Decreased BOLD responses in audiovisual processing

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Abstract

Audiovisual processing was studied in a functional magnetic resonance imaging study using the McGurk effect. Perceptual responses and the brain activity patterns were measured as a function of audiovisual delay.

In several cortical and subcortical brain areas, BOLD responses correlated negatively with the perception of the McGurk effect. No brain areas with positively correlated BOLD responses were found. This was unexpected as most studies of audiovisual integration use additivity and super additivity – that is, increased BOLD responses after audiovisual stimulation compared with auditory-only and visual-only stimulation – as criteria for audiovisual integration. We argue that brain areas that show decreased BOLD responses that correlate with an integrated audiovisual percept should not be neglected from consideration as possibly involved in audiovisual

Introduction

To perceive objects and events in the environment, organisms are equipped with different senses each specialized for the detection of certain physical aspects of the outside world. How the brain manages to combine information that enters through separate sensory channels and forms a unified percept of the outside world is still not well understood.

This study investigates which brain areas are involved in audiovisual (AV) binding using functional magnetic resonance imaging (fMRI) combined with behavioral measurements of the McGurk effect [1]. This effect is very suitable for studying AV binding, as the auditory percept of McGurk stimuli depends on whether AV information is integrated or processed separately. Stimuli that easily elicited the McGurk effect can for instance be made by dubbing the syllables /aba/ and /apa/ on movies of a mouth pronouncing the non-labials /aga/ and /aka/. As the consonants /b/ and /p/ are easily confused with the consonants /d/ and /t/ respectively [2], and because these are visually very similar to the visemes /g/ and /k/ [3], individuals sensitive to the McGurk effect will perceive /ada/ and /ata/ when listening to these incongruent stimuli [1]. Accordingly, the perception of /ada/ or /ata/ indicates that auditory and visual information is fused, whereas the perception of /aba/ or /apa/ indicates that auditory and visual information is processed separately.

In our experiment, the synchronization of the McGurk stimuli was varied to manipulate the strength of the McGurk effect (i.e. the strength of AV binding). We hypothesize that the brain areas involved in the AV binding process will show brain activation patterns correlated to the strength of the McGurk effect. Brain activation patterns as measured using the BOLD response, were therefore correlated to the strength of the AV binding as indicated by the perceptual responses.

To use a McGurk response as evidence for the fusion of auditory and visual information, it is important that the auditory stimulus is easily discerned. If not, the ‘changed’ auditory percept could simply be caused by the absence of auditory information. To ensure the audibility of the relatively brief and weak consonants in the speech stimuli, we used a sparse sampling paradigm [4,5]. Stimuli in this paradigm are presented in periods of relative silence between scanning periods. This ensures that the auditory stimuli are not masked by scanning noise and that the brain activation obtained depends on the stimulus and not on the scanning noise.

Methods

Participants

Twenty healthy volunteers with normal hearing and normal or corrected-to-normal vision participated in this study. None of them reported neurological or language impairments. Four (two females) out of the initial pool of 20 individuals were excluded from the fMRI analysis because of the absence of the McGurk effect as revealed in the psychophysical study. One individual did not complete the scanning experiment and one individual was excluded because of excessive motion during

scanning. We analyzed a total of 14 individuals aged between 22 and 45 years (five females). Before participation, individuals signed an informed consent form. The experiment was approved by the local Medical Ethical Committee, Groningen.

Stimuli

Movies were made with a digital video camera [Panasonic 3 CCD 24 digital zoom (Panasonic, One Panasonic Way, Secaucus, NJ07094, USA)] and external microphone (Sennheiser) in which a female Dutch speaker uttered the syllables /aba/, /aga/, /apa/ and /aka/. The video frame rate was 25 Hz and the sounds were digitized at a sampling rate of 48 kHz with 16-bit resolution. The movies were edited in Adobe Premiere (Adobe Premiere, 345 Park Avenue, San Jose, California, 95110-2704 USA). Incongruent stimuli were produced in which the audio signals of the /aba/ and /apa/ utterances were dubbed onto the videos of the speaker saying /aga/ and /aka/, respectively. Stimuli with AV delays ranging from – 510 ms (audio leads video) to + 420 ms (video leads audio) were prepared. The duration of the acoustic syllables was around 730 ms. The total length of the AV movies was 2.00 s with the auditory utterance temporally centred. Only the mouth was shown. To avoid onset and offset information because of the opening and closing of the mouth, the movies started and ended with an open mouth.

The psychophysical experiment used 14 AV stimuli with different delays (– 510, – 390, – 270, – 190, – 110, – 70, – 30, + 10, + 50, + 90, + 130, + 210, + 290 and + 410 ms). AV stimuli were selected for the fMRI experiment that resulted in minimal (– 510 and + 410 ms), intermediate (– 110 and + 210 ms) and maximal (+ 50 ms) strength McGurk effects. Furthermore, audio-only (A) stimuli (speech sounds /aba/ or /apa/ combined with a blank screen with a fixation cross), and visual-only (V) stimuli (a mouth pronouncing /aga/ or /aka/) were used. The baseline stimulus was a fixation cross on the screen.

Stimuli were presented in the psychophysical and the fMRI experiments against a continuously present pink noise background of 40 dB SPL. Along with the use of ear mufflers, which reduced the scanner noise by approximately 20 dB, this noise background was high enough to mask environmental noise during the relatively silent periods between the acquisitions. The signal-to-noise ratio of the auditory stimuli was 20 dB.

Psychophysical experiment

Individuals were seated in a sound insulated booth (Industrial Acoustic Company, Sohlweg 17, D-71372 Niederkrechten, Deutschland). Auditory stimuli were presented through headphones [Telephonics TDH-49P (Telephonics, 815 Broad Hollow Road, Farmingdale, New York 11735, USA)] and visual stimuli were presented on a computer screen at 60 cm distance. The two AV stimuli with 14 different AV delays were presented seven times in pseudo-random order, resulting in a total of 196 stimulus presentations per session. Individuals had to indicate whether they heard the sound /aba/, /ada/, /apa/ or /ata/ by pressing corresponding keys on a keyboard. Each individual performed three sessions.

Functional magnetic resonance imaging experiment

Functional MR scans were acquired using a 3 T scanner (Philips Intera, Philips Medical Systems, Eindhoven, The Netherlands). Prior to the functional images, a T1-weighted anatomical scan of the entire brain was produced (160 slices; field of view = 256 mm; scanning matrix = 256 256; transverse slice orientation; repetition time = 25 ms; echo time = 4.6 ms; flip angle = 30°). Functional MR images were acquired using echo planar imaging; (46 slices; slice thickness = 3.5 mm; field of view = 224 mm; scanning matrix = 64 64; transverse slice orientation; repetition time = 20 s; echo time = 35 ms; flip angle = 90°). Eight different stimulus conditions were used: 1 to 5 – AV with delays of – 510, – 110, 50, 210 and 410 ms; 6 – A; 7 – V; and 8 – baseline. Each experiment consisted of two functional series in which 74 volumes were scanned (18 volumes at baseline and 56 volumes where the

seven remaining stimulus conditions were presented eight times).

To avoid interference with scanner noise during acoustic stimulus presentation, we applied the sparse sampling method [4,5] with a relatively long repetition time of 20 s. Between two acquisitions, four stimuli of one stimulus condition were presented in pseudo-random order.

The entire experiment, including one anatomical scan and two functional series, lasted approximately 50 min. After each stimulus presentation, except after a baseline stimulus, individuals had to indicate what was said (/aba/, /ada/, /apa/ or /ata/) by pressing a button on a response box with their left or right index fingers, or their middle finger. The individuals had to respond within 1 s. During this second, a window with four buttons corresponding to the possible answers was displayed.

Visual stimuli were projected onto a screen located at the base of the scanner through a LCD projector (Barco G300j, President Kennedypark 35, 8500 Kortrijk, Belgie). Individuals viewed the movies through a mirror angled above the head. Auditory stimuli were presented through the headphones of the scanner's sound system.

Data analysis

The SPM2 software (<http://www.fil.ion.ucl.ac.uk/spm>) was used to process and analyze the data. The echo planar imaging images were realigned to the first volume in the run. These images were co-registered with the individuals' own anatomical images. They were normalized to the standard brain (MNI) and spatially smoothed using a Gaussian kernel with a full width half maximum of 10 mm.

For each individual, weighted effect sizes (con values) were obtained for all stimulus conditions (1–7) against baseline (8). A block design was used for this analysis, without convolution with the hemodynamic response function, as sparse sampling was used. To correlate the individuals' McGurk responses with the brain activation levels, a second level analysis was applied. The con values for conditions 1–5 were correlated to the average McGurk responses across individuals (the regressor is shown in the last graph of Fig. 1, black symbols). We also analyzed the data using the individual mean McGurk responses as regressors (see Fig. 1, 1–14, black symbols). To the resulting t-map, a threshold of $P = 0.001$ (cluster size $Z \geq 20$) was applied. For these regions, the con values per individual were extracted using the MARSBAR toolbox (<http://marsbar.sourceforge.net>).

Figure. 1 Behavioral results for the 14 individual participants that were included in the fMRI experiment. Mean results for all individuals with standard deviations are shown in the last graph. Audiovisual (AV) delay in the synchronization of the AV stimuli is shown on the horizontal axis. The vertical axis represents the percentage of McGurk responses, that is, the mean with standard deviation of the /ada/ and /ata/ responses. Grey symbols represent the psychophysical experiment data. Black symbols represent the data recorded during the fMRI experiment.

Results

Psychophysics

The mean percentage of McGurk responses – that is the mean of the /ada/ responses following auditory /aba/ stimulation and the /ata/ responses after auditory /apa/ stimulation – clearly depends on AV synchronization (Fig. 1). The McGurk response percentages peak in the AV delay range of – 30 to +130 ms. Four out of the initial pool of 20 individuals always heard /aba/ or /apa/, independently of the synchronization of the AV stimulus and were excluded from the fMRI experiment (data not shown in Fig. 1).

Functional magnetic resonance imaging

Psychophysics

We analyzed the whole brain and selected those brain areas in which the BOLD response showed significant correlation with the McGurk response percentages (last graph of Fig. 1, black symbols). Positive correlations were not found. Negatively correlated BOLD responses were found in the supramarginal gyrus, the superior frontal gyrus, parts of the cerebellum and the thalamus (see Table 1 and Fig. 2). All these brain areas show decreased con values after synchronous AV stimulation (see stimulus 3 in Fig. 2b) compared to the maximum response after monosensory stimulation (see stimulus 6 or 7 in Fig. 2b). All con values, except for those in the thalamus, are however positive compared to the rest condition. We also analyzed the fMRI-data using the individual average McGurk response as a regressor (Fig. 1, 1–14, black symbols). The results of this analysis are comparable with the results described (not shown).

Table 1. Brain areas in which the activation showed a significant negative correlation with the number of McGurk responses ($P = 0.001$, uncorrected, cluster size $Z 20$)

		MNI coordinates				Cluster size	<i>t</i> statistics	<i>P</i> value
		Lateralization	<i>x</i>	<i>y</i>	<i>z</i>			
1	Supra marginal gyrus	R	64	–40	36	63	4.16	<0.0005
2	Cerebellum vermis	R	12	–48	–24	25	4.16	<0.0005
3	Cerebellum vermis	L	–12	–44	–26	93	4.01	<0.0005
4	Superior frontal gyrus	L	–14	18	60	67	3.70	<0.0005
5	Thalamus	R	6	–10	2	20	3.82	<0.0005
6	Cerebellum	L	–24	–80	–18	281	3.71	<0.0005
7	Cerebellum	R	32	–72	–20	69	3.60	<0.0005

Figure 2. (a) Brain areas in which the BOLD response showed a significant negative correlation with the number of McGurk responses ($P = 0.001$, uncorrected, cluster size $Z 20$). See Table 1 for details of brain areas 1–7. (b) Mean con values (weighted effect sizes versus baseline) in brain areas 1–7 for the seven stimuli used. Error bars indicate standard errors. Stimuli: 1 = AV – 510 ms, 2 = AV – 110 ms, 3 = AV50 ms, 4 = AV210 ms, 5 = AV410 ms, 6 = A, 7 = V.

Discussion

Audiovisual binding as a function of audiovisual delay

The aim of this study was to correlate the brain activity patterns with a perceptual measure of AV binding as evoked by the McGurk effect. Our psychophysical experiment showed that four out of 20 individuals were insensitive to the McGurk effect. These individuals always perceived the auditory stimulus, /aba/ or /apa/, independently of AV synchronization, and apparently did not combine auditory and visual information in the identification task. Many other studies mention that typically 10–20% of individuals are insensitive to the McGurk effect (e.g. [6,7]) Gentilucci and Cattaneo [8] even report that over 50% of individuals are insensitive. Therefore, non-McGurk individuals form a substantial part of the normal population. In previous fMRI and PET studies that used the McGurk effect to study AV binding [7,9,10], individuals were not screened to see whether they were sensitive to the McGurk effect or not, which might have resulted in contamination of these brain imaging data by including individuals who did not bind AV information.

The psychophysical data as shown in Fig. 1 are comparable with those described in the literature [6,11], with prevalent AV fusion over temporal asynchronies from -30 to $+130$ ms. A window of AV integration of around 200 ms and with an asymmetrical prevalence for audio lags was also found in other studies, such as of a simultaneity judgment task [12] and in an electrophysiological study of the cat superior colliculus [13]. This asymmetric temporal window of integration could be caused by the difference in speed between mechanotransduction and phototransduction, acoustic mechanotransduction being around 60 ms faster than phototransduction [14]. Adaptation of the central nervous system to differences in the speed of light and sound resulting in an audio lag for sources at a distance from the perceiver has also been proposed to account for the facilitated AV integration of stimuli with leading visual stimulation [13].

Brain regions with BOLD responses correlated to AV binding

Our results show that the BOLD response is correlated to the strength of the McGurk effect in a select number of the brain areas: the supramarginal gyrus and superior frontal gyrus, thalamus and parts of the cerebellum. As the McGurk effect indicates AV binding, we hypothesize that these brain areas play a role in AV processing. Several other studies suggest that these brain areas are involved in AV or multisensory processing. The supramarginal gyrus are thought to be involved in AV speech perception [15,16], and the supramarginal gyrus and superior frontal gyrus in AV motion perception [17], whereas several nuclei of the thalamus function as multimodal gateways of sensory information [18]. Further, the cerebellum is mentioned in many studies of AV processing and is thought to be activated during asynchrony detection [19] and AV speech perception [20], for instance.

Decreased BOLD responses as a function of AV binding

Additivity and super-additivity are used as criteria to indicate AV integration sites [21,22] in most brain imaging studies. We were, however, unable to find the brain areas in which the BOLD response positively correlated with the number of McGurk responses. On the other hand, our results are comparable with those of Jones and Callan [10], Miller and d'Esposito [16] and Bernstein et al. [15], who for example found in the supramarginal gyrus larger BOLD responses to temporally offset or incongruent stimuli than to synchronized or congruent AV stimulation. Bernstein hypothesized that in these brain areas temporally incongruent stimuli would give rise to a larger BOLD response because of the mismatch between auditory and visual information. However, as the monosensory A and V stimuli produce BOLD responses that are comparable with those produced by the offset AV stimuli in our study, it appears that the offset stimuli do not cause increased BOLD responses. Instead, the synchronous, integrated AV stimuli seem to produce decreased BOLD responses. Assuming that decreased BOLD responses represent decreased neuronal activity, this finding agrees with recent evidence based on single-cell recordings in cats, that activity is decreased in a substantial part of multisensory neurons in response to simultaneous multimodal stimulation [23]. The positive β values found after auditory-only, visual-only and AV stimulation can be explained by the assumption that these brain areas also contain neurons that are activated during AV or monosensory stimulation.

So far, we can only speculate on why we did not find a single brain area in which the BOLD response increased with AV binding. One difference between this study and many other studies of AV integration is that we used an active AV integration task, rather than a passive paradigm. There is evidence that attention demanding tasks can result in decreased brain activity levels in a network of brain areas [24,25]. However, as the task and probably also attention did not vary with the different stimuli used

in our study, the decreased BOLD response is probably not related to attention. Another important difference between our study and almost all other studies of AV integration is that we used a sparse sampling paradigm. Although we are convinced of the usefulness of sparse sampling because of the importance of a well-defined and easily discerned auditory stimulus, the price paid for using this

paradigm is the reduction of statistical power and/or a longer duration for the scanning experiment.

Perhaps we were unable to identify relatively small positively-correlated BOLD responses because of the reduced statistical power of our experiment. However, it is clear that negatively-correlated BOLD responses were much stronger than the possible positive correlations.

Conclusion

Two cortical brain areas, the supramarginal gyrus and the superior frontal gyrus, part of the thalamus and parts of the cerebellum showed activity patterns that correlated with the perception of the McGurk effect, used to indicate AV binding. BOLD responses decreased with increased AV binding in all these brain areas.

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