinary training programme preparing its students for a research carreer. By selecting the best students and by providing an intensive and in-depth programme by lecturers who are all leading experts in their field, we expect that students with a M.Sc. in Cognitive Neuroscience from the Radboud University Nijmegen will be prime candidates for future Ph.D. positions. Excellence in research shows off by publications in high-ranking peer-reviewed journals. Therefore, a crucial aspect of the training programme is cutting-edge research in one of the research groups of the Radboud University and training in the submission and reviewing procedure of manuscripts, reporting these results. This student journal, edited by students, is a crucial part of the training in submission and review procedure of scientific manuscripts.

The publications of the Nijmegen CNS Proceedings of the Cognitive Neuroscience Master will provide an overview of the research activities of the students. As such it will contribute to dissemination of research activities within the group of students of the master programme CNS, within the group of scientists participating in the Master Programme and to all others interested in Cognitive Neuroscience. I expect that this journal will play an important role to improve the international visibility of our Master programme and that it will serve a major role in public relations.

Inspired by a similar venture of students of Stanford University, this journal is the first one of its kind in Europe. On behalf of the Board of the Research Master Cognitive Neuroscience I wish the editorial board good luck and I hope that this first issue will be the first of a long tradition which will set a standard within Europe.

Prof. Stan Gielen
Programme Director of Master Programme Cognitive Neuroscience

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Nijmegen CNS

Proceedings of the Cognitive Neuroscience Master of the Radboud University

Cover Image by: Yaël Reymer
Journal Logo by: Guido Cavalini & Iris Grothe

Nijmegen CNS, Vol. 1, March 2006

Lateralized activation of the motor system to the observation of left and right hand actions[1]

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A primary feature of the human motor system is its crossed organization (e.g. left motor cortex controls right hand). In the present study MEG recordings were used to investigate whether observation of left and right hand finger movement results in lateralized activation of the motor cortex. Lateralized activation in the form of a lateralized readiness field was found over the motor cortex for both executed and observed finger movements. These results suggest that the basic neural organization that controls left and right limb movements during execution may be used to effectively differentiate between left and right movements of others in action observation.

Keywords: mirror neurons, action observation, cross organization, primary motor cortex, magnetoencephalography, lateralized readiness field.

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[1] Adapted from thesis for MSc Cognitive Neuroscience, Radboud University Nijmegen. Research performed at: F. C. Donders Centre for Cognitive Neuroimaging.

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Introduction

To understand other people's behavior we have to know what their intentions are, their emotional state of mind, and their goals. For this we have to be able to read and interpret their movements, gestures, and facial expressions. Area F5 of the monkey brain contains neurons, called mirror neurons that are active during both goal directed execution and observation of actions (Rizzolatti et al., 1996). Comparable effects have been reported in different parts of the human motor system, i.e. the inferior frontal gyrus, primary motor cortex, and the inferior parietal lobule (Fadiga et al., 1995; Buccino et al., 2004). It is suggested that the mirror neuron system in humans could play a major role not only in our understanding of other people's behavior but also in imitation, learning of motor skills (Jeannerod, 2001), and even language (Rizzolatti and Arbib, 1998).

With respect to action observation neuroimaging results consistently find that motor activation during action observation mirrors the activation that is typically found during action execution. Interestingly, it is not known whether left and right limb movements are represented separately in action observation. That is, it is not known whether the crossed organization of the motor system (Cheyne et al., 1994) that is evident in motor performance (e.g. left motor cortex controls right hand) is also used for the observation of other people's motor actions. Previous studies using transcranial magnetic stimulation (TMS) of the primary motor cortex or EEG recordings over the left and right lateralized motor areas, suggest that there might be lateralized activation of the motor cortex during action observation (Aziz-Zadeh et al., 2002, van Schie et al., 2004).

In this study we would like to focus on this aspect of action observation by answering the following question. Is our motor system sensitive for the laterality of movements during action observation? To study this phenomenon we let our subjects execute and observe left and right hand finger movements. For the observation task pictures were presented of hands performing the same actions that subjects performed in the execution condition. Images of recorded movement are known to have a comparable effect to observation of a live actor (Järveläinen et al., 2001). Brain activity during execution and observation conditions was recorded with 151 MEG channels, and laterality of motor activity in conjunction with left and right hand movement was determent by calculating the magnetic equivalent of the lateralized readiness potential (LRP) (Praamstra et al., 1999). It is hypothesized that activation over the left and right motor cortices will lateralize, as a function of the laterality of the observed hand movements.

Materials and Methods

Subjects

12 healthy subjects (3 female and 9 male, ages between 22 and 33), of which 6 left-handed and 6 right-handed took part in the experiment. All had normal or corrected-to-normal vision. Most subjects were selected from the people working at the F.C. Donders centre, and most of them had prior experience with MEG or other type of neuroimaging experiments. Subjects were informed beforehand about the experimental procedure, and were paid 6 euros per hour. Subjects gave their informed consent, and procedures were approved by the F.C. Donders centre.

Apparatus and stimuli

During the experiment the subjects were seated in a 151-channel axial-gradiometer whole-head MEG system (CTF Systems Inc., Vancouver, Canada) in a magnetically shielded room. In parallel with MEG, EEG was recorded (28-channel, CTF Systems Inc.). Measurements from the locations C3 and C4 were recorded by electrodes located over the left and right motor cortices respectively, and FCz over medial frontal cortex, referenced to both mastoids. To keep track of finger movements during the experiment EMG was recorded bipolarly. For the EMG, electrodes were placed on both arms over the extensor of the index finger halfway on the upper side of the lower arms. Horizontal and vertical eye signals were recorded bipolarly, and trials with eye movements and blinks were rejected from the analyses. All channels were recorded with acquisition software on a Linux computer at a sampling rate of 600 samples per second.

Two LUMITouch (Photon Control Inc. Baxter, Canada) optical button boxes (one for each hand) were used for recording and monitoring subjects' responses, and for triggering the stimulus presentation computer. The two button boxes were placed next to each other in front of the subject. The position of the boxes was adjusted so that the subjects had their arms in a comfortable position. The subject's elbows were supported by cushions to minimize movement of the upper arm to prevent movement artifacts. The index fingers of the subject's left and right hand were placed in a bend posture in front of the buttons to minimize hand movements, and to make sure that contralateral movements were not obstructed by the presence of the other hand.

Stimuli were projected onto a semi-transparent screen with a size of 42x32 cm placed at a distance of 70 cm in front of the subject. Two types of stimuli were shown, cue stimuli indicating how to respond, and response stimuli showing the actual response. The response stimuli show the same button boxes used during the execution task together with two hands shown from a first person perspective. The cue stimuli and response stimuli respectively had a size of 112x112 and 300x174 pixels, a spatial resolution of 72 dpi, and a 24 bit color depth.

Procedure

The experiment existed of 11 execution and 11 observation blocks containing 80 trials each. The blocks were presented in an alternating fashion, and the starting order was counterbalanced over the subjects. The first two blocks were used for practice and were not recorded. The duration of the experiment was approximately 75 minutes.

During the execution task the participants were asked to respond both fast and accurately to the cue stimuli and to try to avoid correcting initial errors. During this task as shown in Figure 1, the cue stimulus was shown for 200ms, and after the response offset recorded by a button press there was a 2000ms interval before the next cue stimulus came on. During all blocks a fixation cross was continuously aligned to the centre of the cue stimulus. The cue stimulus consisted of a square in which four dots were placed. The two dots in the bottom half of the square indicated the starting positions of the two index fingers, and the two dots in the top half of the square indicated the two target positions. The colors of the square and dots could either be red or green. The dot in the bottom half with the same color as the square indicates the index finger that should move, and the dot in the top half with the same color as the square indicates the target that the finger should go to. In case of the cue shown in Figure 1 the right index finger should move to the right target. Eight different cue stimuli could be presented, depending on the response hand (50% left finger movements and 50% right finger movements), movement direction (50% ipsilateral and 50% contralateral finger movements), and color (50% red and 50% green).

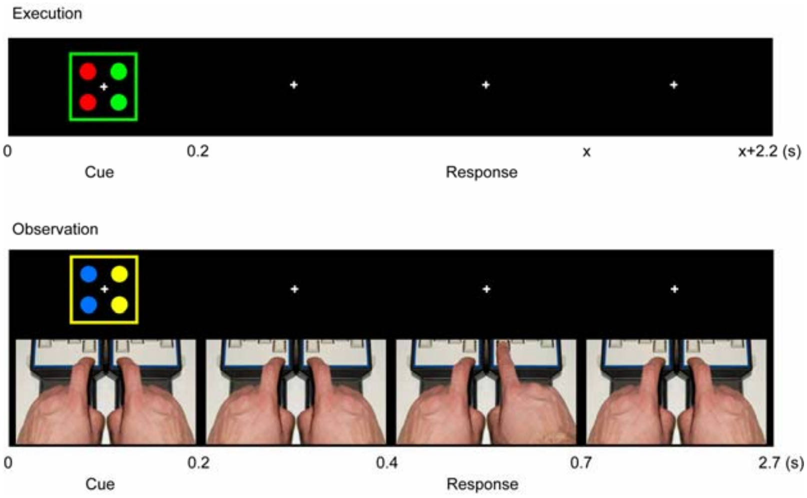

Figure 1. Top, execution task. The cue stimulus is on for 200ms followed by a response. After the response offset (x) there is a 2 sec. interval. Bottom, observation task. The cue is presented for 200ms followed by an interval of 200ms, after which the response stimulus is shown for 300 ms, followed by an interval of 2 sec.

The order of events in the observation task was chosen to be similar to the execution condition. Subjects were first presented with a 200ms cue stimulus showing the same four colored dots presented in a colored frame (see Figure 1). In the lower part of the screen, hands were shown continuously in a starting posture. 400ms after the onset of the cue stimulus, the starting posture of the hands was replaced by a different photo showing a response of the left or right hand (ipsi- or contralateral movement). The response stimulus stayed on for 300 ms after which the hands returned to their starting position. After the response there was a 2000 ms interval before the next trial was presented. To make sure that subjects kept their attention on the screen, and observed responses of the virtual actor, the subject's task was to detect and count occasional errors (e.g. wrong hand moved, or hand moved to the wrong target, or both). To make the task of the observer as unambiguous as possible the square of the cue stimulus was always yellow. Four types of responses were shown: in 70% of the trials a 'correct response' was shown in which the correct index finger went to the correct target, in 10% of the trials a 'hand error' was shown in which the index finger of the wrong hand went to the correct target, in 10% of the trials a 'target error' was shown in which the index finger of the correct hand went to the wrong target, and in 10

% of the trials a 'hand&target error' was shown in which the index finger of the wrong hand went to the wrong target.

Each block started with 8 correct trials, after which the remaining 72 trials were presented in a random order. Subjects were asked to count and report the number of observed errors at the end of each block. The number of errors was the same for each block. The reports show small deviations in counted errors for each block, which suggests that the subjects were not aware that the number of errors was fixed.

During both tasks subjects were asked to keep their eyes on the fixation cross and to minimize blinking. After each block subjects received feedback about their blinking behavior if necessary. There were pauses between the blocks in which subjects were allowed to rest. During both tasks and during pauses subjects were asked to keep their head movements to a minimum.

Data analysis

Behavioral data was analyzed for reaction times, and response types. Reaction times reflect the time between the onset of the cue stimulus and the subsequent button press. Analysis of the EMG data was used to determine which hand was moved for each trial. This was done by calculating the average absolute power for each EMG signal in a time window of 500 ms prior to the button press. The strongest signal corresponded to the responding hand. The signal of the moving hand had to be at least twice the power of the stationary hand, otherwise the trial was marked as ambiguous and discarded during preprocessing. The target of the finger movement was determined by which button was pressed. Four types of responses were classified: (i) a 'correct response' in which the correct index finger went to the correct target, (ii) a 'hand error' in which the index finger of the wrong hand went to the correct target, (iii) a 'target error' in which the index finger of the correct hand went to the wrong target, and (iv) a 'hand&target error' in which the index finger of the wrong hand went to the wrong target.

Analysis of EEG data was done for 7 subjects. Due to excessive noise the EEG signals of 5 subjects had to be discarded from the analysis. Preprocessing involved rejection of trials containing eye artifacts, rejection of trials containing ambiguous responses, and baseline correction over a period of 500 to 400 ms prior to the response offset. After preprocessing the trials were averaged per condition, channel, and separate for left and right hand movements. Averages were used for calculating the LRP according to the subtraction averaging method: LRP = [left hand(erpC4 - erpC3) + right hand(erpC3 - erpC4)]/2. Negative values of the LRP indicate relative activation of the hemisphere contralateral to the correct response hand, and positive values indicate relative activation of the opposite hemisphere associated with the incorrect response hand (Coles, 1989).

The same preprocessing, averaging, and subtraction averaging method that were done for the EEG recordings were also used for the analysis of MEG data. For the MEG data we will refer to lateralized readiness field (LRF) instead LRP because this signal reflects magnetic fields instead of electrical potentials. Before applying the subtraction averaging method, MEG data was converted to planar gradient (Bastiaansen and Knösche, 2000). Instead of C3 and C4 the LRF was calculated for all possible left and right mirror symmetrical channel combinations. In this way a complete topographical plot of the lateralized activation is derived with the left and right sides of the plot showing activation in opposite polarity, but with a symmetrical distribution. In order to allow a direct comparison with LRP effects the results and discussion will focus on effects over the right side of the topographical plots in which relative activation over the hemisphere contralateral to the response hand is indicated as a negative value. Positive values shown in red however indicate relative activation over the other hemisphere in association with the incorrect response hand.

Statistics

Statistics performed on the EEG data was done with a paired-samples t-test using SPSS statistical software. Statistics performed on the MEG data was done by means of randomization test statistics (Maris, 2004), to handle the multiple comparisons problem that arises when performing statistics on a high dimensional dataset (151 channels; 600 Hz sampling). All preprocessing for EEG and MEG data and statistical tests on MEG data were done using Fieldtrip (a biological data analysis software package running in Matlab; www.ru.nl/fcdonders/fieldtrip).

Results

Execution condition

The analysis of behavioral data showed that subjects' reaction times for correct (93.75%, 757 ms) and incorrect (6.25%, 833 ms) responses were not significantly different (t11 = -1.807, P = .098). Incorrect responses were found in the form of hand errors (1.16%, 775 ms), target errors (0.46%, 886 ms), and hand&target errors (4.48%, 840 ms). Reaction times between the three error conditions were not significantly different (F6 = 0.847, P = .474).

For the analysis of lateralized motor activation in association with left and right hand responses, EEG data was analyzed separately for trials with correct hand movements (both correct and target error) and trials with incorrect hand movements (hand error and hand&target error), see Figure 2. The negative LRP shown in blue reflects the relative activation of the hemisphere contralateral to the correct response hand. The positive LRP shown in red shows the relative activation in association with the incorrect response hand. For statistical analysis the mean amplitudes of the LRP in a time window (-356 ms to -16 ms) prior to the offset of the response were calculated. For the correct and incorrect hand responses the means differ significantly (t6 = -4.926, P < 0.003).

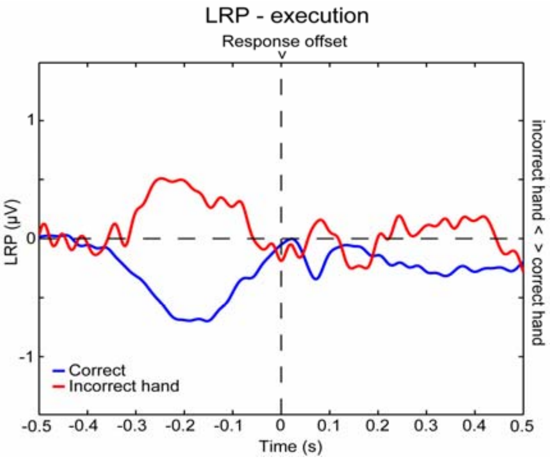

Figure 2. Lateralized readiness potentials for the execution task time locked to the response offset. The blue line shows the LRP for the correct hand responses, and the red line shows the LRP for the incorrect hand responses. Both LRPs were calculated over 7 subjects.

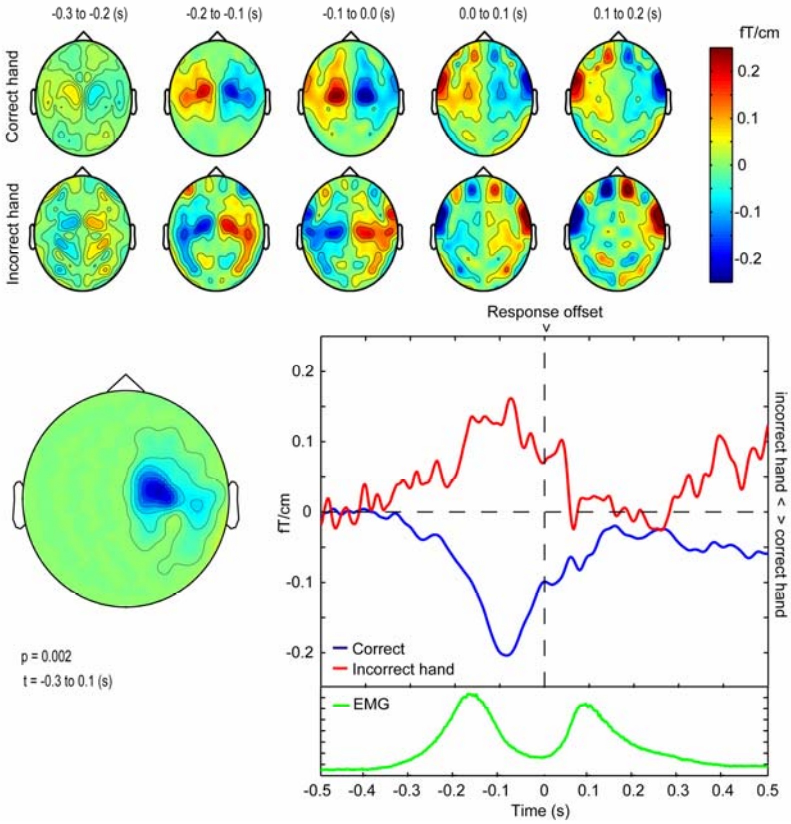

Figure 3. Lateralized readiness fields recorded in the execution task time locked to the response offset. Top, response-locked lateralized readiness fields displayed in topographical plots. The plots range from -0.3 sec. to 0.2 sec., with a time window of 100 ms for each individual plot. The top row of the plots show the topography for correct hand trials, the bottom row shows the topography for the incorrect hand trials. Bottom left, shows the cluster that becomes significant for the comparison between the two conditions (significant between -0.3 and 0.1 seconds). Bottom right, line plot of the LRF for the correct hand actions and incorrect hand actions, derived by averaging the twelve most significant channels. Bottom part of the plot, EMG average for all hand responses

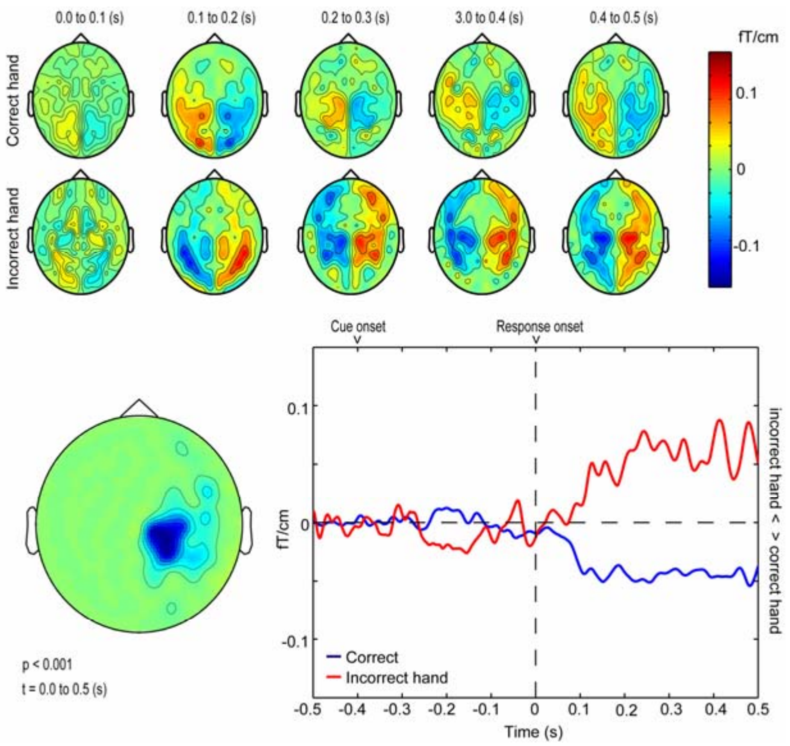

Figure 4. Lateralized readiness fields recorded in the observation task time locked to response onset. Top, response-locked lateralized readiness fields displayed in topographical plots. The plots range from 0.0 sec. to 0.5 sec. with a time window of 100 ms for each individual plot. The top row of the plots show the topography for correct hand trials, the bottom row shows the topography for the incorrect hand trials. Bottom left, shows the cluster that becomes significant for the comparison between the two conditions (significant between 0.0 and 0.5 seconds). Bottom right, line plot of the LRF for the correct hand actions and incorrect hand actions, derived by averaging the twelve most significant channels.

Same procedures were followed for the MEG data with respect to calculating the LRFs for the correct and incorrect hand movements as shown in Figure 3. The top part of Figure 3 shows two rows of topographical distributions of the LRFs ranging from 300 ms prior to the response offset to 200 ms after the response offset. The first row shows the distributions for the correct hand responses, and the second row shows the distribution for the incorrect hand responses. For the correct hand, LRF analysis reveals activation over the motor cortex that is contralateral to the response hand. In this same area and time frame that showed lateralized activation for correct hand responses a cluster with opposite polarity appears for the incorrect hand (Fig. 3, 2nd row). The difference between the two conditions is reflected in the left bottom part of Figure 3 that shows a highly significant cluster in blue located over the motor cortex. In the right bottom of the figure the LRF is presented as the average activation of the twelve most significant channels. The blue line shows the lateralized activation for the correct hand condition over the hemisphere contralateral to the correct hand. The red line shows the relative activation over the opposite hemisphere for the incorrect hand condition as a positivity. The green line in the bottom part shows the average EMG signal for all hand responses.

Observation condition

Figure 4 displays the results for the observation condition in a similar format as for the execution condition in Figure 3. The top part of Figure 4 shows two rows of topographical distributions of the LRFs in a 500 ms interval following the response stimulus. The first row shows the distributions for the observed correct hand responses, and the second row shows the distribution for the observed incorrect hand responses.

For the correct observed hand LRF analysis shows activation that is stronger contralateral to the hand that was used for the response comparable with lateralized effects found with the execution task. In this same area and time frame a cluster with opposite polarity appears for the incorrect observed hand over the motor cortex. The difference between the two conditions is reflected in the left bottom part of the figure that shows a highly significant cluster in blue located over the motor cortex. In the right bottom of the figure a line plot is presented showing the average LRF for the twelve most significant channels. The blue line shows the correct observed hand condition, and the red line shows the incorrect observed hand condition.

Discussion

In this study we used MEG to study the lateralization of motor activation in association with action observation of left and right hand finger movements. The LRF results of the execution task show lateralized activation over the motor cortex in association with the hand that is used during action execution in correspondence with the results of earlier studies (Coles, 1989) that showed lateralization of motor activation using ERPs (van Schie et al., 2004). Comparable with the execution condition, data analysis of the observation task shows lateralized activation over the motor cortex in association with the observation of left and right hand finger movements. Importantly, the finding of opposite lateralized effects to the presentation of incorrect hand movements shows that the observation LRF truly result from action observation, and not in association with the cue.

The significant differences between correct and incorrect hand movements for both the execution and observation tasks are shown as clusters over the motor cortex. These results are in favor of the hypothesis that activation over the left and right motor cortices will lateralize, as a function of the laterality of the observed hand movements.

Even though the results of the execution and the observation task are sufficiently comparable, there are some differences concerning location and timing. Apart from the overlap in topography of lateralized activity during task execution and observation, the lateralized activity seems shifted backwards slightly in the observation condition. One explanation for this difference is that somatosensory cortex is relatively stronger activated than motor cortex in the absence of an executed response, which would be consistent with previous studies that reported somatosensory activation during movement observation (Avikainen et al., 2002; Rossi et al., 2002). Apart from the difference in timing of the LRF between execution and observation conditions that is explained by the different procedures of both conditions, there is also a difference in duration of lateralization. For the execution task the LRF peaks in a narrow time window while for the observation task the LRF is more stretched out. This can be explained by the backwards movement of the index finger observed when turning off the response stimulus 300ms after the onset. This backward movement could evoke a second LRF that adds up to the first, giving the resulting LRF a stretched appearance.

We conclude that the motor cortex is cross activated during the observation of hand movements. The typical crossed organization that is known to underlie motor performance is found to be preserved in action observation. In general this result is consistent with previous reports that have indicated similarity in motor function during the performance and observation of actions. The present findings suggest that even without explicit instructions, the human brain differentiates between observation of left and right hand movements. This ability to represent the left and right hand movements of others separately may provide an important basis for the understanding of other peoples actions where the laterality of movements are considered to be relevant (e.g. in traffic, games, joint action).

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Nijmegen CNS, Vol. 1, March 2006

L2-L1 Word Association in bilinguals: Direct Evidence

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The Revised Hierarchical Model (Kroll and Stewart, 1994) assumes that words in a bilingual's languages have separate word form representations but shared conceptual representations. Two routes lead from an L2 word form to its conceptual representation: the word association route, where concepts are accessed through the corresponding L1 word form, and the concept mediation route, with direct access from L2 to concepts. To investigate word association, we presented proficient late German-Dutch bilinguals with L2 non-cognate word pairs in which the L1 translation of the first word rhymed with the second word (e.g. GRAP (joke) – Witz – FIETS (bike)). If the first word in a pair activated its L1 equivalent, then a phonological priming effect on the second word was expected. Priming was observed in lexical decision but not in semantic decision (living/non-living) on L2 words. In a control group of Dutch native speakers, no priming effect was found. This suggests that proficient bilinguals still make use of their L1 word form lexicon to process L2 in lexical decision.

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Introduction

Bilingualism is becoming a more and more widespread phenomenon. Increasingly it is becoming the norm to be able to speak and comprehend more than one language at least to some extent. There are many questions that are regularly asked by non-experts about bilingualism.

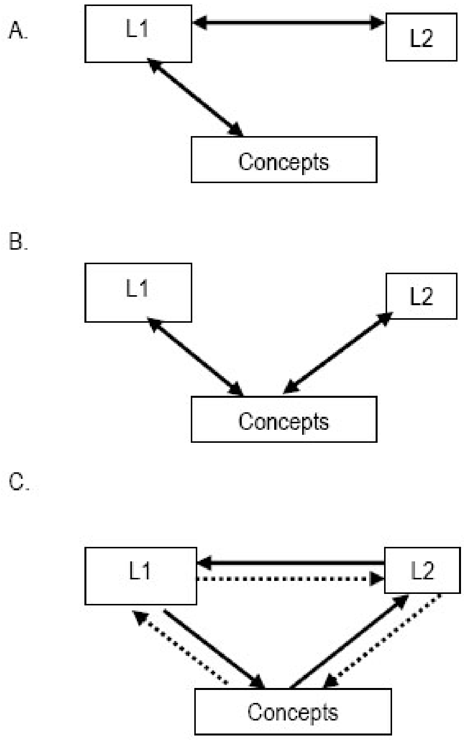

Figure 1. The hierarchical models. A: Word Association Model; B: Concept Mediation Model; C: Revised Hierarchical Model.

Two come to mind: Do bilinguals 'think' in different languages depending on which language they are speaking? If they only think in one language, do they 'translate' to the other language when using it? This latter question, whether bilinguals automatically translate a word in their second language (L2) to the translation equivalent in their native language (L1) has been incorporated in one class of models of bilingual word representation, the hierarchical models.

Hierarchical models of bilingual processing are models that assume separate lexical (word form level) representations but shared conceptual (meaning level) representations for two translation equivalents in a bilingual's two languages. Three such models have been proposed so far. The word association model (Potter, So, von Eckardt & Feldman, 1984, see figure 1A) assumes that an L2 word is connected to its corresponding conceptual representation only through its L1 equivalent. Therefore, according to this model if an L2 speaker needs to access the meaning of an L2 word he or she will first activate the corresponding L1 word form and only then access the meaning of the word. The concept mediation model (Potter et al., 1984, figure 1B) proposes that L1 and L2 word forms are both directly connected to their corresponding concept. Access from L2 to L1 word forms occurs through access to the concept.

Potter et al. (1984) compared these two models in a study in which bilinguals performed picture and word naming in L1 and L2, and both L1-L2 (forward) and L2-L1 (backward) translation. The critical predictions for the word association and concept mediation models were as follows: the word association model predicts that L1-L2 translation will be faster than L2 picture naming because picture naming involves concept retrieval, L1 lexical retrieval and L2 lexical retrieval while forward translation only requires L1 lexical retrieval and L2 lexical retrieval. The concept mediation model predicts that both picture naming and forward translation require concept retrieval (either from an L1 word or a picture) and L2 lexical retrieval. The results were in accordance with the concept mediation model, as L2 picture naming was found to be as fast as forward translation. Potter et al. (1984) found this result to be strikingly similar in proficient and less proficient bilinguals. L2 processing was therefore assumed to occur through concept mediation at all levels of proficiency.

Kroll and Curley (1988) challenged the claim that connections between L1 and L2 always occur through concepts. They proposed that a stage in which L1-L2 word form links mediate the processing of L2 words might still exist, but that the non-proficient bilinguals in Potter et al.'s (1984) study might have already passed that stage. In other words, these bilinguals were already too proficient. In an experiment replicating the Potter et al. (1984) study with a wider range of bilinguals, they found that bilinguals who had known their L2 for less than 2 years conformed to the word association model: translation into L2 was faster than picture naming in L2. For more proficient bilinguals the results replicated those of Potter et al. (1984).

Kroll and Curley (1988) also tested another prediction of the concept mediation model: if forward translation occurs through concept mediation then it should be sensitive to semantic factors. They found that L1-L2 translation took longer when words were presented in semantically categorized lists than when the words were presented at random. This result was only true for the more proficient bilinguals, again confirming the developmental shift from word association to concept mediation.

Kroll and Stewart (1994) posited that translation times from L2 to L1 are faster than vice versa and that this might indicate different processing strategies for the two types of translation. In other words, the lexical and conceptual connections between L1 and L2 might be asymmetric. This idea lies at the basis of the third hierarchical model, the revised hierarchical model (Kroll & Stewart, 1994; figure 1C). Kroll and Stewart (1994) found that the category interference effect occurs for L1-L2 translation but not for L2-L1 translation. This means that concept mediation takes place in L1-L2 translation but not vice versa. The revised hierarchical model (RHM) therefore has two main aspects. First, both lexical and conceptually mediated links between L1 and L2 exist. The lexical link is stronger in the L2-L1 direction than in the L1-L2 direction. The conceptual link on the other hand is stronger in the L1-L2 direction than in the L2-L1 direction. Second, the balance between lexical and conceptual links changes as proficiency increases. The more proficient a bilingual is the more conceptual mediation will occur.

Of the two L2-L1 routes in the RHM, the conceptual route has received the most attention by far. Evidence for this route has been found in quite a number of studies (Dufour & Kroll, 1995; Potter et al.,1984; Zeelenberg & Pecher, 2003). Most studies investigating this route have used some sort of semantic manipulation or semantic task, for example semantic categorization (Dufour & Kroll, 1995; Zeelenberg & Pecher, 2003) or translation of semantically categorized lists (Kroll & Curley, 1988; Kroll & Stewart, 1994). In most of these studies an absence of semantic effects in certain conditions has been taken as evidence for use of the lexical route in these conditions. For instance, L1-L2 translation has been found to be more sensitive to semantic context than L2-L1 translation (Kroll & Stewart, 1994). L2-L1 translation is then assumed to occur through word association because the absence of a semantic effect indicates that it is probably not occurring through conceptual mediation.

One study directly investigating the lexical link was performed by Talamas, Kroll and Dufour (1999). In this study proficient and less proficient English – Spanish bilinguals performed a translation recognition task. The items of interest were the pairs in which the two words were not translation equivalents. There were two types of distractors: if the correct pair was man – hombre, the form related distractor pair would be MAN – HAMBRE (hunger), while the semantic distractor pair was man – mujer (woman). Less proficient bilinguals made more errors on the form related pairs, while more proficient bilinguals made more semantic errors. This indicates that the less proficient bilinguals were relying more on word form while the more proficient bilinguals were relying more on meaning. However, there are two problems with this study. One is that though all bilinguals were categorized as English-dominant, six participants were in fact native Spanish speakers. This may have clouded the distinction between L1 and L2. Second, the direction of translation was also manipulated: half of the pairs were presented in the forward direction and half in the backward direction. The main conclusions are collapsed across this distinction, but this is a mistake. The RHM would predict more semantic errors in forward translation and more form-related errors in backward translation. In fact, the authors found the opposite pattern.

Another frequently used paradigm has not often been studied in direct relation with word association in the RHM, but may still shed some light on it: masked translation priming. In this paradigm, participants perform a monolingual task (mostly lexical or semantic decision) in either their L1 or L2. Preceding a target word, the translation equivalent of this word is presented as a masked prime. A consistent effect in this paradigm is an asymmetry in the two directions of priming. While an L1-prime presented in an L2 task (L1-L2 priming) produces consistent priming effects (De Groot & Nas, 1991; Gollan, Forster, & Frost 1997; Jiang, 1999; Jiang & Forster, 2001; Kim & Davis, 2003), the reverse direction has mostly led to negative or inconsistent results (Gollan et al., 1997; Grainger & Frenck-Mestre, 1998; Jiang, 1999; Jiang & Forster, 2001; Finkbeiner, Forster, Nicol, & Nakamura, 2004). This is in agreement with the word association route: activating the L1 word when viewing the prime saves time when the subsequent L2 word has to be processed, since activating the L1 word form is a necessary step in processing the L2 word. Since processing the L2 word form is not necessary to perform the task in L1, priming of L1 processing with an L2 prime does not occur. However, one problem with the masked priming paradigm is that it introduces a multilingual element in a purportedly monolingual task. It may be the case that the presentation of primes in another language alters the processing of the target words. The fact that primes are masked does not solve this problem: at some level the primes are being processed, or there would not be a priming effect. Another problem is that it is not clear whether it is the activation of the L1 word form or of the concept that produces the effect.

This means that this priming effect is still not conclusive evidence for the existence of the word association route.

For these reasons, the present study aims at directly investigating the word association route in a completely monolingual task. In this study we investigated proficient German – Dutch bilinguals in a novel paradigm, cross-language mediated phonological priming. For this paradigm L2 word pairs are constructed in which the L1 translation equivalent of the first word rhymes with the second word: GRAP (joke) – Witz (joke) – FIETS (bike). Participants only see the first and third word in the triplet, which are both in L2. The L1 word is never presented, but is assumed to be activated by the participant when performing a task. If this L1 word form is activated, a phonological priming effect on the second L2 word will be observed. This paradigm is similar to the semantically mediated phonological priming paradigm, in which word pairs are used of which a semantic associate of the first word is phonologically similar to the second word, e.g. PEN - ink – INCH (see for an example, Farrar IV, Van Orden & Hamouz, 2001). Since the effect we are targeting is phonological, the presence of a priming effect means that the L1 word form has been activated. This is then very strong evidence that L1 word form plays a role in a monolingual L2 setting. Moreover, we test for this effect in semantic decision (SD) and in lexical decision (LD). This allows us to determine whether L1 involvement in L2 processing is dependent on task demands.

The predictions are as follows: if word association (activation of the corresponding L1 word form) is a necessary step in solving the L2 task, then cross-language mediated phonological priming will be observed. Regarding the two different tasks, the RHM predicts that proficient bilinguals are able to use the concept mediation route. They do therefore not need the word association route to access a word's corresponding concept. A priming effect in SD is not predicted by the RHM, but would indicate that even proficient bilinguals use the word association route. For LD no clear predictions concerning cross-language mediated phonological priming are made. It has not been clearly specified which processing steps a bilingual person takes to perform LD in L2. If access to concepts is necessary, then results should be similar to those found in SD. If the L1 word form is accessed to perform the task, then the cross-language mediated phonological priming effect will be found.

Method

Participants

25 Germans (6 male) participated in this experiment. They were students in Nijmegen and followed university education in Dutch, which meant they were relatively proficient in Dutch. All learned Dutch after puberty. L2 proficiency was assessed with a short standardized proficiency test. The test consisted of a text in which 60 words of different categories had to be filled in in gaps in the text. The Germans scored an average of 53 out of 60, with a standard deviation of 5. This is at the lower end of the normal range for native Dutch speakers, which is 53 to 60 out of 60. 26 (8 male) Dutch native speakers, also students, participated as a control group.

Stimuli

34 word pairs were constructed, in which the German translation of the first word rhymed with the second Dutch word. Examples are: GRAP (joke) – Witz – FIETS (bike); ROOSTER (schedule) – Stundenplan – KRAAN (tap). All primes in these pairs were clear non-cognates with their translation equivalent in German, while for the targets an effort was made to keep phonological similarity as low as possible. Control pairs were constructed by shuffling primes and targets (GRAP – KRAAN, ROOSTER – FIETS). All words in experimental pairs were pilot-tested with a group of three beginning learners of Dutch, to test whether the words would be known to the participants. 14 of the German participants in the experiment were also asked to translate the words on a later date. 68 filler pairs were added, which mostly consisted of cognates. This was done because most Dutch and German words are cognates. An experiment with only non-cognates would therefore be odd and this might be noticed by the participants. For lexical decision another 136 pairs containing either one or two nonwords were presented as well. These were constructed by changing 1 – 3 letters in the Dutch filler words. All nonwords were orthographically legal in Dutch.

Design

There were two tasks in this experiment: lexical decision (LD) and semantic decision (SD; living/non living). The lexical decision was always presented first to avoid semantic carry-over effects from the semantic decision. This had the disadvantage that since the same items were presented in the two tasks, repetition priming effects may have occurred in SCT. However, the requirements on the items strongly limited the number of possible items, which made it

		Related RT (ms)	Error(%)	Unrelated RT (ms)	Error(%)	Priming (ms)
LD	Dutch	582	6.73	588	5.36	6
	German	708	4.57	736	4.43	28
SD	Dutch	711	9.75	725	12.36	14
	German	789	10.42	805	11.90	16

Table 1: RTs and error rates per task, condition and group

		Related RT (ms)	Unrelated RT (ms)	Priming (ms)
LD	L1	582	588	6
	L2-long	649	656	7
	L2-short	708	736	28
SD	L1	711	725	14
	L2-long	749	753	4
	L2-short	789	805	16

Table 2: RTs per group, task and condition with L2 group split according to length of stay in the Netherlands.

impossible to split items across the tasks. Both tasks were carried out in Dutch, which was L2 for the Germans and L1 for the Dutch. All experimental pairs were presented both in lexical decision and semantic decision.

Participants had to perform the task (either LD or SD) for both items in a pair. This was done because the question of interest is whether processing the first L2 word activates the L1 word form, which then produces the targeted priming effect on the second word. Also, the question was whether task demands would influence the activation of the L1 word form. Therefore, the task had to be processed on the same item of which L1 word form activation was assessed, namely the prime.

Procedure

Participants sat in a soundproof lab with a PC screen and a button box. Responses were given using the index and middle finger of their preferred hand. For each task, instructions were first shown on screen. After that a practice block started, which consisted of a maximum of 6 blocks of 10 item pairs. During practice participants got feedback on both speed and accuracy after every pair. Practice ended when answers to all 6 words in the last 3 pairs in a block were correct and with an RT under 1000 ms. This was done to train participants in being both fast and accurate. After practice the experiment started, in which no feedback was given. Words were presented in pairs, meaning that the second word of a pair was presented as soon as an answer was given to the first word, with an ISI of 20 ms during which a hash mark mask was presented, while there was a 500 ISI between pairs, in which a fixation cross was presented. Each word remained on screen until a response was given. Pauses were given during the experiment.

Results

The RTs for each condition, group and prime type are shown in table 1. All incorrect answers and RTs more than 3 standard deviations from the group/task mean were removed. One subject was also removed from the SD data because she pressed the same button on 90% of

the trials, indicating that she was not really performing the task. Based on the translation posttest performed by 14 of the German subjects, all items that were not known or given a different translation than our target by 3 or more of the participants, were removed. These items were 3 primes and 3 targets. All pairs containing one of these words were removed from the data. One subject was also removed from the data because she did not know half of the items in the posttest.

Data was analyzed separately for each task in a 2x2 (group x priming) repeated measures GLM. Data was only analyzed by subjects since due to the specific requirements for the item pairs, generalization across many items is not a practical possibility. For LD significant main effects were found for group ($Fs(1,49) = 31.182$, $p<0.000$) and pair type ($Fs(1,49)=9.807$, $p<.003$). The effect of priming was qualified by an interaction between group and priming ($Fs(1,49)=4.159$, $p<0.047$). Planned comparisons for the effect of pair type within the two groups revealed that the effect of

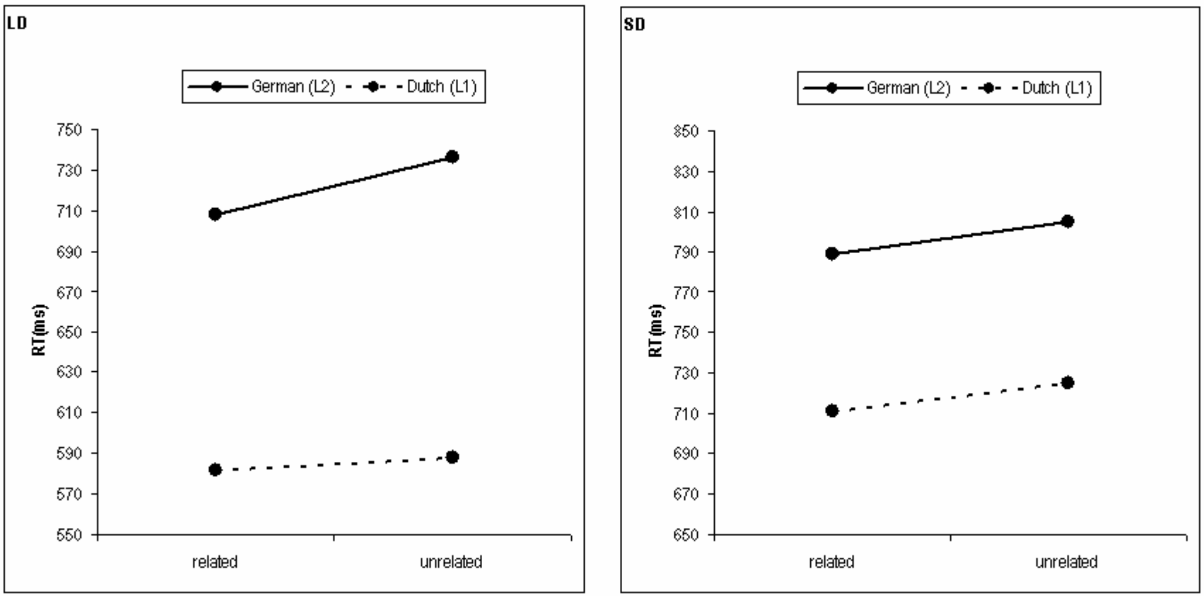

Figure 2: Interaction plots for group and priming

pair type was only significant for the Germans (Fs-L2(1,49)=13.113, p=0.001; Fs-L1(1,49)<1),

In SD only a main effect of group was found (Fs(1,49) = 8.015, p<0.007). The effect of pair type was marginal (Fs(1,49) = 3.965 p<0.052) and there was no interaction between group and priming. Planned comparisons revealed that the effect of priming was significant in neither group (L2: Fs(1,49)=2.152, p<.149; L1: Fs(1,49)=1.817, p<.184). Interaction plots for this effect are shown in figure 2.

In sum, these results show that, as expected, word form association only takes place in the Germans. Moreover, it only takes place in lexical decision, not semantic decision. These results indicate that proficient bilinguals can use the word association route. The RHM model predicts that use of the word association route decreases as bilinguals become more proficient. To test this prediction, we split our bilinguals based on the time they had known Dutch. The shorter stay group had been in the Netherlands for an average of 8.5 months (range 5 to 18, SD = 4.6. the longer stay group had a mean stay of 51.5 months (range 18-120, SD = 30.4).

In this 3x2 (group x priming) repeated measures GLM, the following effects were found for LD: priming had a main effect (Fs(1,48) = 13.895, p<.001), which was qualified by an interaction between priming and group (Fs(2,48) = 6.159, p<.004). Group also had a significant main effect (Fs(2,48) = 31.786, p<.000). Planned comparisons revealed that the effect of priming was only significant for the group that had been in the

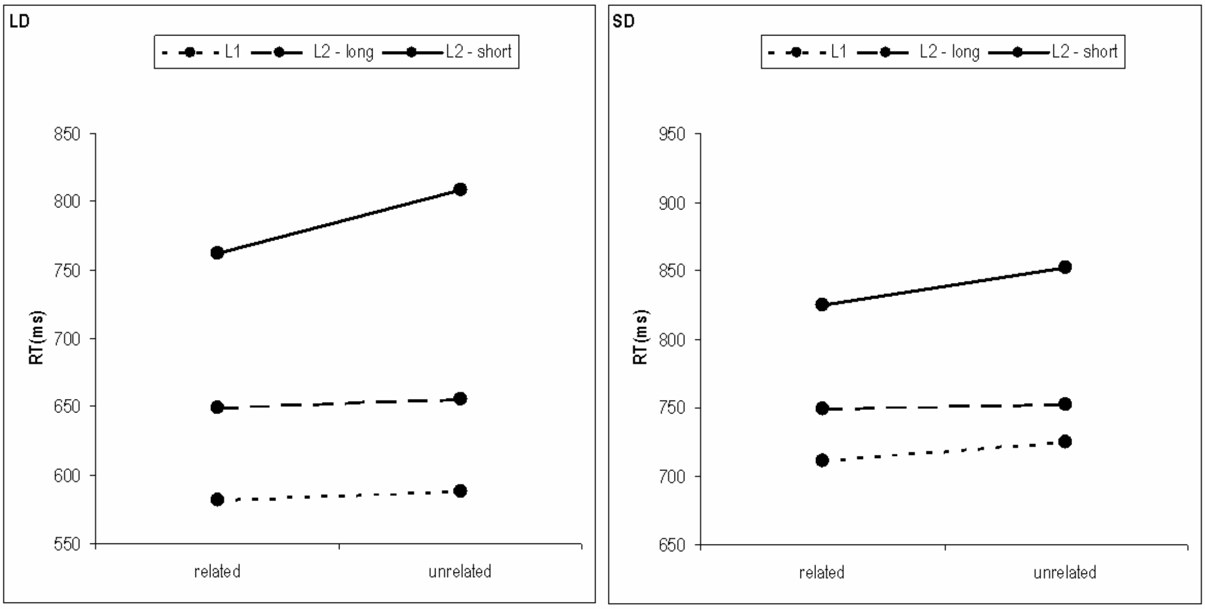

Figure 3: Interaction plots for group and priming. L2 speakers are split in two groups: shorter stay and longer stay.

Netherlands for a shorter time (shorter stay: Fs(1,48) = 22.007, p<.000; longer stay and L1-speakers: Fs(1,48) <1). In SD only the effect of group was significant (Fs(1,48) = 6.997, p<.002). The main effect of priming was marginal (Fs(1,48) = 3.512, p<.067). Planned comparisons revealed that the effect of priming was marginal in the shorter stay group but non-significant in the longer stay group (shorter stay: Fs(1,48) = 3.413, p<.071; longer stay: Fs(1,48) <1; L1-speakers: Fs(1,48) = 1.828, p<.183).

Discussion

In this experiment we investigated evidence for word form association from L2 to L1 in lexical decision and semantic decision. We found evidence for cross-language mediated phonological priming (GRAP – Witz – FIETS) in lexical decision but not in semantic decision. As predicted, the effect was found in the German subjects (L2 speakers) but not the Dutch subjects (L1 speakers). This result is as far as we know the most direct evidence for the existence of the word association route in L2 processing. So far, most studies investigating this issue have introduced primes of one language while the participants were doing a task in the other language. Presenting materials from another language may very well affect the very processes that are under investigation. In this study we presented no L1 materials and therefore obtained strong evidence that when participants are performing a completely monolingual task in their L2, they still make use of their L1. Also, other studies have not been able to fully distinguish form and concept priming effects: L1-L2 translation priming effects can either be due to the shared activation of the L1 word form or of the concept. Since in this study we targeted a phonological effect, the priming effect we find can only be due to L1 word form activation.

The fact that this result is dependent on the type of task participants are performing is also important. So far, most of the studies aiming at the conceptual link have used conceptual tasks or conceptual manipulations (Dufour & Kroll, 1995; Kroll & Stewart, 1994; Zeelenberg & Pecher, 2003), while studies aiming at the lexical link have mostly made use of lexical decision tasks with cross-linguistic primes (De Groot & Nas, 1991; Gollan et al., 1997; Jiang, 1999; Jiang & Forster, 2001; Kim & Davis, 2003). It might therefore also be that the different results these studies have obtained are partly due to the fact that different tasks were used. In the present study we have targeted the word association link but have used both a semantic task and a less semantic task to do so. In the present study, the cross language mediated phonological priming effect appears to be present only in lexical decision, indicating that the lexical route is used in lexical decision but not (or less so) in semantic decision. One drawback is that our semantic task may have suffered from repetition priming effects, since the same items were presented in lexical decision first. Due to the limited number of items they could not be split across the two tasks. We decided that it was more crucial to keep the difference between the semantic and non-semantic task as large as possible by avoiding semantic carry-over effects in the LD. It was also important to do both tasks in the same group of subjects. Since the target population is very heterogeneous in terms of age, age of acquisition, proficiency and use of L2, any differences arising between groups are difficult do interpret.

The finding that lexical mediation is task-dependent within the same group of bilinguals. sheds a new light on the distinction between conceptual links and lexical links. So far, most authors have assumed that the conceptual link is more ‘advanced’ than the lexical link. L2 learners therefore start out using the lexical link but once they are able to conceptually mediate L2 words, they will mostly always do so. Our data on the other hand suggests that even when L2 learners are able to conceptually mediate, they might only do so when this is necessary, i.e. when they have to access the concept. When the concept is needed to solve the task at hand, the most efficient route from the L2 word to the concept is the conceptual link. When access to the conceptual level is not necessary, apparently participants make use of the lexical link and solve the task by accessing the L1 word form.

However, the separate analysis of the two groups of German participants reveals that a developmental pattern does indeed occur. In the group of Germans that had spoken Dutch for a longer time no cross-language mediated phonological priming effect was found, while in the group that had spoken Dutch for a shorter time the effect was strong. Therefore, the more proficient the speaker is in his or her L2, the less he or she makes use of the lexical link. This is exactly what the RHM predicts. It is worth stressing however that all our bilinguals were highly proficient. This was due to a number of factors: first, German and Dutch are very much alike, which facilitates rapid acquisition of Dutch. Second, the participants in our experiment were all taking higher education in Dutch, therefore using Dutch on a daily basis and at a high level.

In conclusion, the current studies provides convincing evidence for the existence of the lexical route in a purely L2 context. In some cases, bilinguals therefore do translate L2 words to L1 words when processing them. As predicted by the RHM, this happens less as proficiency increases. However, the present results show that lexical mediation is dependent on task demands. The same bilinguals appear to use the direct conceptual route when doing SD and the lexical route when doing LD. Further research will be necessary to investigate what task demands influence the use of the lexical link. This is important because neither lexical decision nor semantic decision are very natural tasks. It therefore remains to be seen how much L1 word form access is likely to happen in an everyday context.

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Nijmegen CNS, Vol. 1, March 2006

Modulation of oscillatory neuronal synchrony in the beta band by motor set[1]

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Oscillatory neuronal synchrony is thought to play an essential role in the neuronal processing of information. Modulation of these ongoing oscillations is a possible mechanism by which processing can selectively be biased. Evidence is presented for a modulation of oscillatory neuronal synchrony by motor set, obtained with magnetoencephalography. Subjects performed a bilateral isometric contraction and were cued in some trials to respond at the event of the imperative go-cue with a left and in others with a right wrist extension. The analysis of the period in which subjects could expect the go-cue to occur (stimulation period) revealed that beta power (15-30 Hz) was lower over the motor cortex when it was contralateral to the expected response side compared to when it was contralateral to the side of which no response was required. This difference did not exist in the baseline period in which the go-cue could not occur. The effect was due to a decrease in beta power in the stimulation period compared to baseline that was bigger for the motor cortex driving the cued side. Force output was equal in the two conditions and stratification of the EMG signals did not change the results. The location of the maximal cortico-muscular coherence in an independent data set was highly similar to the location of the maximal decrease in beta power, and analysis within these channels also showed the same results. We conclude that motor set results in a selective modulation of beta power during a steady bilateral contraction.

Keywords: motor set, oscillatory synchrony, MEG, EMG.

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1 Introduction

The active brain

Traditionally, the brain was thought of as a passive stimulus-driven device, triggered by sensory inputs. This device supposedly had the objective to arrive at a context-invariant internal world model by reconstructing object properties in a hierarchical feedforward mode. Such an approach of human information processing tends to deal with perception and action in isolation (Hommel, Müsseler, Aschersleben, & Prinz, 2001). The alternative viewpoint is to see the brain as a much more active and adaptive device (Engel, Fries, & Singer, 2001). The latter view stresses the close linkage between perception and action. Instead of constructing context-invariant world-models, action (planning) guides perception and action is guided by perception. For example, the pattern of saccadic eye-movements during inspection of a painting varies dramatically with a priori instructions (Yarbus, 1967). Findings from single-cell recordings have often seemed to be in line with the traditional view of the brain consisting of hierarchical levels of specialized detectors extracting information from bottom-up input. Recently, however, there has been a great deal of evidence of top-down influence even in cortical areas at the bottom of the hierarchy (Treue, 2001; Lee, Yang, Romero, & Mumford, 2002)

Oscillatory neuronal synchrony

Sensory stimulation evokes responses in brain areas that are time- and phase-locked to the onset of the stimulus. These evoked components therefore survive averaging over trials while the procedure reduces noise that is assumed to be independent between trials and also components that are not phase-locked to the stimulus. A well-known example of such an evoked component is the N400, elicited at a latency of about 400 ms by a semantic violation in a sentence (Kutas & Hillyard, 1980). Another thing we know is that brain shows spontaneous periodic oscillations in activity. By means of spectral analysis we can break down a signal into its different frequency components, like a prism breaks down light into components with different wavelengths. The idea originally proposed by Fourier was that we can decompose any mathematical function into a weighted sum of sinusoids that have a certain frequency and phase. Hence, analysing a signal in terms of its spectral components is called Fourier analysis. It allows for a compact representation of a periodic signal as a function of frequency instead of time. Traditionally, the frequency axis has been subdivided into different bands for classification of neuronal oscillations, namely δ (0.5-4 Hz), θ (4-7 Hz), α (8-12 Hz), β (15-30 Hz) and γ (30-90 Hz). An example of spontaneously occurring oscillations are the different brain rhythms that occur during sleep and wakefulness; whereas the spectrum during slow wave sleep is dominated by high amplitude and low frequency oscillatory components, activated states like wakefulness and REM sleep are characterized by low amplitude and high frequency oscillations (Llinás, Urbano, Leznik, Ramírez, & Marle, 2005). These neural oscillations occur spontaneously but are modulated by (sensory) processing. An example of this is the increase in power at the alpha frequency over visual cortex when the eyes are closed. Recently the term induced component has been coined for components that are time-locked to sensory events but not necessarily phase-locked (see for example Makeig, 1993). In other words the latency of the effects is jittered in the different trials. These components can be detected by first performing spectral analysis on single trials before averaging (Tallon-Baudry & Bertrand, 1999). Evoked components can be considered to be signatures of the passive brain: input at time t leads to a certain component at time t + some fixed latency at a given location. The timing of an induced component on the other hand depends both on the time of input and the ongoing activity in the brain. Modulation of ongoing rhythms in the cortex can make brain regions more or less responsive to input. Besides looking at oscillations at a certain location we can also look at relationships between oscillations at different locations. Coherence and the closely related phase-locking are measures of interdependence in the frequency domain, similar to correlation as a measure of relatedness of signals in time. They quantify the consistency of the phase difference between two signals. Functional coupling of two sources leads to a consistent phase difference between their signals and a high coherence value.

What is oscillatory neuronal synchrony good for?

In the primate visual system more than 30 distinct cortical areas have been identified by physiological and anatomical studies (Felleman & Essen, 1991), reflecting functional specialization. The binding problem is: how do we keep processing together that belongs together and apart from processing that belongs to something else if it is distributed across the brain? One proposal is to use a temporal code that is independent of a rate code (the firing rate of neurons), to code for relations, allowing for selective and dynamic tagging of neurons that currently participate in the same cognitive process by specific yet flexible, context-dependent binding of distributed activation (Malsburg & Schneider, 1986; Engel et al., 2001). Briefly, the advantages of a temporal binding mechanism can be summarized as follows (Engel, Fries, König, Brecht, & Singer, 1999). First, it keeps the general advantages of distributed coding schemes like robustness against loss of network elements (graceful degradation) and representations which contain explicit information about object features instead of just signalling the presence of the object. Second, temporal binding can occur using the very first spikes of a response, suggesting advantages for the speed of processing (Fries, Neuenschwander, Engel, Goebel, & Singer, 2001). Third, temporal binding offers a solution to superposition problems, because it dissociates the relational (temporal) code from the feature code (firing rate). Fourth, temporal binding provides an efficient mechanism for selection of assemblies for further processing because precisely synchronized spikes constitute highly salient events and can be detected from random synchronizations. This can activate coincidence-sensitive neurons in other brain areas (König, Engel, & Singer, 1996). Although the idea of binding by synchrony is still controversial (see for a critical evaluation Shadlen & Movshon, 1999) experimental results point to special role for oscillations in the gamma band in visual binding (Gray, König, Engel, & Singer, 1989; Eckhorn, Frien, Bauer, Woelbern, & Kehr, 1993; Rodriguez, George, Lachaux, Martinerie, & Varela, 1999; Tallon-Baudry & Bertrand, 1999). However, the binding problem is not specific for the visual system and presumably also exists in other brain areas. Recently, an extension of the functional role of neuronal oscillations in visual binding to the coordination of neural processing in general has been suggested (Schnitzler & Gross, 2005): findings suggest that network oscillations bias input selection, temporally link neurons into assemblies, and facilitate synaptic plasticity (Buzsáki & Draguhn, 2004). In line with this general role findings are suggestive of a possible functional significance of oscillatory synchrony in motor functioning (Fetz, Chen, Murthy, & Matsumura, 2000; Salenius & Hari, 2003). Especially oscillations in the beta band have been found to be ubiquitous in the motor system. One suggestion is that the role of beta band activity is similar to that of alpha activity in visual cortex that supposedly reflects cortical idling (Pfurtscheller, Stancák, & Neuper, 1996). Another suggestion is that beta activity may be related to maintenance of posture (Gilbertson et al., 2005).

Attention and motor set

Attention is a cognitive function that is directly linked to neuronal information processing. As Hebb (1949) formulated it: ”in the simplest terms, attention refers to a selectivity of response”. The study of attention is often the study of perceptual selectivity; for example two visual stimuli are present in the visual field and the subject is instructed to attend to only one. The effect of attention is then the difference between the response to the target and the response to the distracter. Again oscillations in the gamma band have been related to visual attention (Fell, Fernández, Klaver, Elger, & Fries, 2003). Fries (2001) recorded neurons in V4 while macaque monkeys attended behaviourally relevant stimuli and ignored distracters and found that neurons activated by the attended stimulus showed increased synchronization in the gamma band (35-90 Hz) but decreased synchronization at lower frequencies (<17 Hz) compared with neurons activated by distracters. The idea is that localized changes in synchronization reflect amplification of behaviourally relevant stimuli because gamma band synchrony may be more effective in activating postsynaptic neurons. These neurons have an enhanced sensitivity to synchronous synaptic inputs that lead to rapid rates of depolarization while they actively compensate for slow changes in mean input rate (Azouz & Gray, 2003). Attention is selectivity in what is responded to or sensory selectivity while the term set is used for selectivity of motor response (Hebb, 1972). In the current study we considered selectivity in the motor system and therefore use the term motor set. By using the term set instead of attention we also mean to avoid the confusion that the latter can cause. Sometimes attention and awareness are seen as related concepts (Crick & Koch, 1990) and selective attention is thought to correspond to selective awareness (for arguments to separate the two see Lamme, 2003). We want to avoid this connotation of awareness that attention has and motor set much less by using the latter term. Oscillatory synchrony is proposed to have a functional role in neuronal information processing. Modulation of this ongoing activity can then selectively bias neuronal information processing in such a way that certain input to a brain region is processed more efficiently than other input. Therefore we hypothesize that motor set modulates ongoing oscillatory activity in the cortex.

Aim of project

We addressed the question whether oscillatory neuronal synchrony is affected by motor set. To this end, we aimed at activating motor cortices in a task that required subjects to use the visual information in order to control the motor output. Subjects were trained to hold both wrists extended during the presentation of a visual stimulus. The visual stimulus displayed a change at an unpredictable moment in time after its onset. Subjects responded to the stimulus change with a further extension of one of the wrists. We wanted to assess the effect of our experimental manipulation during constant and equivalent motor output on both sides. To ensure this, force calibration was necessary: the subject had to move both forces within a narrow window and hold the bilateral contraction steady. Power in the beta band is know to show a rebound after movement (Pfurtscheller et al., 1996), therefore we looked at the periods some time after force was calibrated and steady in order for the beta power to have returned to baseline levels. The crucial experimental manipulation in this experiment was that the subject was cued to respond in some trials with the left and on other trials with the right wrist. In other words, the subject was set to respond on the cued side. Apart from the cuing, the trials were physically identical. We expected that the manipulation of response side would have an effect on oscillatory neuronal synchrony in motor cortex. In particular, activity should be qualitatively different in motor cortex when it is contralateral to the response side compared to when it is contralateral to the side where abstinence of response is required. This effect should be maximal when the subject's set to respond is the biggest, namely in the period in which the go-cue can occur

MEG and EMG

One functional unit of the brain is the neuron and its input stations are the dendrites that receive a combination of excitatory post-synaptic potentials (EPSP) and inhibitory post-synaptic potentials (IPSP) over which integration takes place. Basically the effect of synaptic activity is to determine the frequency with which action potentials are generated. The local field potential (LFP) is an extra-cellular measure of the fluctuations in the membrane potentials of a group of neurons and mainly reflects the input to the population. Oscillations of the LFP therefore reflect regularities in the input of a population (Schnitzler & Gross, 2005). Because were interested in oscillations of the LFP we used MEG to record the electrophysiological signal with the required high temporal resolution. The potential recorded at the scalp consists of spatially averaged LFPs and therefore represents the summated activity of subthreshold soma and dendritic membrane potential fluctuations as well as action potentials (Nunez, 1995). It has been argued that the dominating components in the signal are the post-synaptic membrane potentials of mainly large pyramidal neurons (Baillet, Mosher, & Leahy, 2001). MEG picks up the magnetic fields corresponding and perpendicular to these currents. Since the magnetic field gets through intervening tissues basically unchanged, in contrast to the current, the spatial blurring of the source activity at the sensor level is less in MEG than it is in EEG (Lütkenhöner, 2003). In this study our focus is on the oscillatory neural activity in the MEG sensors overlying motor cortex and visual cortex. The MEG signal is strongly enhanced by temporal synchronization of the underlying activity; therefore power changes in a channel at a certain frequency indicate local changes in synchrony. Importantly, we first calculate the power for every single trial before averaging so that we pick up induced components that are time- but not necessarily phase-locked to events. We also recorded the electromyogram (EMG). Alpha-motor neurons in the spinal cord innervate groups of skeletal muscle fibers at neuromuscular junctions. The neuromuscular junction acts as a single relay synapse: the activity of the motor neuron has a one-to-one correspondence to the activity of the muscle. The motor neuron on the other hand requires concurrent activation of numerous excitatory inputs and is driven predominantly by the contralateral primary motor cortex (Randall, Burggren, & French, 1997). Surface electromyography (sEMG) allows for noninvasive measurement of the electric potential field evoked by active muscle fibers (Zwarts & Stegeman, 2003) and reflects the activity of the alpha-motor neuron that innervates the fibers.

2 Methods

2.1 Participants and paradigm

10 healthy subjects (4 female, mean age 24 years, range: 21-28) participated in the experiment. All subjects gave written informed consent according to the Declaration of Helsinki. We were interested in the activity in the brain (the MEG signal), the activity of the muscles (the EMG signal) and the relationship between the two. For this we designed a cued simple reaction time task. In this task the subjects performed a bilateral isometric contraction of the extensor carpi radialis longus, the muscle that extends the wrist when activated. In an isometric contraction the muscle is activated but held at a constant length so that there is a constant correspondence between force output

and muscle activity. It was important in our paradigm that measurements were obtained during a constant force output. To this end we required the force signal to be within a prespecified range during a trial. A schematic outline of a typical trial is shown in figure 1. In the top of the figure the left and right force traces are shown. The two black lines indicate the upper and the lower border of the desired force output. In the bottom part of the figure the time axis is shown and the corresponding visual stimulation. At the beginning of every trial a cue was presented that was either an arrow to the left or to the right, instructing the subject to respond to the appearance of the go-cue with the left or right hand. After this the force calibration started in which subjects fixated the central cross and extended both their wrists to elevate their hand against the levers of two force meters to bring the measured forces into a prespecified window, the exact settings of which were adjusted to obtain about 15 % motor unit recruitment. When the force got into the window the traffic light turned from red to green. In the figure these two traffic lights can be seen left and right from the fixation point, informing the subject about whether respectively the left force and the right force were in the window (green light) or not (red light). If both forces were in the window for 1000 ms the traffic lights disappeared and the subjects fixated a fixation point while holding the bilateral contraction steady. Then after another 1000 ms the visual stimulation started. The visual stimulus was a concentric sinusoidal grating, contracting towards the fixation point (diameter: 5, spatial frequency: 2 cyc/deg, contrast: 100 %, velocity: 0.8 deg/s) and the speed change (velocity step to 1.6 deg/s) could occur at an unpredictable moment between 150 and 3000 ms after stimulus onset. The speed change of the visual stimulation was the go-cue. The subject had to respond in time by exerting more force to the lever by a more extreme wrist extension at the cued side. Thereby the force moved out of the window while the contraction on the side that was not cued was kept constant. If the subject's force exited the window before the go-cue appeared the trial was stopped and error feedback was given. In both conditions, about 10 % of the trials were catch trials and did not contain a speed change, in which case the correct response consisted of maintaining the wrist extension until stimulus offset. Subjects were given feedback after each trial. The duration of a trial was variable: the cue and the fixation point were on for 1000 ms, force calibration lasted maximally 5000 ms of which both contractions needed to be OK for the last 1000 ms, and finally the period until the speed change was variable between 150 ms and 3000 ms. The trial effectively started when force calibration was successful. The bilateral experiment consisted in total of 300 trials divided over 6 blocks. Summarized, subjects performed a simple reaction time task in which they were cued to respond to a go-cue. Subjects maintained throughout the trial a constant bilateral isometric contraction after the force calibration. In order to be able to localize the motor cortices with the use of an independent data set (see also section 2.3.2) we also let the subjects perform a simple unilateral contraction: in the first block of 20 trials a left wrist extension (LC) was required to bring the force within the force window for the length of 8000 ms, then in the second block of 20 trials the same was asked of the subject for the right side (RC). Every session started with a short training of about half an hour on the bilateral task the subject needed to perform. After this, recording of electrophysiological signals started. First the subjects performed the unilateral contraction task. Finally the subjects performed the bilateral task they had practiced.

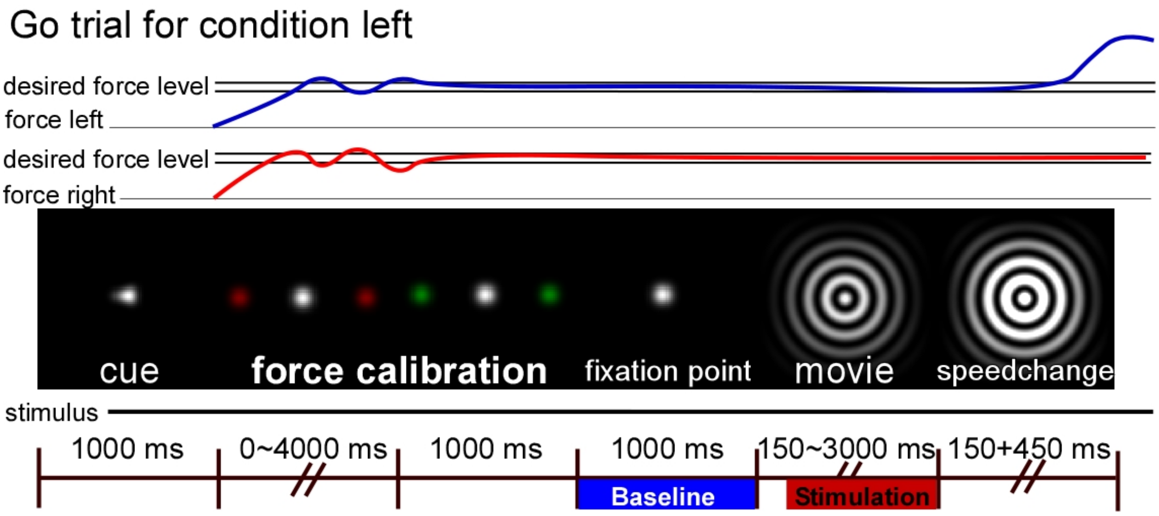

Figure 1: Experimental paradigm.

2.2 Stimulus presentation and data collection

Stimuli were presented with an LCD-projector, with an update frequency of 60 Hz. Control measurements with a sensitive photo-diode showed no 60 Hz component in the luminance time course of the stimuli. Force applied to the levers was measured by strain gauges. For the measurement and real-time control of generated force output we used an A/D conversion system. Apart from being recorded in parallel with the electrophysiological data, custom-made window discriminator software that received the two force signals as input via the A/D convertor was used to detect whether the force was within the prespecified window. For our data collection

we used the CTF MEG system at the Donders Centre, including its EEG and EMG recording capabilities. MEG was acquired with a 151-sensor axial gradiometer system. Bipolar surface EMG was recorded from the left and right m. extensor carpi radialis longus using 2 Ag/AgCl electrodes, which were placed over the muscle with a 2-cm interelectrode distance, with the proximal electrode placed 2 cm distal to the external epicondyle of the humerus. The EOG was recorded from a bipolar electrode pair placed above and lateral to the outer canthus of the left eye. The impedance of the EMG and EOG electrodes was below 20 kOhms. The data were low-pass filtered at 300 Hz and digitized at 1200 Hz. Prior to and after the MEG recording, and between blocks, the subject's head position relative to the gradiometer array was determined using coils positioned at the subject's nasion, and at the bilateral external auditory meatus.

2.3 Data Analysis

2.3.1 EMG- and MEG-signal preprocessing

All analyses were done with Matlab and using FieldTrip, an open source software package for EEG and MEG data analysis, developed at the FC Donders Centre[1]. In a correct go trial the subject kept both force left and right within the window during the period until the go-cue and then responded in time with the cued side while keeping the force on the other side within the window. In a correct no-go trial the subject just had to keep both force left and right within the window during the entire duration of the trial. On average, the experimental sessions with 300 trials yielded 83% correctly performed trials. Data segments that were contaminated by eye movements, muscle activity or jump artifacts in the SQUIDs were discarded. We removed the powerline artifact using a DFT filter and the linear trend in the data. EMG-amplitude was estimated by high-pass filtering the raw EMG signal at 10 Hz and then taking the absolute value of its Hilbert-transform. This procedure enhances firing rate information in the signal and is equivalent to full rectification of the EMG-signal (Myers et al., 2003). The measured axial gradients of the magnetic field were transformed to planar gradients using a nearest neighbour interpolation (Bastiaansen & Knösche, 2000). This facilitates the interpretation of the MEG topography across subjects.

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[1] Fieldtrip toolbox for EEG/MEG-analysis. FC Donders Centre for Cognitive Neuroimaging, Nijmegen, The Netherlands. http://www.ru.nl/fcdonders/fieldtrip

Stratification procedure

One potential problem might emerge if subjects contract to different degrees on the cued and non-cued sides. For this reason we monitored whether the force exerted on the lever was within the force window. However, the activity of the muscles could be different even with equal force output. Different patterns of co-contraction of agonist and antagonist muscles or differences in the position on the lever where the force is exerted could in principle be systematically related to conditions. We therefore wanted to check whether differences between conditions were observed while the distributions of the mean amplitude of the EMG, a measure of the activity of the muscle, were not significantly different across conditions. We first calculated the mean amplitude per trial by bandpass filtering the raw EMG signal between 10 and 250 Hz and subsequently applying the Hilbert transform, which gave us an estimate of the instantaneous amplitude. Stratification ensures that the distribution of the average amplitude in trials of condition left is equal to the distribution of the average amplitude in trials of condition right. We tested the significance of the difference between two distributions by evaluating it under a reference distribution we obtained by shuffling the trials between conditions. To make a selection of trials with similar distributions of the average amplitude both for the left and right EMG in the two conditions we performed the following stratification procedure (see also for example Roelfsema, Lamme, & Spekreijse, 1998). First we chose a number of bins. The choice of the number of bins is arbitrary and has an effect on the number of trials thrown away and the resolution at which we make two distributions equal. In the extreme case of just one bin, only the number of trials will be equated. Using different numbers of bins suggested that choosing 5 bins gave the best trade-off between on the one hand making the distributions similar and on the other hand not throwing away too many trials. We created a common bin space for the two distributions together of which the centres were chosen to maximally account for the spread of the data. Separately for the left and right EMG we had J bins where every bin j contained n trials for condition left and m trials for condition right. We then randomly threw away trials until $n_j = m_j$ so that the number of trials left over in a bin was the minimum of n_j and m_j . Finally we selected the trials that were both left after stratification of the left EMG and the right EMG, that is the intersection.

2.3.2 Analysis of average power and coherence

We used two time periods from the experimental task (see figure 1 on page 7) for the analysis of the average power and coherence spectra. The baseline (B) period is the interval from 1000 ms before the onset of visual stimulation until its onset. In this period the subject performs a steady bilateral isometric contraction and knows that the go-cue cannot occur in this period. The stimulation (S) period is from 300 ms after the onset of the visual stimulus until the speed change. In this period the subject also performs a steady bilateral isometric contraction but knows that the go-cue can occur in this period and is ready to respond. In condition left (L) the subject is cued to respond to the onset of the go-cue with the left wrist and in condition right with the right wrist (R). We calculated the average spectra in both conditions of the baseline periods (LB and RB) and of the stimulation periods (LS and RS). The critical and central comparison was between LS and RS, since we expected the effect of our manipulation of motor set to be mainly revealed in this period. The comparison between LB and RB was made to determine this effect in the baseline period. We also inspected the differences between the stimulation and the baseline period (LS vs LB and RS vs RB) because we expected the subject to be more set to respond in the period in which the go-cue could occur (P(go-cue appears) = 0 in the baseline period and P(go-cue appears) > 0 in the stimulation period). These differences between the stimulation and the baseline period were in turn compared between conditions (LS-LB vs RS-RB). Because the resulting data segments had a variable duration, they were first tapered, then zero-padded to a length of 4 s and then Fourier transformed. The Fourier transform $\tilde{x}(f)$ of a discrete time series $\{x_t \mid t = n\Delta t, n = 1,2,\ldots,N\}$ is given by:

$$\tilde{x}(f) = \sum_{n=1}^{N} x_t e^{-2\pi i f n \Delta t}$$

If T is the length of the time window, the frequency resolution is given by the Raleigh frequency $f_r = 1/T$. The digitization frequency is $f_d = 1/\Delta t = 1200$. According to Nyquist theorem only frequency components that are not bigger than the Nyquist frequency, $f_n = 1/2\ f_d$, can be reconstructed if they are present in the signal. Data was low-pass filtered by an analog filter with a cut-off frequency of 300 Hz. For the tapering of the data segments, we used the multi-taper method. We used a spectral smoothing of ±2 for the cluster level test statistic, focusing on the lower frequency bands, and we used ±5 for the group level statistics in the selected sensor set (see for details on the statistical methods section 2.3.3), focusing on a wider range range of the frequency axis. The direct multitaper spectral estimate of time series x_t, is defined as the average over individual tapered spectral estimates,

$$S_X(f) = \frac{1}{K}\sum_{k=1}^{K}\left|\tilde{x}_k(f)\right|^2$$

with:

$$\tilde{x}_k(f) = \sum_{n=1}^{N} w_t(k) x_t e^{-2\pi i f n \Delta t}$$

where $w_t(k)$, $k = 1, 2, \ldots, K$ are K orthogonal taper functions (see Mitra & Pesaran, 1999, and references therein). The number of tapers for a data segment is determined by the frequency smoothing S and the length of the segment: $K = 2(ST)-1$. So for a data segment of 1 second 9 tapers are used with a frequency smoothing of ± 5 Hz. The spectra we obtain are complex valued, containing in polar notation an amplitude and phase at every frequency:

$$S_X(f) = A(f)e^{i\phi(f)}$$

We estimate the expected value of the spectrum by averaging over multiple realizations, i.e. number of trials in a certain condition (Bruns, 2004). From the spectra we can compute the power and coherence: The power is defined as the squared modulus of the spectrum and is also called the auto-spectrum (Challis & Kitney, 1991). The (squared) coherence between signals X and Y is the squared cross-spectrum divided by the auto-spectra of the signals:

$$C_{XY}(f) = \frac{\left|S_{XY}(f)\right|^2}{S_{XX}S_{XY}}$$

The cross-spectrum is:

$$S_{XY} = S_X \cdot S_Y^* = A_X(f)A_Y(f)e^{i(\phi_X(f)-\phi_Y(f))}$$

From this can be seen that coherence represents the consistency of the phase difference and that it is normalized between 0 and 1. Coherence estimates have a positive bias that decreases with an increase in the amount of data. To correct for this, a non-linear transformation can be applied to the coherence spectra (Jarvis & Mitra, 2001). In the following we will refer to the corrected coherence estimate as the z-transformed coherence (see also Schoffelen, Oostenveld, & Fries, 2005). We also used the simple unilateral contraction task for analysis. The trials were first cut into segments of 1000 ms after which the z-transformed coherence was calculated separately for the unilateral contraction left (LC) and right (RC) between the MEG sensors and the left and right EMG. After inspection of the coherence spectra a frequency band of 10 Hz was selected around the peak frequency in every subject. Coherence was averaged in this band. Subsequently we took the difference between LC and RC, calculated the z-score over channels (so that the average was not dominated by subjects with the largest z-transformed coherence) and finally averaged over subjects. We then selected the 5 channels that were maximally coherent with the left EMG and the 5 channels that were maximally coherent with the right EMG. See figure 6 on page 15 for a sketch of the procedure.

2.3.3 Statistics

A prominent feature of cognitive processes is the large intersubject variability and a statistical analysis on the group level is therefore necessary to reveal the most prominent responses across the group (Hillebrand, Singh, Holliday, Furlong, & Barnes, 2005). We used two approaches to test the differences between conditions at the group level. The first approach was using a cluster level test statistic. The second approach was evaluating effects only in a prespecified region of interest. The rationale of using two different approaches is the following. First of all, if we find the same results with two different approaches this will cross-validate the two methods and provide further support to the results. Another reason is that two methods have different advantages. The cluster-level test statistic makes no prior assumptions about where the effects are located and therefore shows the most prominent effects in the entire sensor space. The region of interest approach uses the sensible criterion of the maximal coherence with the EMG in an independent data set for localizing motor cortices, since the motor cortex is known to drive the contralateral muscle. Therefore it supports the idea that we are looking at motor cortex if we limit our analysis to the two regions that are selected on the basis of this criterion. Furthermore, we would expect increased power of detecting effects in motor cortex with this approach. Moreover, the channel selection can be used as a reference region for computing cortico-muscular or corticocortical coherence. The two approaches will be described in more detail below.

Cluster level randomisation test

The multiple comparisons problem is the name for the fact that the false alarm rate (the probability with which we reject our null hypothesis while it is true) increases with the number of comparisons. This problem is often encountered in cognitive neuroimaging because of the high dimensionality of the data. Nonparametric statistical inference is well suited for dealing with this kind of data (Maris & Oostenveld, 2005) and the multiple comparisons problem can be solved by reducing multiple test statistics to just one aggregate test statistic. This approach also allows us to use a test statistic that incorporates a priori constraints that are biophysically plausible. The cluster level randomisation test uses a test statistic at the cluster level since effects in planar MEG sensors are clustered in space and frequency. For every subject we compute an average spectrum in condition A and B giving us a paired sample. Our null hypothesis of no effect is that conditions are exchangeable within subjects. The cluster level randomisation test works in the following manner. First a test statistic is calculated for every frequency channel combination, in this case by using a paired samples t-test. Connected clusters are then constructed of samples that have the same sign of the test statistic. The test statistics of the clusters are obtained by taking the sum of the individual samples' test statistics in the cluster. These cluster level test statistics are evaluated under the randomisation distribution of the maximum of the cluster-level statistics: for 1000 randomisations conditions are randomly shuffled within subjects and the maximum cluster level statistic is put in the reference distribution. Evaluating significance under this reference distribution will control the false alarm rate. See Maris (2004) for an extensive discussion of the rationale behind the cluster level randomisation test. In the following, whenever we use the term cluster analysis, we mean the approach that uses a cluster level randomisation test.

Group level statistics in selected sensor set

In our second approach we reduce the number of comparisons by first averaging over a selection of 5 sensors based on an independent data set. The independent samples t-test is calculated as a measure of the difference between the two conditions at the single subject level.

$$t = \frac{(\bar{x}_1 - \bar{x}_2)}{\sqrt{\frac{s_1^2(n_1-1)+s_2^2(n_2-1)}{(n_1+n_2-2)}\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}}$$

We now have a matrix T_{diff} with dimensions number of subjects x number of frequency bins containing in every cell a t-statistic of the difference between conditions A and B. Our teststatistic simply is the average over N subjects for every frequency. To test the significance of the effect at the group level we again use a non-parametric test. Under the null hypothesis of no effect conditions are exchangeable within subjects. The t-statistic of the difference between condition A and B basically is a paired sample. We obtain a reference distribution by calculating the value of the test-statistic for every possible relabeling of conditions within subjects by multiplying the t-value of one subject with a multiplication factor of either $m = 1$ or $m = -1$. The number of relabelings R is 2^N. The multiplication factor matrix has dimensions number of relabelings x number of subjects. Multiplying the multiplication factor matrix with T_{diff} results in a distribution T_{rlb} of the test-statistic for every frequency band with dimensions number of relabelings x number of frequency bins. To solve the multiple comparisons problem across frequencies and control for the false alarm rate we created a reference distribution by putting the maximum t-value over all frequency bands of a given relabeling in the reference distribution. Concretely, we take the maximum of T_{rlb} over the second dimension frequency and normalize for the number of subjects. The p-value is given by the proportion of relabelings that is more extreme than the test-statistic and the critical values are the $1/2\alpha \cdot R + 1$ smallest and largest members of the reference distribution in a two-sided test (Nichols & Holmes, 2002).

3 Results

Behavioural results

The average performance of the subjects in the task was as follows. The mean reaction time was 376 ms and subjects performed on average 83 % correct. Neither the average mean reaction time nor the percentage correct were significantly different in condition left and right in a paired sample t-test (respectively p=0.449 and p=0.447, randomisation tests).

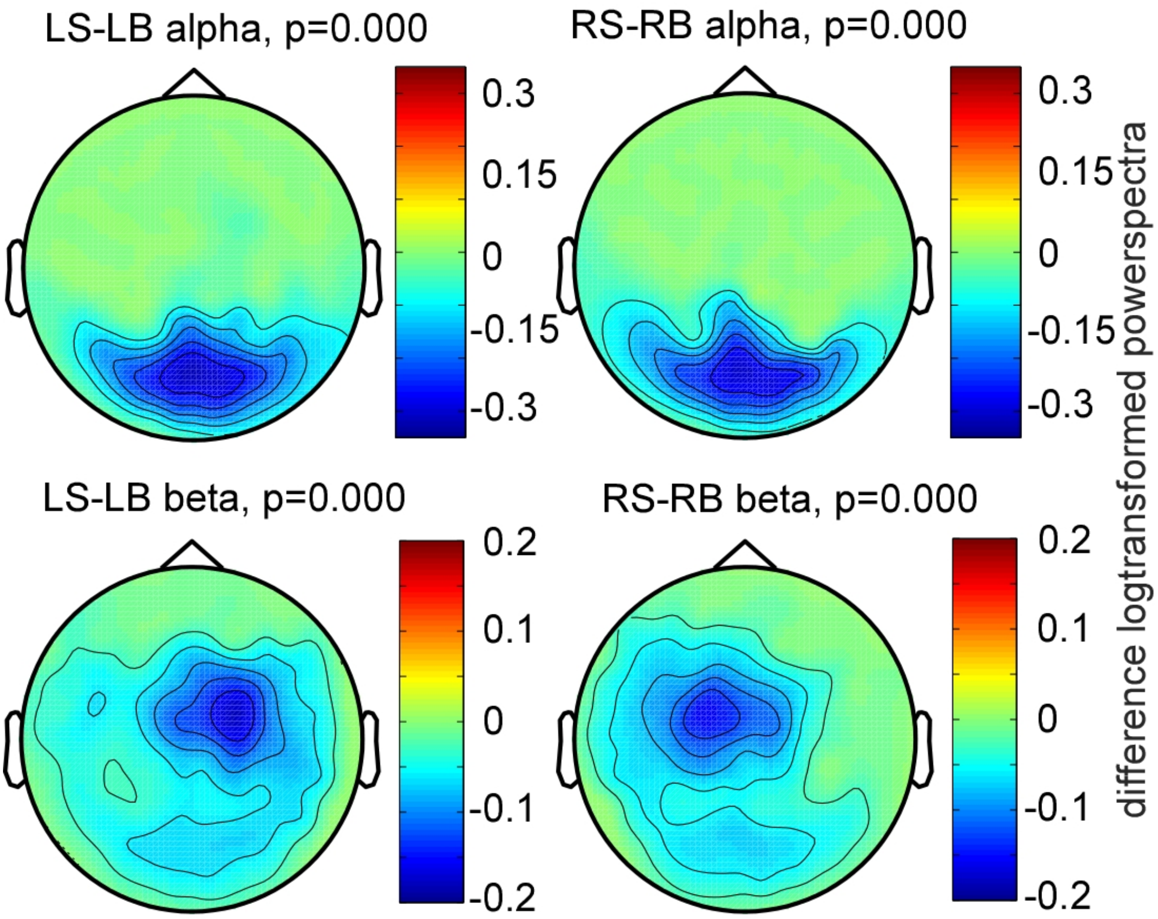

Figure 2: Cluster analysis Results. Alpha band is 8-12 Hz, Beta band is 15-30 Hz. Plotted and on the colorbar are the differences in the logtransformed powerspectra of the two conditions that were significant.

MEG power in stimulation and baseline period

The comparisons we make are between the estimates of the average spectra in both conditions of the baseline periods (LB and RB) and of the stimulation periods (LS and RS) that we calculated for every subject. We test significance at the group level of differences between the averages over subjects. We first discuss the results of the cluster analysis we applied to test significances. Second, we will show the results of the region of interest approach.

3.1 Cluster level randomisation test

Power is known to drop off roughly according to 1/f; the power of the spectrum *S*(f) obtained with MEG is inversely proportional to the frequency. 1/f power drop-off is a phenomenon observed in a wide variety of signals, for example the velocity of ocean waves and the loudness of natural sounds (Yu, Romero, & Lee, 2005). However, we are not interested in the absolute magnitude of signals at a certain frequency but rather in the relative differences between conditions. We therefore use the difference of the logtransformed powerspectra in condition A and B, which is equivalent to the ratio of the powerspectra, to inspect relative differences.

Cluster analysis: alpha and gamma power

Comparing the stimulation period to the baseline period within conditions we observe the following results. First the alpha band power (8-12 Hz) decreases dramatically (see top of figure 2) while the gamma band (40-80 Hz) power increases in the occipital sensors in the stimulation period (see figure 3). This effect appears both in condition left and right.

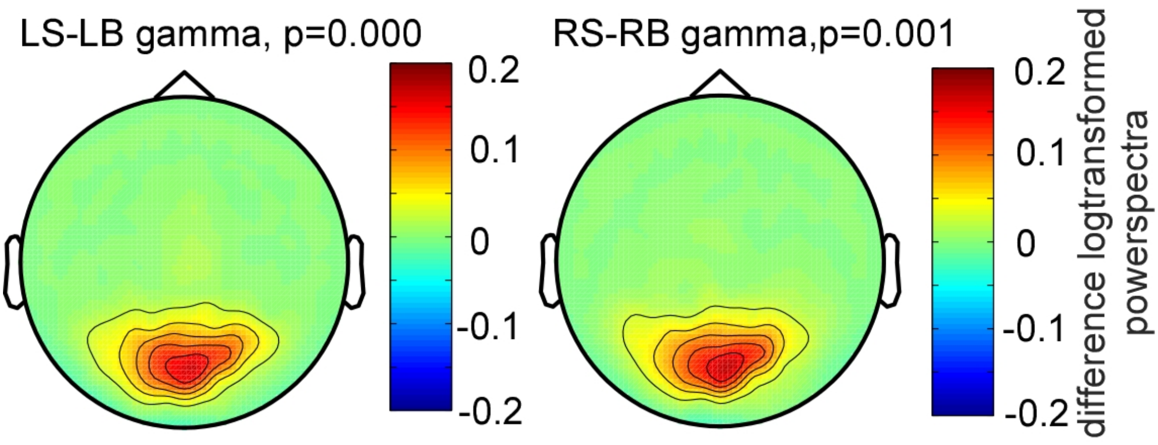

Figure 3: Cluster analysis Results. Plotted and on the colorbar are the differences in the logtransformed powerspectra of the two conditions that were significant. The comparison between the logtransformed powerspectra in the stimulation and baseline period reveals an increase on gamma power (40-80 Hz) in both conditions left and right.

Cluster analysis: stimulation vs baseline: beta power

Second, the power in the beta band (15-30 Hz) decreases significantly in the stimulation period relative to the baseline period. This decrease is lateralized in that it is bigger over the motor cortex contralateral to the side that needs to respond compared to the motor cortex that needs to abstain from responding (see bottom of figure 2).

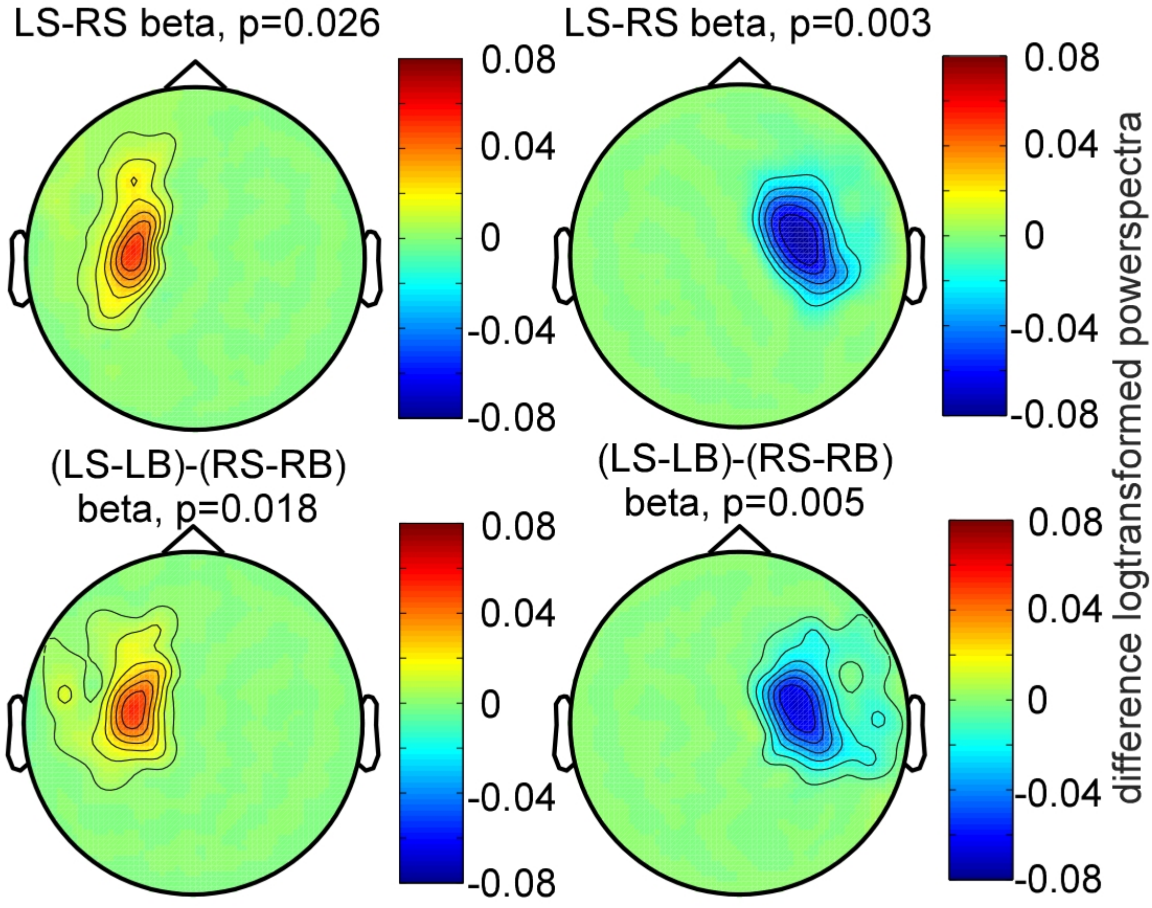

Figure 4: Cluster analysis results. Plotted and on the colorbar are the differences in the logtransformed powerspectra of the two conditions that were significant. In the upper panel the comparison is between the logtransformed powerspectra in condition left and right in the stimulation period yielding a significant positive and a significant negative cluster in the beta band (15-30 Hz). In the lower panel the comparison is between condition left and right after correction by the baseline period.

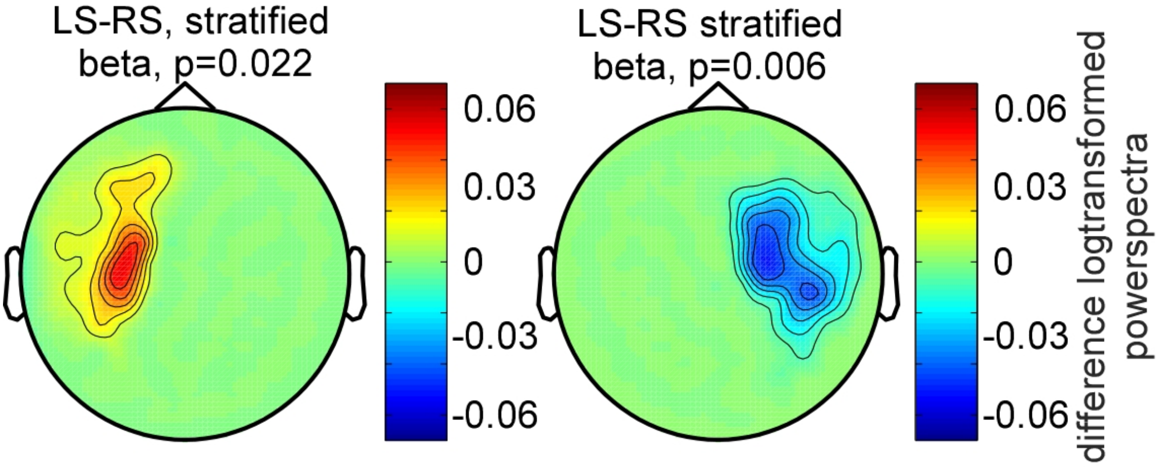

Figure 5: Cluster analysis Results. The same comparison and general format as in figure 4 after stratification.

Cluster analysis: condition left vs condition right: beta power

The results of the comparison between condition left and right (L-R), where the only difference is that the subject is set to respond with the left respectively right hand, are shown in figure 4. The power in the beta band (15-30 Hz) in condition left is bigger over left motor cortex and lower over right motor cortex compared to condition right (top of figure 4). In other words, beta activity over left motor cortex is lower in condition right and beta activity over right motor cortex is lower in condition left. In the baseline period no significant differences are revealed by cluster analysis. We have also made the comparison between the baseline controlled stimulation periods in both conditions. To this end we first took the difference between the stimulation period and the baseline period within a condition and subsequently compared these between the conditions. Again we see the left lateralized increase and a right lateralized decrease. That is, power in the beta band decreases more when the hemisphere is contralateral to the side that needs to respond than when it is contralateral to the side that is not cued (bottom of figure 2 and bottom of figure 4). Besides the significant differences over motor cortex no differences were found. This is clear support for the notion that only activity over motor cortices was lateralized.

Stratification procedure

In order to exclude the alternative explanation that observed differences were due to lowerlevel differences between condition left and right we performed a stratification procedure on the EMG. The stratification was dependent on the amount of spectral smoothing since we first had to select the trials that were long enough for a given smoothing. The stratification was then performed on this pre-selection. The stratification procedure resulted in a trial selection in which the distributions of the mean amplitude of the left and right EMG were not different across the two conditions (for all subjects $p > 0.25$, randomisation test). As shown in figure 5 the difference between condition left and right in the stimulation period is still present after stratification (for the result without stratification see top figure 4). This supports the idea that this effect does not result from differences between conditions at the level of the EMG.

3.2 Group level statistics in selected sensor set

Defining a region of interest using prior information

The result of the channel selection based on the unilateral contraction task is shown in figure 6. This procedure gives us an independent and sensitive indication of the location of the motor cortices.

The topography of the two selected groups is highly similar to the two clusters in which the maximal decrease in the beta band power was observed. The average z-transformed coherence in the unilateral task is shown in figure 7. During an extension of the left wrist coherence exists almost exclusively between the left sensor group and the right EMG and during an extension of the right wrist coherence is mainly observable between the right sensor group and the left EMG.

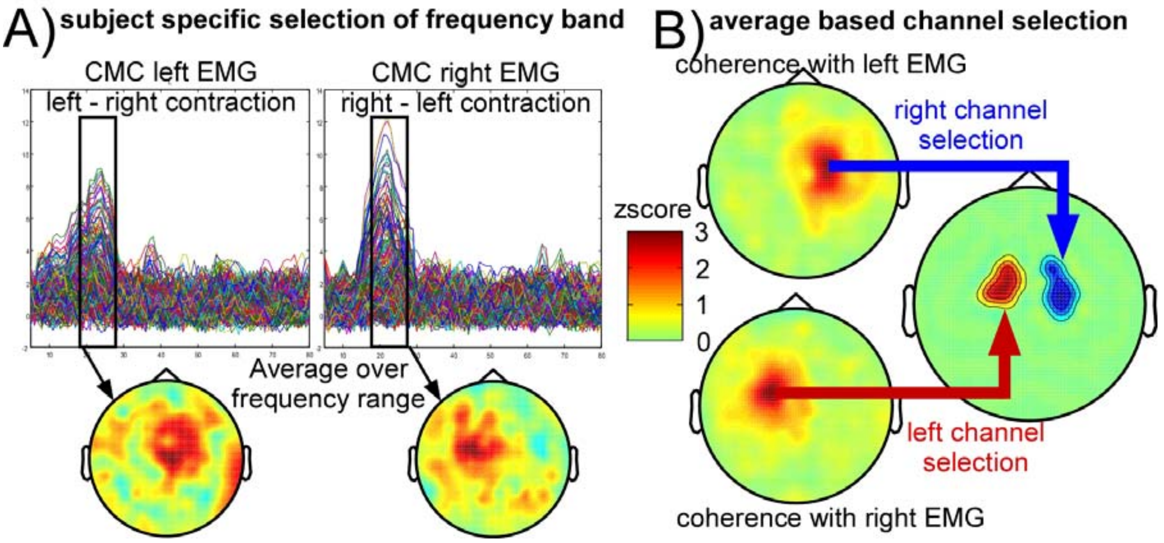

Figure 6: Coherence in a unilateral contraction. In A the CMC of all MEG channels with the EMG is shown. We first select a subject specific frequency band over which we average the CMC with the left and right EMG. The z-score is then taken, indicating which channels show the largests deviations in a subject, and subsequently averaged over subjects. Finally, the 5 channels with the maximum CMC with the left (channel sel right, since left EMG is maximally coherent with contralateral MEG sensor group) and right EMG (channel selection left) are selected (B).

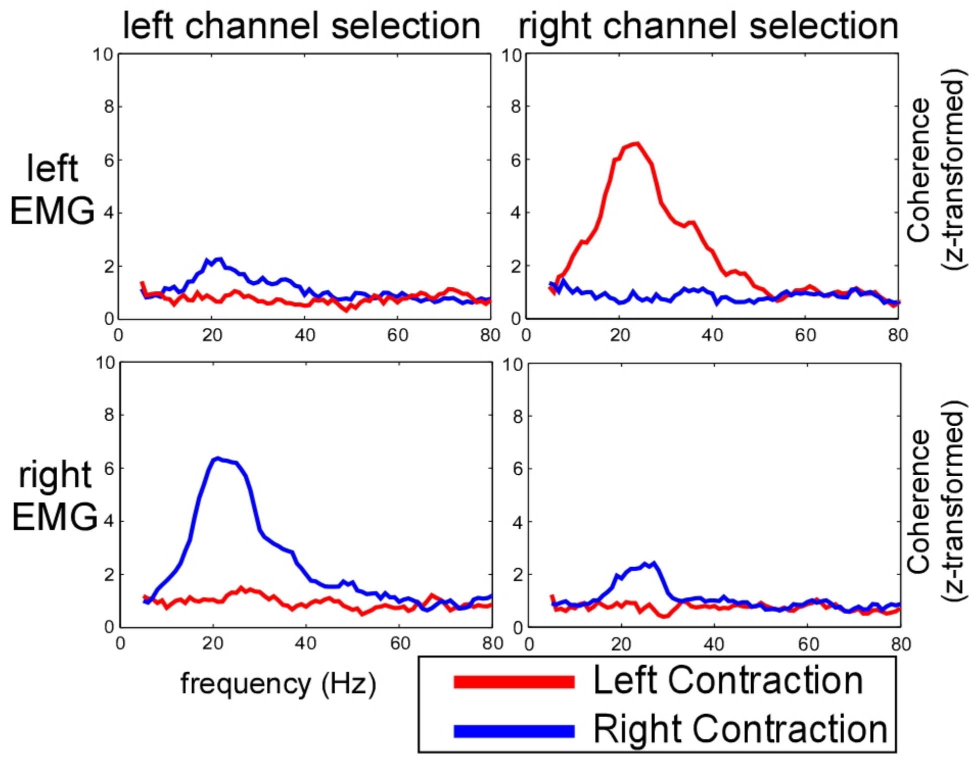

Figure 7: Coherence in channel selection during unilateral contraction task.

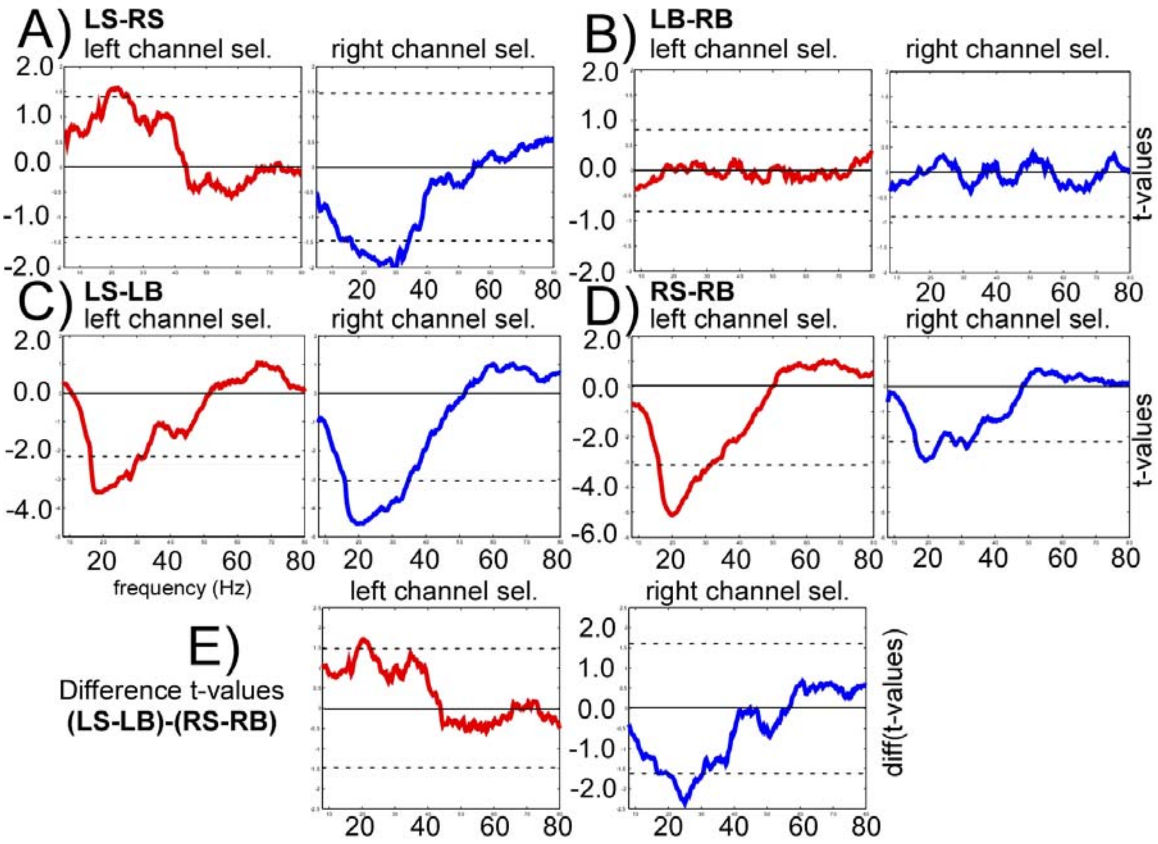

Figure 8: T-values of differences between power in experimental conditions. Dotted lines are the critical values with α = 0.05, corrected for multiple comparisons.

Analysis in ROI

In the channel selection, that had been determined with the procedure described above, we were able to confirm the results of the cluster analysis. Depicted in figure 8 are the average t-values of the differences for all considered comparisons and the corresponding critical values of the reference distribution with α = 0.05, corrected for multiple comparisons (see methods section). The left channel selection shows both in condition left and right a significant decrease relative to baseline (left plots 8C and 8D) but this decrease is bigger in condition right (left plot 8E). The right channel selection shows both in condition left and right a significant decrease relative to baseline (right plots 8C and 8D) but this decrease is bigger in condition left (right plot 8E). The direct comparison of the stimulation periods (8A) shows that the beta power is bigger in the left and lower in the right channel selection in condition left relative to condition right. Interesting is furthermore that the plots suggest that the effect at the higher frequencies (50-80 Hz) is inverted to the beta power effect in that it is bigger in the hemisphere that has to become active, although this is not significant. The direct comparison of the baseline periods (8B) in the two conditions shows no difference.

Cortico-muscular coherence

Cortico-muscular coherence was calculated between all pairs of the EMG channels and the MEG channels. Although the focus in this article is on the effects in power, we make some observations about the cortico-muscular coherence at a descriptive level. In figure 9 we compared condition left to condition right, both in the stimulation and the baseline period. Shown is the average z-transformed CMC in the left channel selection with the left EMG and with the right EMG, in the stimulation period and in the baseline period. The same is shown for the right channel selection. It appears that the average z-transformed coherence is not different across condition left and right. Again, only the coherence spectra between the EMG and the MEG group contralateral to it show convincing peaks. In figure 10 we compared the stimulation period and the baseline period, both in condition left and condition right. Shown is the average z-transformed CMC in the left channel selection with the left EMG and with the right EMG, in condition left and in condition right. The same is shown for the right channel selection. Here it appears that the average z-transformed coherence in the beta band is generally lower in the stimulation than in the baseline period and this only holds for the coherence between the EMG and the contralateral

4 Discussion

Stimulation versus baseline period

In advance we hypothesized that motor set would modulate oscillatory neuronal synchrony in motor cortices. One of our expectations was that this effect should be maximal when the subject's set to respond was maximal. During the experimental task, the subject needed to monitor the visual stimulus for the imperative go-cue that occured at an unpredictable moment in time. However, the subjects did know that the go-cue had zero probability of appearing in the baseline period and nonzero probability of appearing during the stimulation period. Motor set will be bigger when the subject's expectancy to respond is bigger and therefore reflects knowledge about the likelihood of the occurrence of the go-cue. This can be the result of behavioural experience that allows a probalistic estimate of the time of the go-cue. Schoffelen (2005) showed that subjects can implicitly learn the so-called hazard rate, the probability that the go-cue occurs given that it hasn't yet occurred; the reaction time was inversely correlated with the hazard rate. Interestingly, power over motor cortex in the gamma band correlated positively while power in the beta band correlated negatively with the hazard rate. Riehle (1997) also found that go-cue expectancy affects spike synchronization in primary motor cortex in the absence of firing rate modulations. The comparison between the baseline and the

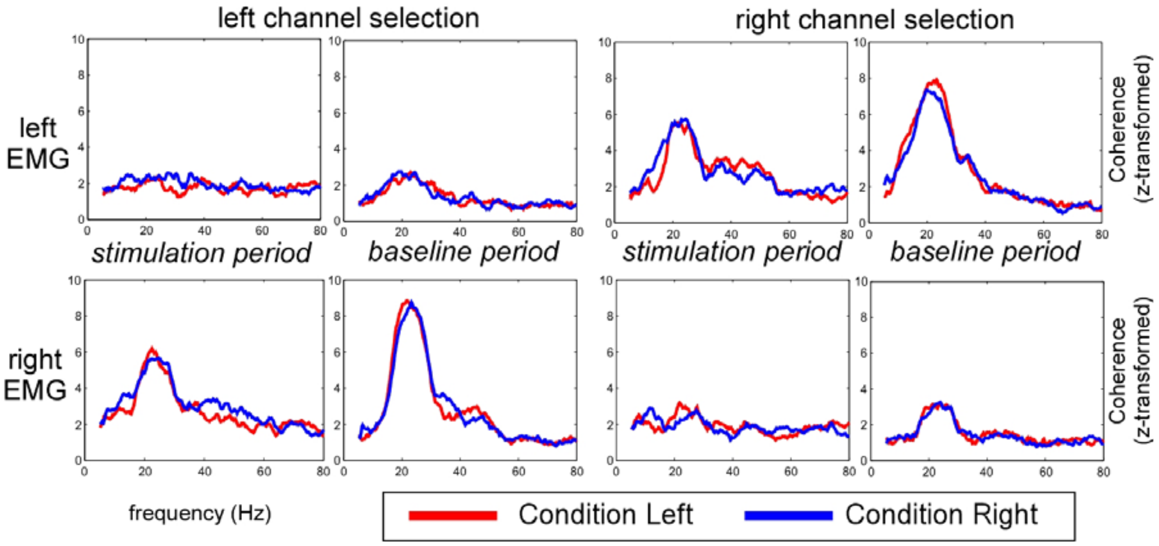

Figure 9: Coherence in channel selection during bilateral contraction task. Comparison between coherence in condition left and in condition right.

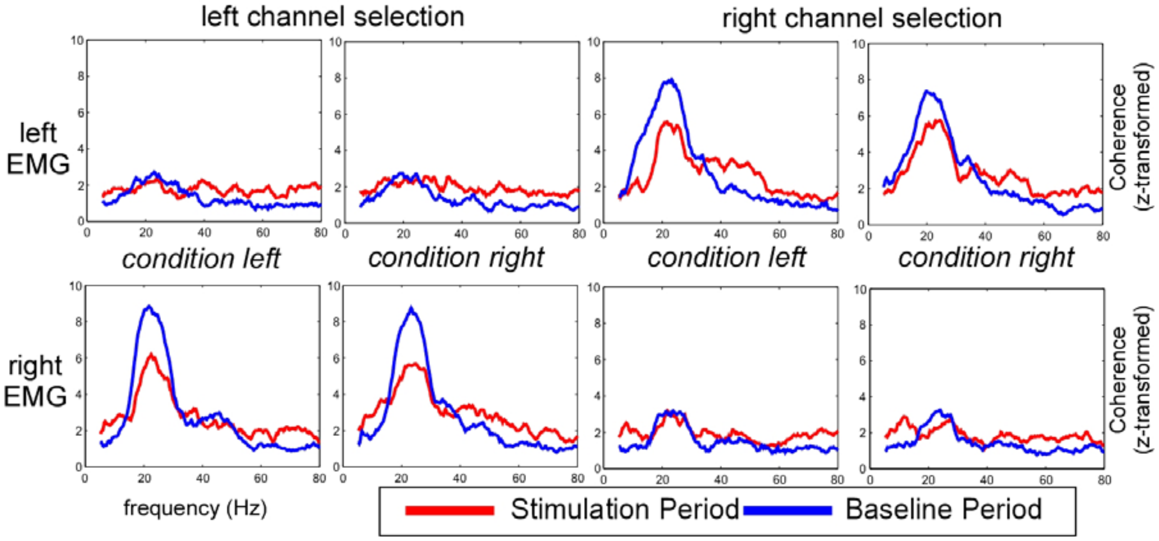

Figure 10: Coherence in channel selection during bilateral contraction task. Comparison between coherence in stimulation period and in baseline period.

stimulation period in condition left revealed a decrease in beta power both in the sensors overlying left and right motor cortex although the decrease was bigger in the sensors over right motor cortex. In condition right the decrease on both sides in beta power was also evident and bigger in the left sensor group. The comparison between the cortico-muscular coherence in the baseline and the stimulation period suggested that beta band coherence is generally more pronounced in the baseline period than in the stimulation period both in condition left and right. This had been previously shown by Schoffelen (2005) in a unilateral contraction.

Condition left versus condition right

We also predicted that activity in the motor cortex contralateral to the response side should show a qualitatively different pattern of activation compared to the motor cortex contralateral to the side where abstinence of response was required. At the start of every trial the subject was cued whether to respond with left or right wrist to the appearance of the go-cue. Thus, the subject is set to respond at one side to the go-cue: the contralateral motor cortex needs to drive the response while the ipsilateral motor cortex should not drive a response in the side that is not cued. The well known pre-cue utilization effect (see for example Gottsdanker & Shragg, 1985) describes the finding that reaction times become shorter when the subject is told in advance what the required response is to the imperative stimulus. This effect has been interpreted as the deletion of the response-selection stage; the subject already knows he has to respond in the case of a go-cue with the motor effector indicated by the cue. Described in the section above is the finding that the decrease in beta power in the stimulation period compared to the baseline period in condition left was bigger over right motor cortex while in condition right it was bigger over left motor cortex. The direct comparison between condition left and right reveals that in the stimulation period of condition left the beta band power is higher in the sensors overlying left motor cortex and lower in the sensors overlying right motor cortex compared to condition right. This effect of the cue that allows for response selection is present in the stimulation but not in the baseline period: so the difference in motor cortex when it is ipsilateral and when it is contralateral to the response side is only apparent in the stimulation period in which the go-cue can appear and the subject should be more set to respond than in the baseline period. The comparison between the cortico-muscular coherence in condition left and right showed no obvious difference across conditions. Baker (2003) also found a relative constancy of corticomuscular coherence despite perturbations of the power of the EEG by pharmacological agents and interpreted this as suggestive for a functional role of cortico-muscular coherence in itself.

Motor set or preparation

It is possible to distinguish between motor set and motor response preparation. Motor response preparation denotes the processes that precede a motor response. It is here defined as preparation while you know you can respond. Certain preparatory components have been identified that are time-locked to and precede the movement onset. For instance the readiness potential or Bereitschaftspotential is a slow negative potential preceding self-paced movements (Doyle, Yarrow, & Brown, 2005). The subject can start motor response preparation after he has perceived the imperative go-cue; we only consider the periods that precede the go-cue and don't look at these time- and phase-locked components. Motor set is located earlier in the causal chain that can eventually end with a movement. It is preparation while you know you may have to respond. In our task the subject is cued to respond either on the left or right side if and only if the go-cue appears. Thus, the subject can expect that he has to make a certain response but cannot set into motion the cascade of events that unavoidably lead to a movement before the go-cue appears. First, in some percentage of the trials the go-cue does not appear in which case the subject needs to abstain from responding (no-go trial) and second, the go-cue appears at a certain time with a certain probability: although over multiple trials it may be more likely that it will appear at a certain time, in a given trial it can appear over a wide range in time with some small probability.

Motor set modulates beta band power over motor cortex

Our main conclusion is that motor set modulates oscillatory synchrony in the beta band in the motor cortices. Beta power was lower over motor cortex if it had to become active in case of the appearance of the go cue and less so if it had to keep a steady contraction. Crucially, these differences were observed during steady contraction and equivalent motor output and sensory input. Clearly, this modulation of activity by motor set pleads against the simple view of the motor cortex as an independent output module for motor commands. Although electrical stimulation of motor cortex can evoke predictable behavioural responses and motor cortex is the cortical source that drives the muscles, this does not mean that processing in motor cortex is not influenced by factors not directly related to force output, like motor set. In this study the subject knew he had to make a response on one side but not on the other: response times are known to decrease as a result of this prior knowledge that allows for response selection. We find that reduction in beta power over motor cortex is a correlate of this response selection. Beta power decreases more over the motor cortex contralateral to the response side, thereby reflecting an expected functional involvement. The subject's set to respond only selectively modulates oscillatory neuronal synchrony in the period in which the go-cue can occur. This makes sense if beta power indeed corresponds to a mode in which the steady state is maintained; only in the period in which a response can be required this modus should be turned off to allow for dynamic changes in motor output.

The functional role of beta band synchrony

Oscillations in the beta band are an ubiquitous feature of human and nonhuman primate motor cortical areas and findings accumulate on the functional role of these oscillations. Beta band synchrony decreases before voluntary movement (Pfurtscheller, 1981), shows a rebound after movement (Pfurtscheller et al., 1996) and is strongly present during a steady contraction (Farmer, 1998). Although the role of beta synchrony has been compared to that of the alpha rhythm in visual cortex, that is thought to reflect cortical idling; this is probably too simple. Maintenance of balance is a highly active and demanding process that is normally accomplished without conscious thought. Recently, Gilbertson (2005) found that intrinsic fluctuations in the degree of beta band synchronization within the motor system were associated with a measurable impairment in movement performance in subjects. Their interpretation is that beta synchronization reflects a state in which the existing motor state is favoured at the cost of processing related to new movements. Beta band synchrony is also pathologically increased in Parkinson's disease (Schnitzler & Gross, 2005) and Parkinson patients have in particular difficulties with initiating movements. The benzodiazepine diazepam increases the size of $GABA_A$ IPSPs while the antagonist flumazenil has the reverse effect: Baker (2003) showed that EEG power in the beta band was greatly enhanced after diazepam injection and returned to normal levels following flumazenil. In this experiment beta band activity was selectively reduced over the cortical area that was expected to be involved in responding to the go-cue. Beta band synchrony may act as a safety lock to maintain posture and balance. Reduction of this component may be an essential prerequisite for allowing efficient neural processing related to dynamic changes in motor output to take place. An area in a cortical state dominated by beta band synchrony is possibly less sensitive to small fluctuations of input and the current status can then be maintained with a minimum of computational effort. Motor set can selectively modulate the cortical state of a certain area to make it more responsive to changes in input. Doyle (2005) showed that lateralized EEG changes occur in the beta band only when informative warning cues allow early motor selection, as suggested by the shortened reaction times in that case. Thus, selective modulation can occur only as far as allowed by prior information. To conclude this section, evidence suggests that a reciprocal relationship exists between cortical beta activity and dynamic motor processing.

Reciprocal coupling of different bands

Instead of only looking at effects within a frequency band it is also possible to look at covariations among different frequencies (Friston, 1997). The general idea is that activity in lower frequency bands is reciprocally coupled to activity in higher frequency bands. Spatially restricted fast oscillations are thought to play an essential role in the formation of neuronal cell assemblies (Llinás et al., 2005). Therefore the disappearance of slow and extended oscillations in favour of oscillations that are faster and more localized is a signature of increased involvement in information processing. An example of this is found in visual cortex. In this experiment we confirmed the following result of the study by Hoogenboom (2006) who used a paradigm highly similar to ours: in the stimulation period gamma power was enhanced while alpha and beta power were reduced compared to baseline in occipital sensors with high signal-to-noise ratio. They found that this effect was found reliably across subjects and across multiple recording sessions of a given subject. Furthermore, the gamma power enhancement seemed to be more localized than the alpha power reduction. Thus, gamma power was increased in the period in which the visual stimulus was on and the subject expected the go-cue while power at lower frequencies was reduced. Tentatively, this reflects increased functional involvement and reduced cortical idling. The reciprocal relation we observe between the power in the gamma and the alpha band in visual cortex is also thought to exist for the gamma and beta band in motor cortex. For example, the correlation with the readiness to respond is positive in the gamma band and negative in the beta band power over motor cortex (Schoffelen et al., 2005). Here we have shown directly that beta power over motor cortex goes down with motor set. We also show that the effect is lateralized giving bigger decreases over motor cortex contralateral to the side that needs to respond. The direct comparison between the stimulation period in condition left and condition right reveals a smaller power in the beta band over motor cortex when it needs to respond compared to when it needs to abstain from responding. Concluding, the power in the beta band seems to correspond to a mode of control suited to exerting constant force output. Importantly however, the amount of beta power can be modulated by cognitive factors such as motor set. This modulation is detectable during constant motor output. Gamma oscillations seem to come into play during dynamic changes or contraction with higher force (Brown, 2000). For instance, signal power in the gamma band in sensorimotor cortex is enhanced during performance of visuomotor tasks (Aoki, Fetz, Shupe, Lettich, & Ojemann, 1999). A consistent gamma band enhancement was not detected at the group level. The 1/f frequency drop-off inherent in biological signals, combined with measurement noise that is constant over frequencies, will lead to a worse signal to noise ratio for higher frequencies. The gamma band also compromises a bigger range on the frequency axis compared to lower frequencies. Both factors are unfavourable to group statistics that basically test the consistency of an effect. The fact that we did not find the effect in the gamma band could be the result of signal-tonoise or statistical issues we discussed or because it was not present. Reduction of synchrony in lower frequency bands and enhancement in higher bands could be modulated separately. In the stimulation period the subject needed to be ready but steady; one could already remove the safety lever (beta band reduction) of a gun when the command to fire is expected but not yet put his finger on the trigger (gamma band enhancement) to prevent premature acting.

Two different approaches provide cross-validation

Cluster analysis is an approach that makes no use of prior information about the location of the effect. Instead it gets its sensitivity from incorporating an assumption in the test statistic that is biophysically plausible, namely that effects at the sensor level are clustered in space and time. Cluster analysis can then reveal the most prominent effects in the entire sensor space. We note that a log transformation of the power spectra seems advisable in order to avoid that the high power of the MEG signal at lower frequencies dominates the signal. Cortico-muscular coherence is modulated by task parameters (Kilner, Baker, Salenius, & Hari, 2000), but its functional role is still debated. We have shown how unilateral coherence in an independent data set can be used to select a group of channels that presumably represents motor cortex. This selection can subsequently be used as a starting point for the analysis of cortico-muscular and cortico-cortical coherence. This informed selection of a region of interest in advance reduces the multiple comparisons problem, simplifies data exploration and increases the power of the statistical test. The fact that the two different approaches reveal the same effects is supportive both for the effect as for the methods, providing cross-validation.

Stratification

In this experiment force output was required to stay within a narrow range so that subjects had to keep steady and controlled contractions. However, a difference in the point of applied force on the levers or a different pattern of co-activation of agonist and antagonist muscles could lead to the same force output with differences in EMG activity. These differences could in principle be systematically related to conditions. Stratification of the EMG resulted in a trial selection in which the distribution of the mean amplitude of the EMG left and the mean amplitude of the EMG right were not significantly different. Although this procedure reduced the number of trials in the analysis the difference between condition left and right remained present: with equivalent force output and equivalent EMG activity on both sides, beta power was lower over motor cortex when it was contralateral to the expected response side compared to when it was contralateral to the side that was not cued to respond.

Final conclusion

Oscillatory neuronal synchrony is likely to have a functional role in neural information processing. In the motor system a special role seems to be reserved for oscillations in the beta band in maintaining constant motor behaviour. A reduction in the dominance of beta power synchrony in motor cortex is then perhaps an essential prerequisite for allowing dynamic changes in motor output. Motor set can enhance the efficacy of motor behaviour by selective modulation of oscillatory synchrony in the beta band. We believe that future research on oscillatory network dynamics can bring us further towards a mechanistic understanding of cortical information processing

Acknowledgements

I wish to express gratitude to JM. Schoffelen and P. Fries for their contributions and supervision in this research project and to R. Oostenveld and E. Maris for helpful discussions and suggestions. I also thank B. Hommel and three anonymous reviewers for their comments.

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Distinguishing between prelexical levels in speech perception: an adaptation-fMRI study

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Behavioural studies of speech perception indicate a dissociation of acoustic-phonetic and a more abstract level of prelexical processing. Here we used functional magnetic resonance imaging, in combination with an adaptation paradigm to distinguish between the neural correlates of acoustic-phonetic and phonological processing of the fricative speech sounds [S] and [s] by Dutch listeners. To manipulate the perceived quality of the fricatives while keeping their acoustic properties constant, we varied the sounds' vowel-context: Dutch listeners are more likely to classify an ambiguous fricative from an [S] – [s] continuum as [S] when it is followed by [i], and as [s] when it is followed by [y] (Smits, 2001a). Syllable pairs were presented consisting of an [S], an [s], or an ambiguous fricative, followed by an [y] or an [i] vowel. The most ambiguous fricative was identified individually for each subject in a pretest. During the fMRI scanning session syllable pairs were presented rapidly and randomly intermixed. A sparse scanning paradigm was used, in which auditory stimuli were presented during silent gaps between image acquisitions. We hypothesized that syllable pairs in which the fricatives were perceived as the same would lead to larger adaptation in brain regions responsible for phonological processing as compared to syllable pairs in which the fricatives were perceived as different. Distinct fMRI adaptation patterns were observed corresponding to acoustic-phonetic and phonological processing respectively, supporting the functional distinction between these processing levels. No cortical regions showed both patterns: the cortical regions underlying the acoustic-phonetic and phonological stages in prelexical processing appear to be anatomically distinct.

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Introduction

Prelexical processing levels in speech perception

During speech perception, continuous and infinitely variable sound waves must be mapped onto stored lexical representations in the listener's brain. These lexical items are discrete. The task the listener has is to match every particular token to a word type. Analogue representations therefore have to turn into discrete representations, and how exactly this happens is one of the greatest mysteries of speech perception. One solution is that there are prelexical levels, where representations of speech sounds mediate between the speech signal and the lexicon. As McQueen (2005) has argued, prelexical levels could be an efficient way to partially solve the mapping problem.

A possibly important step on the prelexical stage could be the phenomenon referred to as categorical perception. The definition of categorical perception is based on identification and discrimination experiments with a continuum of speech sounds varied in an acoustic parameter and ranging across two (or more) unambiguous consonants. The defining properties are (1) an abrupt increase of steepness in the identification function for a speech sound at the phoneme boundary, and (2) an abrupt increase of the discrimination accuracy function for across-category stimulus pairs from the continuum as contrasted to the poor discrimination accuracy of within-category pairs.

The phenomenon of categorical perception was first described by Liberman (1957), and was claimed to be a speech-specific phenomenon from the beginning. Later, general auditory mechanisms were shown to contribute significantly to the categorical perception of speech sounds, questioning that it is specific to speech and even that it is specific to humans. But it was repeatedly shown that language experience does play an important role in categorical perception. Today it is hardly debated that at least a certain kind of categorical perception is speech- and language-specific: although languages, on the one hand, exploit natural boundaries, but, on the other hand, they are also able to modify them (for an overview, see Diehl et al., 2004).

But the explanatory power of categorical perception is often exaggerated. Models with a prelexical level that makes discrete categorical phoneme decisions are clearly simplistic (McQueen, 2005). Indeed, categorical perception seems to reveal categories that are organised around prototypes and have an internal structure (Phillips et al., 2000). But these categories cannot be discrete phonological categories, because the defining property of discrete categories is that all within-category contrasts are lost. Therefore, categorical perception in itself is not a sufficient mechanism to phonologically categorize speech sounds, and this does not appear to be the right phenomenon to demonstrate the presence of phoneme categories either. To make things even worse, in a general critic of categorical perception research Schouten et al. (2003) have pointed out that the discrimination task might be measuring a task-inherent bias, in fact, an artefact only. All in all, categorical perception does not solve the invariance problem.

We will argue for a more plausible view of prelexical processing which consists of minimally two processing stages. There were several attempts to make similar distinctions. Phillips (2001) has distinguished three levels of prelexical processing: acoustic, phonetic and phonological processing levels. According to his view, acoustic processing is a not speech-specific, not language-dependent auditory processing, which is sensitive to fine-grained differences of speech sounds, independently of their phoneme category membership; phonetic processing is a speech-specific, language-dependent processing, where the processing function of the input sounds is nonlinear, but within-category differences are still relevant; and finally, phonological processing is a speech-specific, language-dependent processing, where the processing function of the input sounds is discrete categorical, and within-category differences are irrelevant. We believe that this analysis rightfully shows that acoustic-phonetic processing involves various, both speech-specific and not speech-specific sub-processes; and it also rightfully points out that phonological processing is necessarily more than just speech-specific processing, but it fails to present distinctive behavioural evidence for each stage and it also fails to note that there is no clear proof for the presence of discrete phonological categories at the prelexical processing stage, even though Scott and Wise (2004) have warned that a phonemic level of representation is not logically necessary. Similarly, Indefrey and Cutler (2005) have noted that there is evidence compatible with models involving alternative intervening representations or no intervening representations.

Here we test a simpler framework for prelexical processing. On logical grounds, assuming that there are prelexical phonological representations to help solve the invariance problem, it is motivated clearly that there should also be at least one earlier stage of acoustic-phonetic processing. The role of this early processing stage would be to generate more abstract phonological output from the speech signal for the later stage (McQueen, 2005). Behavioural evidence suggests there are early processes, which are sensitive to fine physical differences in the speech signal; and speech-specific processes, which depend on the categorical identity of speech sounds (e.g., Samuel and Kat, 1996). Smits (2001b) has proposed that the decoding of continuous, coarticulated speech is based on hierarchical categorization dependencies, suggesting there are at least two distinct, cascadic processing stages and no discrete phonemic representations on the prelexical level. We hypothesize that there are (minimally) two processing stages at the prelexical level, one acoustic-phonetic and one more phonologically abstract, with these two stages acting in cascade and passing information on continuously to the lexicon. In the present study we will examine whether there are neural correlates of this two-way distinction (acoustic-phonetic processing versus phonological processing).

Neuroanatomical correlates of prelexical processing levels

This section reviews recent neuroimaging literature in light of the proposed two-way distinction to see what previous studies have said about neural correlates of separate prelexical processing levels. Most models of speech processing assume that processing is hierarchically organised and that this hierarchy might be mapped onto auditory anatomy. Primate and human studies indicate the interconnectedness of adjacent regions in the auditory cortex, with an information flow from core, to belt, to parabelt, and to more distal regions, such as more distant parts of the superior and middle temporal gyri and the left inferior frontal gyrus (Davis and Johnsrude, 2003; Scott and Johnsrude, 2003). Scott and Wise (2004) proposed that there are two distinct processing pathways involved in speech perception, both having a network of connections spreading from primary auditory areas: an anterior stream of processing, running lateral and anterior to primary auditory cortex is implicated in the mapping of sound onto meaning, while a divided posterior stream including the temporo-parietal junction and the posterior superior temporal sulcus is involved in a mapping of speech sounds onto motor representations of articulation.

A large number of studies have reported the involvement of superior temporal regions in speech-specific processing in adults (Zatorre et al., 1992; Binder et al., 2000, Scott and Wise, 2003), in young children (Ahmad et al., 2003) and even in infants (Dehaene-Lambertz et al., 2002). The most commonly found area is the left posterior superior temporal gyrus (Benson et al., 2001; Ruff et al., 2003; Zevin and McCandliss, 2005; Dehaene-Lambertz et al., 2005). There is evidence for its involvement in speech sound discrimination (Jacquemot et al., 2003; Callan et al., 2004) and in using phonetic experience (Liebenthal et al., 2003). The superior temporal gyrus was also claimed to have more general and more specific roles, like processing spectrally complex sounds (Belin et al., 1999; Joanisse et al, 2003), processing transient acoustic features of speech (Poldrack et al., 2001) or detecting rhymes (Seghier et al., 2004; Burton et al., 2005). Bilateral activation of the superior temporal gyri in speech processing tasks was shown too (Demonet et al., 1992; Hugdahl et al., 2003). The superior temporal sulcus also seems to have a role in speech-specific processing (Jäncke et al., 2002; Dehaene-Lambertz et al., 2005), and its posterior part is even claimed to be involved in the manipulation of phonological representations (Seki et al., 2004). Although these studies have provided clear evidence for the involvement of the superior temporal regions in prelexical stages of speech processing, their exact function is still largely unknown.

There is also considerable evidence for the involvement of inferior frontal regions, with left dominance, in phonetic or phonological processing (Zatorre et al., 1992; Demonet et al., 1992; Hsieh et al., 2001; Gandour et al., 2002; Sharp et al., 2001; Golestani and Zatorre, 2004; Seghier et al., 2004; Burton et al., 2005; Deheane-Lambertz et al., 2005), but how and how much is this involvement related to speech-specific processes and how much is it a consequence of more general processes, is debated. It is often claimed that the inferior frontal gyrus has a more general role and its activation reveals a general mechanism for selecting among competing phonetic categories (Thompson-Schill et al., 1997; Zhang et al., 2004) or a phonologically based working memory mechanism (Nixon et al., 2004). Poldrack et al. (2001) have found that a subset of phonological processing left inferior frontal regions is also sensitive to acoustic-phonetic features. Jacquemot et al. (2003) suggested that activations in the inferior frontal regions are related to explicit extraction of abstract linguistic features, or to the segmentation of the auditory stimuli.

These results show that functional imaging studies aiming to distinguish prelexical levels successfully showed that processing speech and non-speech has separate neural correlates (Zatorre et al., 1992; Demonet et al., 1992; Binder et al., 2000; Benson et al., 2001; Jäncke et al., 2002; Scott and Johnsrude, 2003; Zevin and McCandliss, 2005). But regions that are found to be speech-specific are often presented as findings of phonological processing areas (Poldrack et al., 2001; Burton et al., 2005; Dehaene-Lambertz et al., 2005), without making a further distinction between speech-specific processing levels, or without suggesting the possible relevance of such a separation. Other studies even consider any acoustic-change related activations as correlates of phonological representations, in case the stimuli are speech stimuli (e.g., Seki et al., 2004). Although it is mainly an issue of clarity in defining processing levels, the inconsequent use of terms often results in claims about phonological representations and phoneme categories in these studies whose design did not allow for an acoustic-phonetic versus phonological distinction. Phonological processing refers to something qualitatively more than just speech-specific processing. But the precise role of cortical areas that are claimed to be speech-specific, and whether it is possible to assign certain areas to certain prelexical, speech-specific levels, remains unclear in all these studies.

Only few neuroscientific studies, and especially few functional magnetic resonance imaging studies aimed for the distinction of phonological processing and earlier prelexical, acoustic-phonetic processing levels. Phillips et al. (2000) conducted an MEG mismatch study in which they tried to cancel out acoustic effects by grouping several acoustically different stimuli from the same phoneme category in one condition and claimed to have found that auditory cortex accesses phonological categories, although they did not claim that they had found neural correlates of phoneme categorization or phonological processing there. In a cross-linguistic design, Dehaene-Lambertz et al. (2000) exploited the mismatch negativity effect with EEG, and showed the effects of a phonological change in the brain. Using a very similar design to that of Dehaene-Lambertz et al., Jacquemot et al. (2003) carried out an fMRI experiment. In their study, French and Japanese volunteers were scanned while performing a discrimination task. Three pseudowords were presented in each trial; the first two were always identical, and the third one was either identical (acoustically the same) or different. The key of the manipulation was that while the change was phonological for one population, it was only acoustic for the other. This way, they could subtract the activations involved in the phonological versus the acoustic discriminations. Jacquemot et al. have found superior temporal activation as a cortical response for a phonological change, and therefore they have claimed that the language-specific phonological grammar can shape the auditory cortex. Their design, however, could not entirely exclude the effects of the fact that the phonological change was a not well-controlled or well-balanced acoustic change at the same time.

To conclude, most previous neuroimaging studies to date are inadequate in that they do not allow for conclusions about the neural correlates of an acoustic-phonetic versus phonological distinction to be made. In fact, there seems to be an agreement about the mysterious nature of phonemes in the brain. As Scott and Wise (2004) have noted: “there is a lack of evidence for post-acoustic, prelexical, perceptual processing of phonemes in the functional imaging literature” (p. 21). Similarly, in a recent meta-analysis of hemodynamic studies on prelexical and lexical levels in listening, Indefrey and Cutler (2005) have argued that “at present, neuroimaging data do not allow for a distinction between phonetic and phonological processing” (p. 14).

In the present study, we aim to show that a phonological level of processing can be anatomically distinguished from earlier processing levels. More specifically, we attempt to find a functional and anatomical distinction of acoustic-phonetic processes which are sensitive to fine physical differences in the speech signal; and phonological processes which depend on the categorical identity of speech sounds. Consequentially, we aim to localize acoustic-phonetic and phonological processes and describe the differential activation pattern of the responsible cortical areas.

Vowel-context effect as a tool

Speech sound perception studies are sensitive to stimulus properties, to the precise nature of contrasts. For example, the difficulty in testing acoustic versus phonetic-phonological processing was that stimuli had to be manipulated in a way that the only difference between conditions is their perception as speech or non-speech. Testing acoustic-phonetic versus phonological processing seems to be even more difficult: one has to manipulate within-category / across-category property of stimulus-pairs without manipulating any other properties of the stimuli. For that, a strict definition of the phonological contrast is needed. This contrast should be balanced in all other, irrelevant aspects (such as the physical distance of the stimuli). At the same time, all stimuli in a phonological contrast should be contrasted to an unambiguously identified speech sound. Thus, phonemic identity of the speech sound stimuli should be manipulated while their acoustic properties remain constant.

Our solution to the problem of finding a sensitive contrast to test phonological processing is based upon the fact that the phonemic categorization of a consonant can depend on the neighboring vowel. The phenomenon which is responsible for such vowel-context effects is referred to as compensation for coarticulation. Phonemes are coarticulated in continuous speech, and coarticulation results in context-sensitive acoustics of phonemes. Listeners compensate for the effects of coarticulation: perception of a speech sound depends both on its acoustic properties and its context, and the direction of this context-moderated perception is opposite to the effects of coarticulation (Diehl et al., 2004).

The underlying mechanisms of compensation for coarticulation, whether it is caused by general auditory processes or is phonologically mediated, were long debated. Mitterer (submitted) recently suggested that compensation mechanisms depend on the type of coarticulation. He showed evidence that certain context-effects are based in audition (see also Mitterer et al., 2003; Mitterer and Blomert, 2003), while other context-effects, mainly those in which acoustic cues are more dissimilar and thus little room is left for auditory interactions, act on the phonetic/phonemic level. One such phonetically or phonologically mediated compensation effect is the vowel-context effect with fricative-vowel syllables. In his sushi experiment, Whalen (1989) has shown with English listeners that phonemic categorization of an ambiguous fricative depends on the quality of the following vowel. Similarly, Smits (2001a) has found that Dutch listeners classify the same ambiguous fricative as [S] (as in “sjaal”) in [i]-contexts but as [s] (as in “saai”) in [y]-contexts. Smits has suggested that sounds in the syllable are categorized in a hierarchical manner, as a consequence of a statistical learning mechanism: the fricative identification is preceded by the vowel identification. Manipulating sine-wave speech and audio-visual speech stimuli Mitterer (submitted) has recently found supporting evidence for Smits’ conclusion that the fricative-vowel context effect depends on the phonemic identity of the vowel, and as such, it necessarily acts on a phonological processing level. We used the same fricative-vowel syllables as stimuli in our experiment.

The vowel-context effect causes a shift of the identification function, a shift of the fricative category boundary for fricative-vowel syllables. For our purposes, the value of this late context-dependency in perception is that we can manipulate phonemic categorization of a fricative without actually changing the sound. As a consequence, we can create a “within-category versus across-category” type contrast while (1) keeping the same stimulus distance within a comparison, between the conditions; and at the same time (2) comparing each and every stimulus to an unambiguous phoneme. This way, we can define a strictly phonological contrast. Vowel-context effect also makes it possible to create a well-balanced “within-category versus identical” type contrast, so acoustic-phonetic processing can also be tested.

Adaptation-fMRI in a sparse scanning paradigm

Neural dishabituation as a sign of change detection in a neuronal population on different speech processing levels was found with EEG (and with MEG) earlier in mismatch negativity studies (e.g., Näätänen et al., 1997). A great advantage of MMN is that it can be elicited in the absence of parallel behavioural responses. Functional magnetic resonance imaging research was long lacking a method that combines the advantages of the MMN paradigm (being a similarly sensitive measure of neuronal change detection) and those of fMRI (providing a high spatial resolution). Grill-Spector and Malach (2001) have recently suggested a novel experimental paradigm, called adaptation-fMRI to study the invariant properties of specific neuronal populations to changes in the environment. Its application proceeds in two stages. As they describe: “First, the neuronal population is adapted by repeated presentation of a single stimulus. Second, some property of the stimulus is varied and the recovery from adaptation is assessed. If the signal remains adapted, it will indicate that the neurons are invariant to that attribute. However, if the fMRI signal will recover from the adapted state it would imply that the neurons are sensitive to the property that was varied.” (p. 293). The adaptation-fMRI paradigm was first used in object recognition studies, but after combining it with the technique of sparse scanning (Hall et al., 1999) in order to avoid interference with the scanner noise, auditory adaptation-fMRI paradigms (or auditory habituation paradigms) are also being developed and are used efficiently (e.g., Zevin and McCandliss, 2005). The value of adaptation-fMRI for our purposes is that it may efficiently be used as a tool to test fast neuronal responses to fine acoustic-phonetic or phonological changes on anatomically precisely defined loci in the human brain.

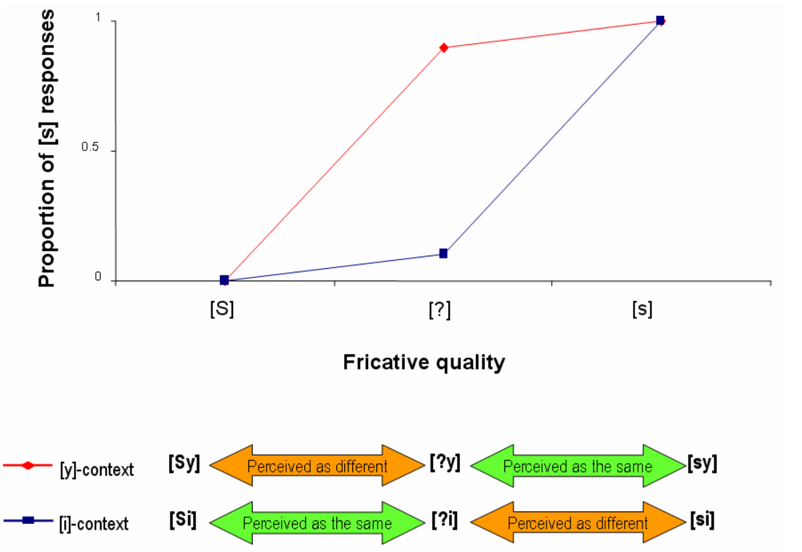


FIGURE 1 : Vowel-context effect, illustration. An ambiguous fricative [?] from the [S] – [s] continuum is usually classified as [S] when heard in context of an [i] vowel, but classified as [s] when heard in context of an [y] vowel. Arrows show which syllable pairs are usually perceived as the same and which ones are usually perceived as different.

Design of the present study

In this study, we have combined the advantages of a phonological vowel-context effect and those of the auditory adaptation-fMRI paradigm. The units of our stimuli were fricative-vowel syllables. We used three fricatives: [S], [s] and an ambiguous fricative [?] from the [S] – [s] continuum, each of them in [i] and [y] vowel contexts. The most ambiguous fricative [?] was identified individually for each subject in a pretest in a phonemic categorisation task, using a 9-step [S] – [s] continuum.

In the fMRI experiment, pairs of fricative-vowel syllables were presented auditorily. In the test conditions we varied the relation of the members within a syllable pair: in certain trials, fricatives in the pair-members were previously identified as the same or as different phonemes. Brain responses to syllable pairs were recorded during pseudo-passive listening. Following the logic of adaptation-fMRI, we expected that if pair-members are treated as the same by a cortical area, the repeated firing of neurons will lead to adaptation and thus to a reduction in overall activity in that area, as compared to pair-members that are treated as different by that area. We expected that already one presentation of a syllable establishes sufficient context to generate this adaptation effect.

We could manipulate acoustic properties and distance of the fricative sounds while keeping the perception of members of a syllable pair unaffected. For example, fricatives of both the syllable pair Si-Si and the syllable pair Si-?i were perceived as the same, although the acoustic-phonetic relations were different in the two pairs. We used this manipulation for testing the sensitivity of a cortical area to acoustic-phonetic changes.

But the key property of the individually identified ambiguous sound was that it was classified as [S] in [i]-contexts, but as [s] in [y]-contexts by the listener. And by exploiting this vowel-context effect, we could perform the inverse test as well: we could manipulate the perception of members of a syllable pair as the same or different while keeping the acoustic properties and distance of the sounds constant. For example, fricatives of the syllable pair Si-?i were perceived as the same, while fricatives of the syllable pair Sy-?y were perceived as different, although the acoustic-phonetic relations were not different in the two pairs (see Figure 1). This was our critical manipulation for testing the sensitivity of a cortical area to phonological changes.

The present study has focused on the tests of specific contrasts of four conditions, which were the following (see also Table 1):

SAME (identical pairs): pairs of syllables with perceptually unambiguous, acoustically identical fricatives, referred to as "SAME".

CRITICAL-SAME (within-category pairs): pairs of

Conditions	Unambiguous sound compared to unambiguous	Ambiguous sound compared to unambiguous
Pair-members identified as the same phoneme	SAME: identical pairs (Si-Si, si-si, Sy-Sy, sy-sy)	CRSA: Critical-same: within-category pairs (Si-?i, ?i-Si, sy-?y, ?y-sy)
Pair-members identified as different phonemes	DIFF: different endpoint stimuli (Si-si, si-Si, Sy-sy, sy-Sy)	CRDI: Critical-different: across-category pairs (si-?i, ?i-si, Sy-?y, ?y-Sy)

TABLE 1 : Experimental conditions

syllables with a context-independently perceived (unambiguous) and a context-dependently perceived (ambiguous) fricative which are in a large proportion of trials identified identically in the pretest, referred to as “CRSA”:

CRITICAL-DIFFERENT (across-category pairs): pairs of syllables with a context-independently perceived (unambiguous) and a context-dependently perceived (ambiguous) fricative which are in a large proportion of trials identified differently in the pretest, referred to as “CRDI”.

DIFFERENT (different endpoint stimuli): pairs of syllables with perceptually unambiguous, acoustically and phonologically different fricatives, referred to as “DIFF”.

Importantly, the vowel did not change within a pair, and every pair consisted of a comparison of a given syllable to an unambiguous syllable. (We use the term “unambiguous syllable” for syllables with an endpoint fricative [S] or [s], whose classification is context-independent.)

Acoustic-phonetic processing areas were assumed to be sensitive to any physical differences of speech sounds. Phonological processing areas, or areas that code a phonologically abstract representation, were assumed to follow the behavioural pattern in making distinctions between syllables perceived as the same and syllables perceived as different. When defining the contrasts, we followed two principles: first, we used the minimal possible comparison; and second, we required that our contrasts contain the SAME condition as the only legitimate base for an interpretable comparison. For acoustic-phonetic processing, the minimal contrast was SAME (identical pairs) < CRSA (within-category pairs) – and we also expected that these areas would show less adaptation in all other conditions than in the SAME condition: indeed, it would be difficult to interpret areas that show a SAME < CRSA effect but not a SAME < CRDI or SAME < DIFF effect. For phonological processing, the minimal contrast was the conjunction of two simple contrasts: SAME (identical pairs) < CRDI (across-category pairs) and CRSA (within-category pairs) < CRDI (across-category pairs).

Following this logic, we aimed to distinguish a phonological processing level from an earlier, acoustic-phonetic processing level along two simple predictions: First, if a cortical area shows adaptation in the identical (SAME) condition as compared to all other conditions, then this area plays a role in acoustic-phonetic processing. Second, if a cortical area shows adaptation both in the identical (SAME) and within-category (CRSA) conditions as compared to the across-category (CRDI) condition, then this area is involved in phonological processing. We also hypothesized that the areas characterized this way are both functionally distinct (thus follow different SAME-CRSA-CRDI patterns) and anatomically distinct.

Method

Participants

Thirty subjects participated in the study (19 female). None of them had participated in any of our pilot studies. All participants were right-handed, native Dutch speakers with no known hearing disorders. Mean age was 23 years (range 19-26). All participants gave informed written consent before participating in the experiment.

Materials and procedure

In a series of pilot experiments we optimized the stimulus set of fricative-vowel syllables and learned that (1) compensation for coarticulation was a strong effect when using synthetic stimuli, and that (2) there was a large intersubject variability both in phoneme categorization and in the size of the vowel-context effect. Thus we needed to know on an individual base how each subject perceives each stimulus type from a fine-grained continuum without actually asking them during the fMRI experiment. At the same time, we wanted to minimize the number of stimuli used in the experiment, in order to maximize the number of repetitions for each stimulus type. To solve this problem we ran a pretest before the fMRI experiment with each subject, in which both the unambiguity of the endpoints was checked and the most ambiguous fricative was identified individually in a phonemic categorization task. In the fMRI experiment, only these individually fine-tuned stimuli were presented.

Therefore, the experiment consisted of two parts: a behavioural pretest phase and an fMRI experiment phase. The pretest was immediately followed by the fMRI experiment.

Pretest

Materials

Syllables in the pretest consisted of a fricative from an [S] – [s] continuum and an [i] or an [y] vowel. Both the male voice vowels (mean F0 was 127 Hz) and a 9-step fricative continuum were synthetized by Holger Mitterer, using Praat 4.0 (Boersma and Weenink, 2004). The fricatives were varied in the frequency at which the most energy in the frication noise was concentrated. For an exact physical

Figure 2: Scanning with silent gaps

description of the stimulus synthesis, see Mitterer (submitted). Endpoints of the continuum were unambiguously identified as [S] and [s] in a preliminary identification test with the stimulus set by 6 native Dutch speaking subjects. Seven middle steps of the continuum were linearly distributed in a narrower interval which covered enough of the continuum to contain the most ambiguous sound as determined by 14 native Dutch speaking subjects' individually averaged responses in our pilot studies. 18 syllables were synthetized by concatenating each of the 9 fricatives with each of the 2 vowels. Length of the fricative and the vowel were 180 ms and 200 ms, respectively, adding up into 380 ms long syllables.

Procedure

Stimuli were displayed in a sound-proof room through headphones at a constant, comfortable listening level. A trial consisted of one syllable presentation and one button response. The pretest consisted of a short practice (6 trials) and the experiment with one self-terminated break after the first 8 chunks. Participants had a phoneme identification task: they were instructed to decide whether the first sound in the syllable heard was an [s] (described as "s" in the Dutch word "saai") or an [S] (described as "sj" in the Dutch word "sjaal"). Participants had to give a button press response with their left or right index finger, according to the "s" or "sj" sign on the corresponding side. The coupling of sound and side was balanced across subjects. Participants were instructed to respond as accurately and as fast as possible. Each trial began with the stimulus presentation and lasted 2500 ms. The offset of the response-window was determined by the onset of the next trial. The pretest lasted 12 minutes.

Experimental design

Each of the 18 syllable types was presented 15 times. Trials were clustered into 15 chunks of 18, where each chunk contained each syllable once. These chunks were then randomized and ordered with the constraint that the last trial of each chunk had to be different from the first trial of the consecutive chunk. Thus, two consecutive syllables were never identical during the whole test, and the distance of two identical trials was never larger than 35, with an average distance of 18 for each syllable-type. This was to minimize the biasing effects of task-internal probability learning. The experiment was run and data were collected by a Presentation software.

fMRI experiment

Materials

Stimuli in this test were syllable pairs. Three levels of the pretest's 9-step fricative continuum were used: the two unambiguous endpoints [S] and [s]; and one of the seven middle steps, the most ambiguous level [?], which was determined individually for each participant on the base of the pretest. The fricative was followed by an [i] or an [y] vowel: either by the same vowels as the ones in the pretest, or by the gender-changed version of the same vowels (for that, PRAAT's change gender function was used, the resulting new mean F0 was 260 Hz).

Syllable pairs consisted of two 380 ms long fricative-vowel syllables, separated by a 370 ms long silent gap. Trial types and conditions were defined on the basis of the relation of the two syllables within a pair. Test trials and their types, distractor trials and their types, and silent trials were distinguished. In silent trials, both syllables were substituted by a 380 ms long silence. The vowel quality did not change within a pair in any of the trial types: in test trials, vowels from the pretest were used and they were identical in the two syllables; in distractor trials, the vowel of the first syllable was one from the pretest, while the vowel of the second syllable was the gender-changed version of the same vowel quality.

Test trial types varied in vowel quality across pairs and in the relation of the fricatives within a pair. Given that there were 3 fricatives, there were 9 possible combinations of fricative-fricative couplings for each vowel, so the 2 vowel contexts resulted in 18 different types of syllable pairs. This way every syllable-pair appeared equally often with both possible orderings (e.g., Si-?i and ?i-Si). Each of these 18 types were repeated 35 times during the experiment.

Distractor trial types, similarly to the test trial types varied in vowel quality across pairs and in the relation of the fricatives within a pair. Only the two unambiguous fricatives were used in these trials, the 4 possible fricative-fricative couplings and the 2 vowel contexts resulted in 8 different types. Each of these 8 types was repeated 10 times during the experiment.

The silent trial was repeated 70 times during the experiment.

Procedure

Participants had a distractor task during scanning: they were instructed to listen to the syllable pairs and to press a button only when the second syllable is uttered by a different speaker, a female voice. Participants were instructed to respond with the left index finger. There was a short practice session after the pretest.

Button response was expected for 80 out of 780 trials (10%), with an average time-gap of 36 s between 2 distractor trials. There was a 22 second (6 pulses) long break after every 9,5 minutes (two chunks). During the break the scanner was on, but no stimuli were presented. Participants were informed about the beginning and the end of the break visually.

Experimental design.

We applied a rapid event-related paradigm. But in order to increase the power of the statistical analyses, most of the test trials and the silent trials were presented in clusters of 3, meaning that the same syllable pair or the same silent trial was presented three times in a row. In order to reduce predictability of the consecutive trials on the other hand, one out of 7 test trials and one out of 7 silent trials were presented non-clustered. Thus, 3-clusters of a given test or silent trial type appeared twice as often as their non-clustered variant, and 86% of a given type appeared in 3-clusters. Distractor trials always appeared non-clustered. The experiment consisted of 780 trials.

To minimize probability learning effects and the effects of attentional fluctuation, an equal distribution of trial types was ensured throughout the experiment. Furthermore, for ordering purposes, trials were grouped into five categories: same, critical, different, distractor and silent categories. Trial ordering was based on these categories. Units (3-clusters and non-clustered trials) were randomized with the restriction that no 2 consecutive units came from the same category.

The clustering, equal distribution and restricted randomization of trials were done in order to create a well-balanced, powerful, rapid event-related design.

fMRI scanning parameters

Whole-brain functional images were acquired on a 3-Tesla MRI system (Siemens TRIO). Using a gradient echo planar scanning sequence, 26 axial slices were obtained for each subject (voxel size $3{,}5 \times 3{,}5 \times 4$ mm^3, field of view = 224 mm, TA = 1800 ms, TR = 3670 ms, TE = 35 ms, flip angle = 70°). To avoid interference with the scanner noise, we used the technique of sparse scanning (Hall et al., 1999). All stimuli were presented between volume acquisitions, during silence (see Figure 2).

We expected that the BOLD signal would peak between 4 and 6 sec, and thus we assumed that the largest proportion of activation corresponding to a given trial would be acquired in the second volume acquisition following a syllable pair (the volume acquisition between 4040 ms and 5840 ms after the beginning of the second syllable within a pair).

All functional images were acquired in one run that lasted 50 minutes and contained 820 pulses, including 3 dummy scans at the beginning and 5 extra scans at the end of the run. After the acquisition of functional images, a high-resolution anatomical scan (T1-weighted MP-RAGE, 192 slices) was acquired.

Data analysis

Pretest

Boundary determination

The most ambiguous sound of the fricative continuum (i.e., the category boundary) was determined individually, on the basis of the fricative identification curves for the two vowels (see Figure 3 for an example for an individual identification curve). The selection algorithm had five steps, which were applied sequentially, but the algorithm terminated immediately when the boundary level was determined. The five consecutive steps were the following:

(1) Normally, that sound level was chosen for which the [S] responses were the closest to 50%, for vowel-contexts collapsed.

(2) In ambiguous cases, that level was chosen for which the neighbouring levels were more ambiguous, more precisely that one of the competing ambiguous levels for which the least ambiguous, non-shared neighboring level had responses closer to 50%, for vowel-contexts collapsed.

(3) In still ambiguous cases, that level was chosen for which the difference of the identification curves for the two vowel-contexts was greater.

(4) In still ambiguous cases, the level closer to the middle of the continuum was chosen.

(5) In still ambiguous cases, one of the competing levels was chosen randomly.

To have a sensitive tool for checking the category boundary, based on our pilot studies the differences between neighbours of the seven middle steps of the fricative continuum were set rather small. However, it was theoretically possible that a subject's fricative category boundary falls between two stimulus levels, and the identification curve is so steep that both levels neighbouring the hypothesized position of this category boundary are too far, and the perceptual balance of the stimulus set is not ensured by choosing any of the levels. For this reason, an inclusion criterion was set to check whether our pretest continuum was fine-grained enough for the participant's perceptual system.

Furthermore, we expected great intersubject variability in the position of the category boundary and in the size of the vowel-context effect. The selection algorithm of the most ambiguous sound was optimized firstly for finding the most ambiguously identified fricative level, for vowel-contexts collapsed; and not, or only secondarily for finding the fricative level with the greatest identification difference between the two vowel-contexts. This choice was made to ensure a perceptually balanced stimulus set for the fMRI experiment.

But on the other hand the manipulation in the fMRI experiment was sensitively based on the vowel-context effect, and thus the presence of unambiguously, context-independently and ambiguously, context-dependently perceived fricatives was going to be critically important there. For this reason, two further inclusion criteria were set: a criterion to check whether endpoint sounds were indeed unambiguously identified in each vowel-context; and another criterion to check whether the vowel-context effect is strong enough for the selected ambiguous level.

Only those subjects entered the fMRI data analysis whose pretest responses to the selected stimuli had passed all three criteria.

Inclusion criteria

Criterion 1 - fine-grained continuum: the percentage of [s] decisions at the boundary level is between 33% and 66%, for the vowels collapsed.

Criterion 2 - unambiguity of phonemic decision at the extremes: the percentage of [s] decisions at level 0 ([S] endpoint) is less than 40%, at level 8 ([s] endpoint) is greater than 60%, for the vowels collapsed; the percentage difference of [s] decisions at level 0 and level 8 is greater than 33%; and both endpoints receive decisions that are less ambiguous than the boundary level.

Criterion 3 - vowel-context effect: either at the boundary level or at one of its non-endpoint neighbouring levels the percentage of [s] decisions for vowel [y] is at least 25% greater than for vowel [i].

fMRI experiment

fMRI image preprocessing

fMRI data were analyzed with BrainVoyager QX 1.2.6 and 1.3.8 (Brain Innovation). Functional images were corrected for motion and slice time acquisition. Functional images were coregistered with the anatomical scan and transformed into Talaraich coordinate space (Talaraich and Tournoux, 1988). Images were spatially smoothed with a full-width at half-maximum (FHWM) Gaussian kernel of 6 mm.

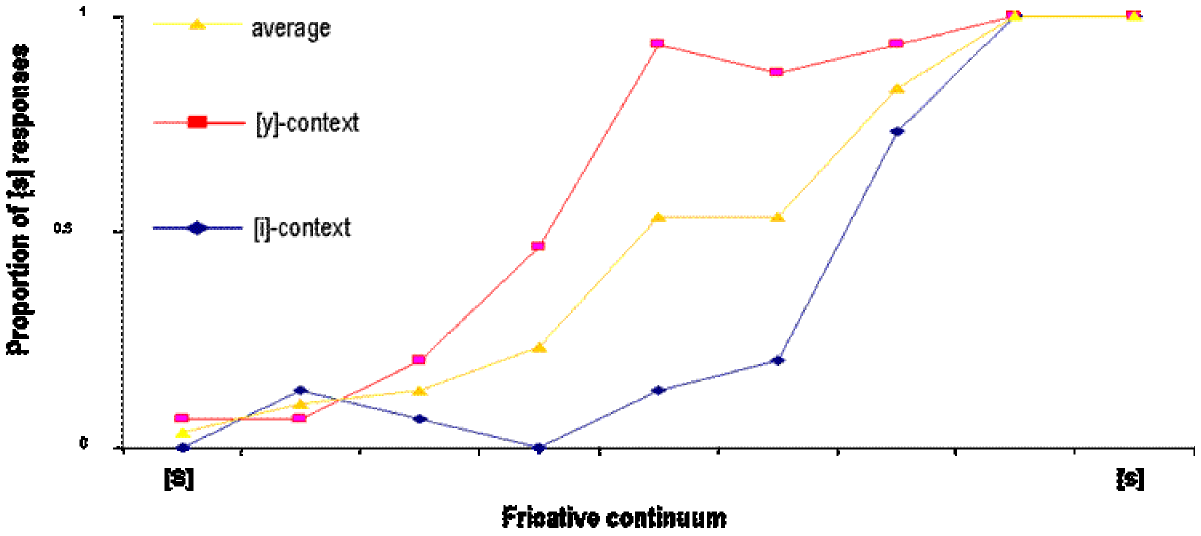


FIGURE 3: Vowel-context effect for an individual subject. Responses in the phoneme identification task (pretest) for fricatives from an [S] – [s] continuum in [i] and [y] contexts.

Statistical analyses

Statistical analyses were performed in the context of the general linear model. Regions of interest were defined based on fixed effects analyses. Maximum cluster spread range was 25 mm. Single contrast analysis was performed with a statistical threshold set at $P < 0.001$ at the voxel level, uncorrected for multiple comparisons. Conjunction analysis of two contrasts for fixed effects was performed with a standard "minimal t-statistic" approach (Nichols et al., in press) that BrainVoyager uses, which is equivalent to a logical AND of the contrasts at the voxel level. In order to get a statistical threshold for the conjunction analysis that is comparable to our single contrast analysis, we estimated the probability of finding a voxel that is independently significant in each and both contrasts (i.e., the joint probability), by multiplying the probabilities for each contrast (e.g., Allan et al., 2000; Cabeza et al., 2002). Thus, both contrasts in the conjunction were assigned a threshold set at $P < 0.033$, the square-root of $P < 0.001$.

Beta weights (regression coefficients) as indices of effect size were then obtained for all voxels included in these regions of interest, per subject and per trial type. These beta weights, averaged first regionally and then across those trial types that were collapsed within one condition in a specific contrast, were normalized for all conditions (that is, the average of the beta weights for all conditions was set as baseline, it was assigned the weight zero, and the set of all conditions was linearly shifted accordingly) per ROI and per subject. Random effects analyses were performed applying t-tests to the averaged and normalized beta weights, with a threshold set at $P < 0.05$.

Only regions that were defined in a fixed effects analysis and then passed the t-test for a specific contrast are reported. To reduce the risk of reporting false positive activations, only regions including more than 10 contiguous voxels were considered.

Fricative level	[i]-context	[y]-context	average	difference between vowel-contexts
level 0	0.049	0.137	0.093	0.088
level 1	0.080	0.341	0.211	0.261
level 2	0.096	0.509	0.303	0.413
level 3	0.126	0.565	0.346	0.439
level 4	0.197	0.726	**0.462**	**0.529**
level 5	0.324	0.813	**0.569**	**0.488**
level 6	0.478	0.864	0.671	0.386
level 7	0.707	0.915	0.811	0.208
level 8	0.928	0.979	0.953	0.051

TABLE 2: Proportion of [s] decisions (25 subjects)

Fricative level	[i]-context	[y]-context	average	difference between vowel-contexts	number of included subjects
boundary -6	0.000	0.033	0.017	0.033	2
boundary -5	0.028	0.156	0.092	0.128	12
boundary -4	0.061	0.245	0.153	0.183	23
boundary -3	0.075	0.410	0.242	0.334	23
boundary -2	0.106	0.511	0.308	0.406	24
boundary -1	0.155	0.640	0.369	0.485	25
boundary	0.221	0.781	**0.501**	**0.560**	25
boundary +1	0.432	0.851	0.649	0.419	25
boundary +2	0.624	0.891	0.757	0.266	25
boundary +3	0.814	0.947	0.868	0.132	23
boundary +4	0.856	0.990	0.923	0.133	13
boundary +5	0.500	1.000	0.633	0.733	2
boundary +6	0.667	1.000	0.833	0.333	2
boundary +7	0.600	0.867	0.733	0.267	1

TABLE 3: Proportion of [s] decisions, levels centered around the selected boundary level for each subject (25 subjects)

Results

Pretest results

All subjects passed the “fine-grained continuum” test and the “unambiguous endpoints” test, but 5 subjects failed on the “vowel-context effect” test. Therefore, 25 out of the 30 subjects passed all 3 inclusion criteria. Our inclusion criteria were quite liberal. In fact, half of the subjects would have passed much stricter criteria as well: 15 out of the 30 participants had a boundary level with 50 +/- 10% [s] decisions (fine-grained continuum), had identified the endpoint in each vowel-context with an unambiguity greater than 80% (unambiguous endpoints) and finally either at the boundary level or at one of its non-endpoint neighbouring levels the percentage of [s] decisions for vowel [y] was at least 33% greater than for vowel [i] (vowel-context effect). Figure 3 shows the vowel-context effect for an individual subject.

The selection of the fricative category boundary level, which could have been between level 1 and level 7 from the fricative continuum (level 0 and level 8 were the endpoints) showed little variance (mean = 4.5; sd = 1.01) for the 25 subjects who passed the inclusion criteria. However, picking a middle step from the continuum as a standard boundary level for all participants would have clearly weakened the phonetic balance of the stimulus set used in the fMRI experiment. Choosing level 4 as the boundary level for all participants would have resulted in 46% [s] decisions; choosing level 5 for all would have resulted in 57% [s] decisions at that level. By applying individual fine-tuning, the overall percentage of [s] decisions was 50% at the individually selected boundary level, thus it was indeed ambiguous.

As a secondary effect, individual fine-tuning also increased the context-effect at the selected ambiguous level: the percentage difference of [s] decisions for the two vowels was higher (56%) at the individually selected ambiguous level as compared to the hypothetical case of choosing level 4 (53%) or level 5 (49%) of the continuum as the ambiguous sound for all participants. (See the Tables 2 and 3 for an overview of the pretest results.)

The context-effect at the selected ambiguous level was strong, behavioural responses to [?i] and to [?y] were highly different (see Figure 4). This confirmed that the critical CRSA and CRDI conditions are indeed different.

fMRI results

Performance data

Two subjects had to be excluded because of movement in the fMRI scanner, a third subject was

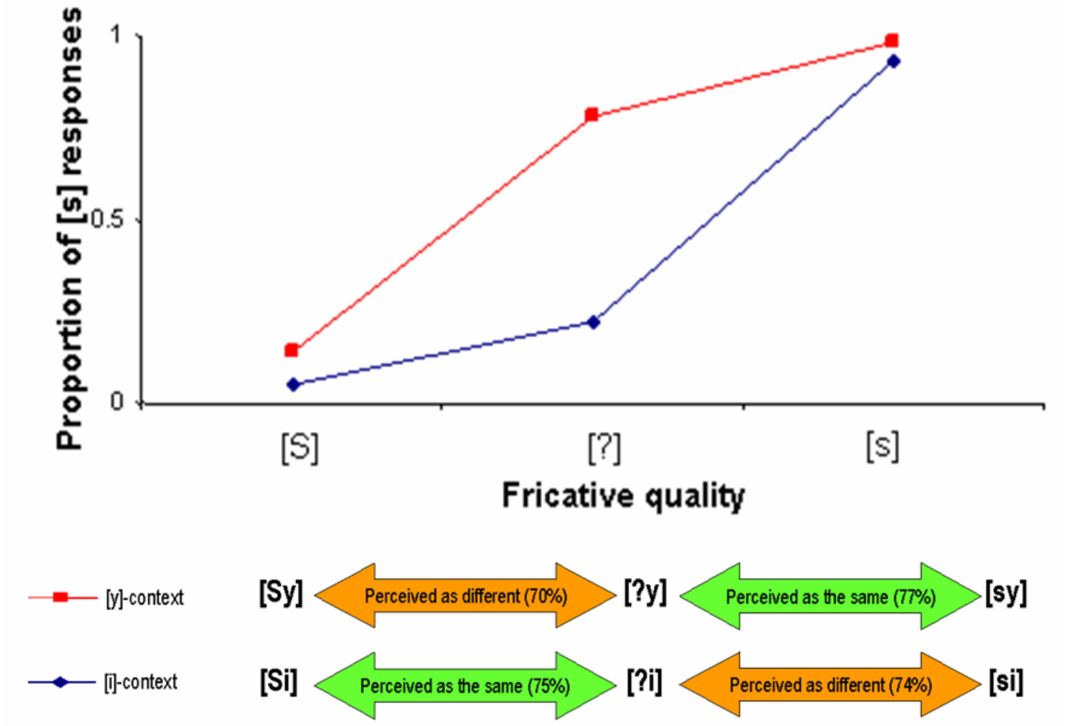
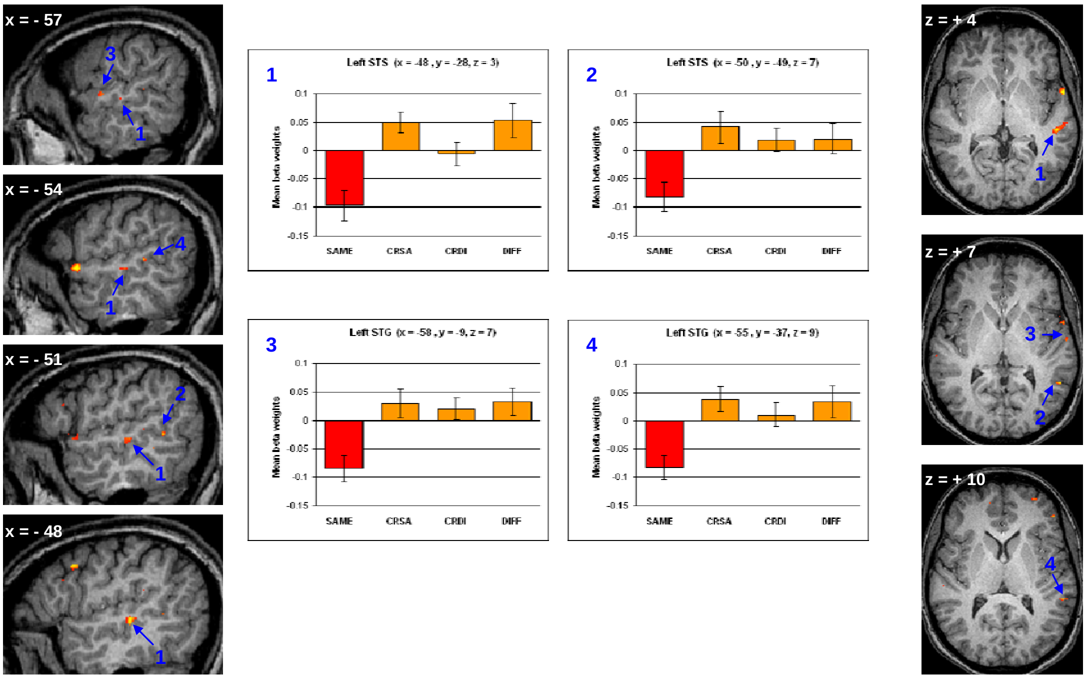


FIGURE 4: Vowel-context effect, group average (25 subjects)

FIGURE 5. Four left superior temporal regions showing an acoustic-phonetic pattern. Sagittal and axial maps showing significant clusters (P < 0.001) of the fixed effects analysis superimposed on a representative brain. Bar diagrams indicate mean beta weights and standard errors for the four conditions. Color coding of the bars signals significant comparisons between the conditions.

🟥<🟧 (p < 0.05 for each pair of conditions)



excluded because his scanning was accidentally interrupted. So in the context of the group analyses below, the fMRI data of 22 subjects are presented.

Participants performed well on the voice-change detection task. Only one subject made more than one false alarms, 17 out of the 22 subjects made no false alarms during the whole fMRI experiment. The percentage of false alarms was below 0.7%.

This shows that the task was indeed very easy.

Acoustic-phonetic test

The first test aimed at identifying cortical areas that are involved in the acoustic-phonetic processing of speech sounds. We assumed that these areas have undergone habituation in the SAME condition, caused by the repetition of the syllable, while remained dishabituated in the CRSA, CRDI, DIFF conditions. To focus on an acoustic-phonetic level of processing, a minimal (SAME < CRSA) contrast was used: regions being significantly less activated when the fricatives in a syllable pair were physically the same opposed to when they were physically different but perceived as the same fricatives, were determined in a single contrast fixed effects analysis. Paired-samples t-tests – a random effects analysis – were then applied on these regions (SAME < CRSA, SAME < CRDI, SAME < DIFF) to filter those with an interpretable acoustic-

Acoustic-phonetic processing	voxels	Talx	Taly	Talz	BA	SA<CS	SA<CD	SA<DI
L STS	129	-48	-28	3	22	.001	.029	.005
L STS	16	-50	-49	7	22	.012	.017	.017
L STG (anterior)	14	-58	-9	7	22	.016	.003	.004
L STG	15	-55	-37	9	22	.000	.011	.016
L middle frontal gyrus	87	-30	11	38	8	.000	.012	.001
L superior frontal gyrus	29	-8	10	49	6	.000	.012	.012

(Talx, Taly, Talz refers to the Talaraich coordinates, BA refers to the Brodmann areas. The last three columns show significance levels in the paired-samples t-tests for the comparison of the denoted conditions. SA: same, CS: critical-same, CD: critical-different; D: different. See the text for details.)

TABLE 4: List of brain areas, acoustic-phonetic test

phonetic pattern as characterized by our four conditions.

Areas following an acoustic-phonetic pattern (SAME < CRSA, CRDI, DIFF) were all left lateralized and included regions of the superior temporal gyrus and the superior temporal sulcus (BA 22), the middle frontal gyrus (BA 8) and the superior frontal gyrus (BA 6). See Table 4 for details.

Figure 5 shows the similar acoustic-phonetic patterns of four clusters from the left superior temporal sulcus and gyrus.

Phonological test

The second test aimed at identifying the regions involved in phonological processing. We assumed that these areas work with discrete, categorical representations of speech sounds, and are insensitive to within-category variations. Thus, a similar level of adaptation and therefore a similar amount of activation decrease was expected in the SAME and CRSA conditions as compared to the CRDI condition in all phonological processing regions. To make the determination of the regions of interest specific, a conjunction analysis of the minimal contrast (CRSA < CRDI) and the contrast to the no-change condition (SAME < CRDI) was performed for fixed effects. Then the behaviour of each identified area was further checked in t-tests (SAME < CRDI, CRSA < CRDI).

Areas showing a phonological pattern as characterized by these three conditions, were the following: the left superior temporal gyrus (BA 22), the right anterior superior temporal gyrus (BA 38), the right inferior temporal gyrus (BA 20), the right fusiform gyrus (BA 20), the left inferior frontal gyrus (BA 9), regions in the right inferior frontal gyrus, the right superior frontal gyrus, regions in the medial frontal cortex and in the basal ganglia. See Table 5 for details.

Interaction of acoustic-phonetic and phonological patterns

No regions passed both the acoustic-phonetic and the phonological tests.

The SAME-CRSA-CRDI pattern for each ROI from the acoustic-phonetic test was paired with the SAME-CRSA-CRDI pattern for each ROI from the phonological test, resulting in 270 ROI-pairs altogether. These ROI-pairs entered a repeated measures ANOVA in which the interaction of the two main effects (effect of test, effect of condition) was tested.

85% of all ROI-pairs showed a significant interaction ($p < 0.05$), and 96% of all ROI-pairs showed a trend for an interaction ($p < 0.1$). Thus, on a global level activation patterns of areas from the two tests are distinct.

Specific interactions of neighbouring areas determined in different tests were also tested. We identified superior temporal areas, close to the superior temporal sulcus with an acoustic-phonetic pattern; and areas with a phonological pattern in the left superior temporal sulcus and in the right anterior superior temporal gyrus. These subregions were distinct both anatomically and functionally. For instance, Figure 6 shows the two largest left superior temporal area in each contrast (both from BA 22). Both areas followed the curve of the superior temporal sulcus, the area in the phonological contrast was slightly more anterior. Their activation

Phonological processing	voxels	Talx	Taly	Talz	BA	SA<CD	CS<CD	SA<DI	CS<DI
L STS	75	-45	-23	-8	22	.017	.024	.365	.426
R STG (anterior)	57	44	12	-11	38	.009	.006	.205	.339
R inferior temporal gyrus	23	40	-5	-20	20	.021	.005	.946	.783
R fusiform gyrus	20	36	-21	-14	37	.003	.045	.740	.733
L inferior frontal gyrus	184	-39	9	30	9	.017	.011	.108	.272
R inferior frontal gyrus	24	39	27	-11	47	.006	.050	.139	.331
R inferior frontal gyrus	21	32	20	16	45/46	.002	.039	.015	.019
R inferior frontal gyrus	14	42	12	16	45/46	.011	.022	.075	.015
R superior frontal gyrus	44	16	34	46	8	.029	.002	.126	.028
Medial frontal cortex	72	3	23	-11	25	.009	.001	.064	.126
Medial frontal cortex	58	3	14	1	25	.032	.004	.047	.039
Medial frontal cortex	50	5	-11	27	23	.009	.013	.057	.021
Basal ganglia	38	28	-15	26		.026	.018	.779	.763
Basal ganglia	36	26	2	22		.001	.006	.126	.129

(Talx, Taly, Talz refers to the Talaraich coordinates, BA refers to the Brodmann areas. The last four columns show significance levels in the paired-samples t-tests for the comparison of the denoted conditions. SA: same, CS: critical-same, CD: critical-different; D: different. See the text for details.)

TABLE 5: List of brain areas, phonological test

patterns showed a significant interaction ($p < 0.01$).

We also found near sites of the left inferior/middle frontal gyri that were functioning differentially. Figure 7 shows two larger inferior/middle frontal areas: a cluster from the left middle frontal gyrus (BA 8) shows an acoustic-phonetic pattern, while a cluster on the superior part of the left inferior frontal gyrus (BA 9) shows a phonological pattern. Their activation patterns also showed a significant interaction ($p < 0.02$).

Discussion

Acoustic-phonetic and phonological contrasts

An overwhelming majority of neuroimaging studies of prelexical processing was aiming to make a distinction between not speech-specific (acoustic) and speech-specific (phonetic-phonological) processing levels, but were not designed to separate a phonological processing level. Our experiment was designed to make a distinction between acoustic-phonetic and phonological processing levels.

The acoustic-phonetic test (SAME < CRSA) had a controlling function: it was designed to check for the effects of all non-phonological changes in our speech stimuli. On the first level of group analyses we made a minimal comparison and contrasted syllable pairs with an acoustic-phonetic (but not phonological) change (CRSA) to unambiguous syllable pairs with no change (SAME). If a cortical area is involved in acoustic or phonetic processes, then it should be sensitive to fine changes of speech sounds and thus it should be differentially activated by the two conditions. We expected neuronal adaptation and thus a decreased level of activity in the identical condition.

For the phonological test we applied a strict and minimal critical contrast (CRSA < CRDI) and combined it with a comparison to the no-change condition (SAME < CRDI) in a conservative conjunction analysis (Nichols et al., in press) on the first level of group analyses. Below I discuss the validity of this test in more detail.

The critical contrast (CRSA < CRDI) was indeed a minimal comparison. In all syllable pairs of the contrast, the same ambiguous fricative sound was coupled with one of the two unambiguous fricative sounds. Thus, acoustic properties of the displayed stimuli and physical distances of the fricatives within a syllable pair were identical in the two conditions. If a cortical area is involved in acoustic processes, then it should not be differentially activated by the two conditions. Inversely, if an area is differentially activated by the two conditions, then there is good reason to assume that this area is involved in a process which makes a difference between certain groups of syllable pairs in synchrony with our grouping into the two conditions, along more abstract than acoustic dimensions.

Further characterizing the syllables in the critical contrast, it is important to point out that the ambiguous fricative sound was indeed ambiguous, it was identified as [s] or as [S] in exactly 50% of all cases, also as a result of the individual fine-tuning of the critical stimulus at the category boundary. That is, phonetic properties of the displayed stimuli were balanced between the two conditions. If a cortical area is involved in phonetic (speech-specific, but not yet phonological) processes, then again, this area should not be differentially activated by the two conditions. That is, if an area is differentially activated, then we can assume its involvement in a process which differentiates syllable pairs along other than acoustic or phonetic dimensions.

However, there was a clear difference between CRSA and CRDI conditions. Fricatives in the CRSA condition were identified as the same phonemes, while fricatives in the CRDI condition were identified as different phonemes. It was the vowel-context effect on the fricatives that made this crucial difference. As we have seen, there is evidence that this specific compensation effect acts in a late phonetic phase or more probably on a phonological level, since phonemic categorization of the fricative seems to be preceded by the phonemic categorization of the vowel (Smits, 2001a; Mitterer, submitted). Since this is the effect that makes our two critical conditions contrastive, we can suppose that only dimensions higher than the dimension of the vowel-context effect can be causally involved in eliciting differential cortical responses to CRSA and CRDI conditions.

FIGURE 6. Regions in the left STS with different activation patterns. Sagittal, coronal and axial maps showing significant clusters (P < 0.001) of the fixed effects analysis superimposed on a representative brain. Yellow/red: acoustic-phonetic contrast. Light/dark green: phonological contrast. A: area with acoustic-phonetic pattern. P: area with phonological pattern. Bar diagrams indicate mean beta weights and standard errors for the four conditions. Color coding of the bars signals significant comparisons between the conditions. 🟥<🟧 (p < 0.05 for each pair of conditions)

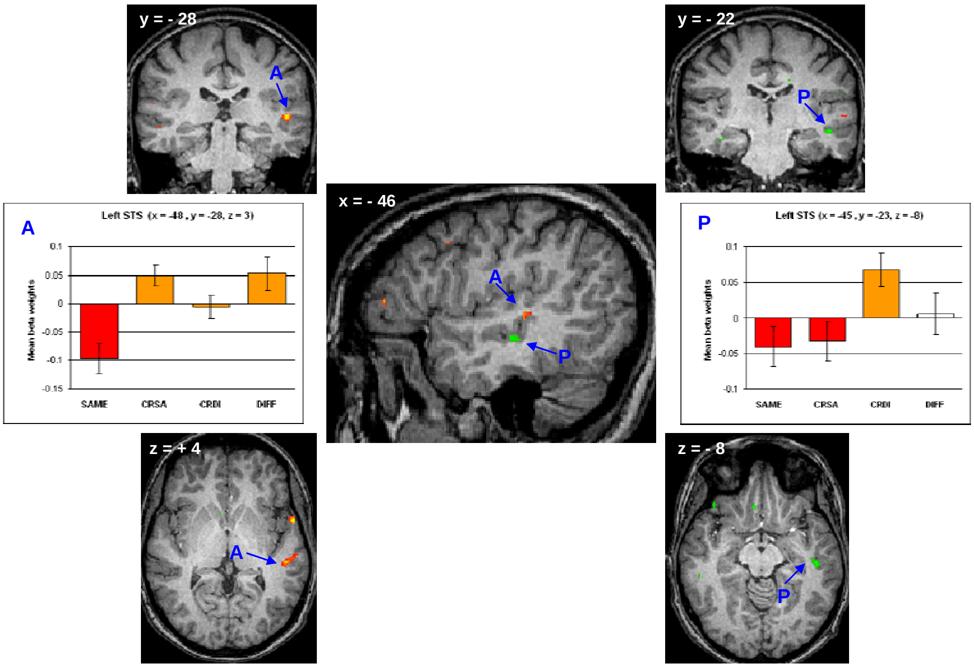
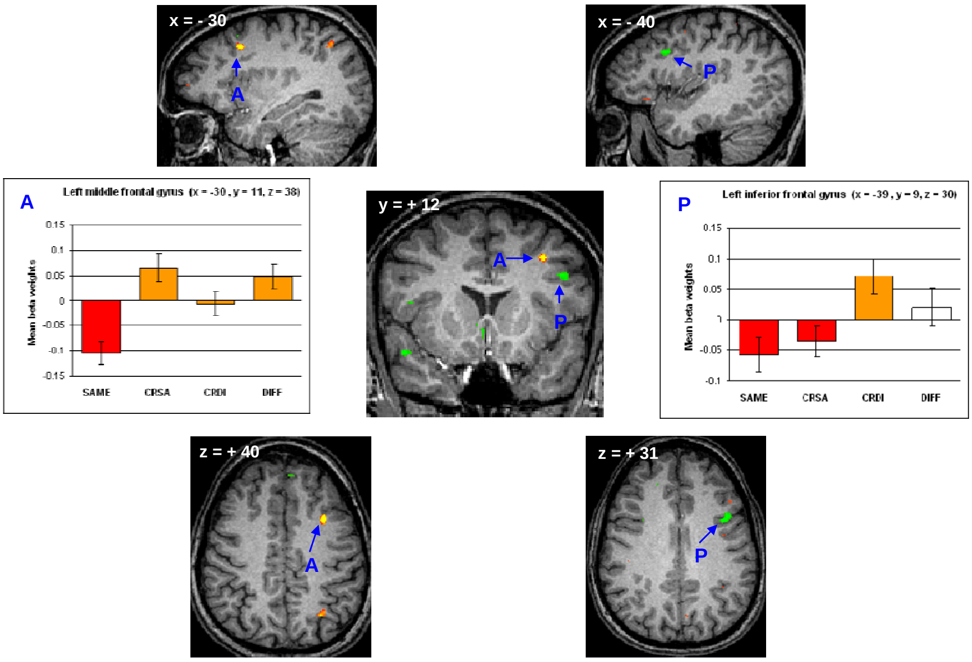


FIGURE 7. Regions in the left inferior and middle frontal gyrus with different activation patterns. Sagittal, coronal and axial maps showing significant clusters (P < 0.001) of the fixed effects analysis superimposed on a representative brain. Yellow/red: acoustic-phonetic contrast. Light/dark green: phonological contrast. A: area with acoustic-phonetic pattern. P: area with phonological pattern. Bar diagrams indicate mean beta weights and standard errors for the four conditions. Color coding of the bars signals significant comparisons between the conditions. 🟥<🟧 (p < 0.05 for each pair of conditions)



It has to be noted that unambiguous speech sounds played a central role in our study: every syllable pair presentation consisted of a comparison of a certain speech sound to a context-independently unambiguously identified speech sound. In case of the critical contrast, it increased the chance that although our comparison was strict, the resulting findings remained relevant for speech. To further reduce the possible danger of reporting artifacts resulting from contrasting activations in different conditions instead of contrasting them to any sort of baseline activation, we considered the critical contrast in conjunction with a second contrast (SAME < CRDI) in the phonological test. This contrast ensured that only such areas were characterized as areas following a phonological pattern which also survived a comparison to the pair of identical, unambiguous syllables, meaning that the activation difference observed for that area indeed reflects a response to a change versus no-change relevant in normal speech processing.

On the basis of the above listed reasons we suggest that activation increase for the critical-different (CRDI) condition as compared to both the critical-same (CRSA) and identical (SAME) conditions at a certain cortical area would be caused by the dishabituation of a group of neurons as a response to a phonologically (but not acoustically or phonetically) relevant change.

All in all, we defined a strictly phonological contrast, where the acoustic properties were identical and the phonetic properties were balanced in the conditions; and all the stimuli were compared to an unambiguous phoneme (instead of simply being compared to each other). We claim that our phonological test was sufficiently strict and had the potential to reveal the neural correlates of phonological processing.

Cortical regions in prelexical processing

We showed that certain subregions of the superior temporal gyrus and sulcus seem to have a role in acoustic-phonetic processing of speech sounds; while other subregions here seem to be involved in phonological processing. This way, we found supporting evidence for the claims that there are phonetic processing areas (e.g., Demonet et al., 1992) and also for the claims that there are phonological processing areas in the superior temporal gyrus (e.g., Jacquemot et al., 2003), with the important note that these are highly specialized, differentially functioning subregions. Similarly, we have found differentially functioning, adjacent regions in the left inferior and middle frontal gyri, suggesting that certain subregions here play a role in acoustic or phonetic processing, while others in phonological processing. This result is in line with Poldrack et al. (2001) who have found that a subset of phonological processing left inferior frontal regions is also sensitive to acoustic-phonetic features. Importantly, we also found a clear anatomical separation.

The supramarginal gyrus was often found in studies of phonetic or phonological processing (e.g., Benson et al., 2001; Golestani and Zatorre, 2004; Jacquemot et al., 2003; Dehaene-Lambertz et al., 2005). Here we found no differential supramarginal activity in any of the tests. One reason might be that none of those studies used fricatives as critical stimuli. It can be that the supramarginal gyrus is involved in the phonological processing of certain speech sound categories only.

Distinct processing levels

It is theoretically possible that areas showing an adaptation effect in the phonological test (decreased activity in certain conditions as compared to other conditions) also show an adaptation effect in the acoustic-phonetic test. The finding of cortical areas that show the expected adaptation effect in both tests; or finding that a considerable proportion of the areas that showed the effect in one of the tests follow a similar pattern, would question the relevance and plausibility of separating speech processing levels. We expected, however, that this would not be the case, for two independent, complementary reasons. First, our phonological test was supposed to be free of acoustic-phonetic confounds; and second, the phonological processing level was characterized by its insensitivity to within-category differences (that is, differences between the SAME and CRSA conditions).

Our expectations were met. There were several regions showing the expected adaptation effect in each contrast, but no regions passed both the acoustic-phonetic and the phonological tests. That is, the processing levels described by our tests are anatomically distinct. Also, we found significant interaction between the regions with acoustic-phonetic pattern and the regions with phonological pattern, and it clearly suggested that the acoustic-phonetic and phonological processing levels as characterized by the activation patterns are functionally distinct. The functional distinction of areas determined in our two tests also suggested that in the CRSA and SAME conditions phonological areas did not show a significantly different level of activation, that is, within-category contrasts were lost. It is, according to Phillips (2001), a defining property of phonological categories. In short, these results mean that it is plausible to assume that separate speech-specific processing levels exist; they have neural correlates with separate localizations and can be characterized by different neural activation patterns.

On the basis of our results we can distinguish two levels of speech sound processing. The first level is clearly an earlier than phonological level: when being processed by these areas, speech sounds are not yet categorized phonologically. This is a prelexical, acoustic-phonetic processing level. The second level is a clearly phonological level: when being processed by these areas, speech sounds are either being categorized or are already categorized phonologically. This is the level of phonological processing. Although there is no logical reason to assume the involvement of lexical processes, it may be that some regions what we have identified as phonological processing areas may reflect lexical or postlexical stages. But it is reasonable to suppose that at least some of the phonological processing regions are involved in prelexical processing, given that compensation for coarticulation and hence the vowel-context effect are presumably learned so that they can assist in speech decoding during word recognition.

It is important to point out what we do claim and what we do not claim on the basis of this distinction concerning phonemic representations. We claim that our second level is involved in prelexical processing; and also that our second level is involved in phonological categorization. We do not claim, however, that there is a distinct prelexical level in speech processing that represents discrete phoneme categories.

What we suggest, in short, is that the separate localization of the neural correlates of acoustic-phonetic processing and phonological processing can be better described by our study than by those, which did not define a phonological processing level as strict as we did here. Nevertheless, to specify more precisely what various cortical areas underlying acoustic-phonetic and phonological processing are actually doing, and to clarify what further prelexical processing stages can be distinguished, will be subject of future research.

Methodological notes

Our study has demonstrated that the novel combination of a phonetic phenomenon (vowel-context effect) and a neuronal phenomenon (adaptation) resulted in an effective and powerful paradigm. We have also shown that the adaptation-fMRI method works efficiently with item-trains which are only 2 items long.

Individual fine-tuning has proven to be very useful in our study: it has significantly increased the behavioural effect that was exploited in the fMRI scanner. Speech perception studies that did not take intersubject variability into consideration, might fail to draw proper conclusions because of the decreased signal-to-noise ratio originated in the stimulus set and because of the ineffective exclusion of confounding effects in the design.

Acknowledgements

I thank my supervisors for their careful, promoting and demanding guidance – I have gained much more during our discussions than what this paper can reflect. I thank my fellow students in the master’s programme for sharing the pioneering experience. I also thank Holger Mitterer for his help with the speech sound stimuli. Finally, I thank my wife, Agnes for her patience and her continuous support, and my family in Hungary for bearing the lack of me.

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Abstracts

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Bilingual word representation: a multi-task fMRI investigation

Laura Menenti, Supervisor: Peter Indefrey

The Revised Hierarchical Model (Kroll and Stewart, 1994) assumes that words in a bilingual's languages have separate word form representations but shared conceptual representations. Two routes lead from an L2 word form to its conceptual representation: the word association route, where concepts are accessed through the corresponding L1 word form, and the concept mediation route, with direct access from L2 to concepts. The implications of the RHM for fMRI data were investigated. Proficient German-Dutch bilinguals carried out three tasks (voice decision, lexical decision and semantic decision) in their L1 and L2. LIFG and the left superior temporal gyrus were among the many areas responding more strongly to L2 than L1, while the right middle temporal gyrus was the only area responding more strongly to L1. Data from a previous behavioral experiment suggest that word association takes place in lexical but not semantic decision. An interaction between task and language was therefore expected in an area that processes L1 word forms. In a volume-of-interest analysis, such an area was found in the right posterior middle temporal gyrus. This area may therefore be involved in processing L1 word forms, in particular in the L1 processing that serves word association from L2.

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