Cognitive conflict and inhibition in primed dichotic listening

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Abstract

In previous behavioural studies, a prime syllable, was presented just prior to a dichotic syllable pair, with instructions to ignore the prime and report one syllable from the dichotic pair. When the prime matched one of the syllables in the dichotic pair, response selection was biased towards selecting the unprimed target. The suggested mechanism was that the prime was inhibited to reduce conflict between task-irrelevant prime processing and task-relevant dichotic target processing, and a residual effect of the prime inhibition biased the resolution of the conflict between the two targets. The current experiment repeated the primed dichotic listening task in an event-related fMRI setting. The fMRI data showed that when the task-irrelevant prime matched the task-relevant targets, activations in posterior medial frontal cortex (pMFC) and in right inferior frontal gyrus (IFG) increased, which was considered to represent conflict and inhibition, respectively. Further, matching trials where the unprimed target was selected showed activation in right IFG, while matching trials where the primed target was selected showed activations in pMFC and left IFG, indicating the difference between inhibition-biased selection and unbiased selection.

Keywords: Priming; cognitive conflict; inhibition; dichotic listening; event-related fMRI.

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The dichotic listening experimental task (Broadbent, 1954; Kimura, 1967) creates an ambiguous situation for the subject by presenting two simultaneous auditory stimuli, one in each ear. The task activates mental representations of both stimuli in the dichotic pair, and asking the participant to select one of them constitutes the cognitive challenge. Functional neuroimaging studies have shown that the consonant-vowel dichotic listening task activates the superior and middle temporal gyrus with a left-sided lateralization (Hugdahl, 2000; Hugdahl et al., 1999; Hund-Georgiadis, Lex, Friederici, & von Cramon, 2002; Jäncke, Buchanan, Lutz, & Shah, 2001; Jäncke, Specht, Shah, & Hugdahl, 2003; O'Leary et al., 1996; Sommer, Ramsey, & Kahn, 2001). It has also been reported that when participants are instructed to attend to either the left or right ear stimulus, correct reports from the attended side increase, indicating that response selection can be modulated by endogenous top-down attention (Bryden, Munhall, & Allard, 1983; Hugdahl & Andersson, 1986). Corresponding functional neuroimaging studies have shown additional activations in the inferior parietal and prefrontal cortical areas when subjects are instructed to attend to a side, interpreted as the involvement of selective attention (Hugdahl et al., 2000; Jäncke & Shah, 2002; Lipschutz, Kolinsky, Damhaut, Wikler, & Goldman, 2002; Thomsen, Rimol, Ersland, & Hugdahl, 2004).

In two previous studies (Sætrevik & Hugdahl, 2007a, 2007b) it has been shown that the responses in dichotic listening can also be modulated by a priming procedure. In these studies, a binaural prime syllable that participants were instructed to ignore was presented immediately before each dichotic syllable pair. On ”matching prime condition” trials, the ignored prime stimulus was the same syllable as one of the subsequently presented dichotic syllables, while on ”non-matching prime condition” trials, the ignored prime syllable was different from the two dichotic syllables (see Figure 1). Results showed that for ”matching prime condition” trials, the unprimed syllable (the syllable from the dichotic pair that was not the same syllable as the prime) was reported more frequently than the primed syllable. Separate experiments showed that the effect was evident both when the prime was presented as a spoken syllable and when presented as a written syllable (Sætrevik & Hugdahl, 2007b). The fact that the priming had an effect when it was cross-modal, indicated that the effect is not due to perceptual saliency, but relies on processes at a higher cognitive level. The priming effect was not significantly modulated by varying the interval between prime presentation and target presentation between being adjacent, a 500 ms interval and a 3000 ms interval (Sætrevik, unpublished). An additional study showed that the effect of priming interacted with instructions to attend to and report from one side (Sætrevik & Hugdahl, 2007a), further indicating a top-down mechanism. It was argued that there is cognitive conflict between the different response alternatives activated by the two target stimuli in the primed dichotic listening task. In this context we understand cognitive conflict to be the coexistence of incompatible information processes, and that the amount of cognitive conflict influences the application of cognitive control (Braver & Barch, 2006; Egner & Hirsch, 2005; Miller & Cohen, 2001). A dichotic presentation would in itself create conflict, as there are two inputs of equal (or close to equal) salience that can not both be processed to the same cognitive level. This assumption is supported by neuroimaging studies which show that compared to binaural presentations, dichotic presentations activate medial frontal structures (Thomsen et al., 2004), an area often associated with conflict detection (see e.g. Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Thus a primed dichotic listening task overall (whether prime matches or not) would evoke conflict due to the three syllable presentations needing a single response. Additionally, the perceptually most salient input is the task-irrelevant binaural prime, but this signal must be suppressed by cognitive control in favour of processing the task-relevant dichotic syllables. This suppression may cause cognitive conflict to be stronger when the task-irrelevant prime is the same syllable as one of the task-relevant dichotic targets (matching prime trials). In the terminology of Botvinick and colleagues (Botvinick, Braver, Barch, Carter, & Cohen, 2001), the cognitive conflict in this experiment would arise both as an effect of underdetermined responses (the left and right dichotic syllable are equally relevant signals) and of response override (the task-irrelevant binaural prime syllable is a more salient signal than the task-relevant dichotic syllables). Whereas underdetermined response conflict can be assumed to be largely stable across the experiment, response override conflict can be assumed to vary with prime-target match[1]. We have previously proposed (Sætrevik & Hugdahl, 2007a, 2007b) that in the primed dichotic listening situation the conflict between the salient prime and the ambiguous targets was resolved through inhibition of the prime signal. This is in line with Tipper’s account of data from a study by Milliken and colleagues (Milliken, Joordens, Merikle, & Seiffert, 1998), in which it was stated that “the act of ignoring a prime word probably involves selective inhibition” (Tipper, 2001, pp 333). As a consequence of the prime inhibition, the processing of a syllable similar to the recently inhibited prime syllable (the primed syllable in the dichotic target pair on ”matching prime condition” trials) will have a relative processing disadvantage, and the unprimed syllable is thus more

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[1] It could, however, also be argued that in the “matching prime” trials the inhibition of task-relevant information could reduce the underdetermined response conflict while increasing response override conflict. However, the current study was not designed to test this hypothesis, and it was no supported by indirect indicators (no significant increase in RT or fMRI signal for “non-matching prime condition” > “matching prime condition”, see results section).

likely to be reported. This would account for the previously reported behavioural effects (Sætrevik & Hugdahl, 2007a, 2007b). Such a model of cognitive control would involve cognitive mechanisms related to detecting cognitive conflict and inhibiting prime processing.

Several studies have shown that posterior medial frontal cortex (pMFC) areas, involving dorsal anterior cingulate cortex and more dorsal frontal areas, including the pre-supplementary motor area are involved in the detection and resolution of cognitive conflict (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Braver & Barch, 2006; Ridderinkhof, Ullsperger et al., 2004; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). Activation of right inferior frontal gyrus (IFG) on the ventrolateral frontal cortex has been found for tasks that require inhibition (Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Aron & Poldrack, 2006; Aron, Robbins, & Poldrack, 2004; Chikazoe, Konishi, Asari, Jimura, & Miyashita, 2007; Rubia, Smith, Brammer, & Taylor, 2003), and perturbing brain activity in right IFG with transcranial magnetic stimulation has been shown to cause an inability to inhibit initiated actions (Chambers et al., 2006). The present task shares some experimental and theoretical features with the concept of negative priming, in the sense that the task shows a behavioural effect of directing attention at a previously ignored item. It has been argued that negative priming is due to attention inhibition applied to resolve cognitive conflict (Houghton & Tipper, 1996; May, Kane, & Hasher, 1995; however, see Neill, Valdes, Terry, & Gorfein, 1992, for an alternative account; Tipper, 1985, 2001). It has been found that frontal lobe lesions result in positive priming effects in experimental tasks that would otherwise result in negative priming (Metzler & Parkin, 2000), and right hemisphere lesions have resulted in loss of negative priming (Stuss et al., 1999).

The aim of the present study was to follow-up on previous studies (Sætrevik & Hugdahl, 2007a, 2007b) by adding fMRI to study neuronal activation when subjects resolve the cognitive conflict caused by primed dichotic listening. As in the previous studies, subjects listened to dichotic syllables that were preceded by a binaurally presented prime syllable. In half of the trials, the prime syllable was the same as one of the two dichotic syllables (”matching prime condition”), and in half of the trials the prime syllable was different from both the dichotic syllables (”non-matching prime condition”). It was predicted that the ”matching prime condition” would increase cognitive conflict, reflected in pMFC activation, and attention inhibition, reflected in right IFG activation. It was further predicted that “matching prime condition” trials where the unprimed syllable was selected (trials that showed the expected behavioral effect of the manipulation) would be associated with additional inhibition and less conflict, and would thus show an increase in right-sided frontal cortex activation and a decrease in pMFC activation, compared to “matching prime condition” trials where the primed syllable was selected. These predictions are in line with the cognitive mechanisms previously proposed to be involved in the primed dichotic listening task (Sætrevik & Hugdahl, 2007a, 2007b), and the localization of these mechanisms according to current neuroimaging literature (for reviews, please see Aron, 2007; Ridderinkhof, Ullsperger et al., 2004).

Methods

Participants. Eighteen university students (10 female, 8 male) aged 21 to 29 participated in the study. All participants were right-handed (as measured by the Edinburgh Handedness Inventory, Oldfield, 1971), had Norwegian as first language, and had normal hearing when tested with audiometer screening. The participants had no history of neurological or psychiatric illness. Written informed consent was collected from all participants.

Stimuli. The experiment used consonant-vowel syllables consisting of the six stop-consonants and the vowel “a”, constituting the syllables /ba/, /da/, /ga/, /pa/, /ta/ and /ka/. The syllables were pronounced by a Norwegian male voice. The syllables had durations of 450-500 ms, and were digitized and edited for simultaneous sound onset. The prime stimulus was a binaural presentation of one of the six syllables. The targets two of the syllables (one in each ear) in a synchronized dichotic presentation. All 30 combinations of unique syllable pairs were used in random order.

Pre-test training. One to two days before the fMRI scanning, participants were pre-tested in a mock-MR situation (NordicNeuroLab Inc., www.nordicneurolab.com) with a similar experimental set-up as in the ensuing fMRI scanning. The purpose of this was to familiarize the participants to the experimental procedure and to train them to the response scheme. Participants were fitted with video goggles, headphones and two response grips (NordicNeuroLab), with buttons that corresponded to the six response alternatives on screen. The programming platform E-Prime (Psychology Software Tools, www.pstnet.com) was used for stimulus presentation and response collection. The pre-test consisted of three blocks of trials with different tasks, using the same stimuli and response scheme, but otherwise different from the actual experiment[2]. By the end of the pre-test session, all participants mastered the tasks with few errors and reported feeling confident about the task and the response scheme.

Trial procedure: In the fMRI setting, the trial procedure was similar to the procedure in a previous experiment (Experiment 1 in Sætrevik & Hugdahl, 2007b). Each trial consisted of the prime stimulus (500 ms), a 500 ms inter-stimulus-interval, the dichotic target stimuli (500 ms) and a response phase (1500 ms). Throughout the experiment a response screen displaying the six syllables as black text inside white boxes on a black background was visible in the goggles. The positions of the syllables on the screen were counterbalanced across participants. The participants were informed that they would hear two sounds in succession, and that they should not pay attention to the first sound, but report the identity of the second sound. Participants were encouraged to respond as soon as they had made a decision, due to the 1500 ms response deadline. An overview of the trial procedure is shown in Figure 1.

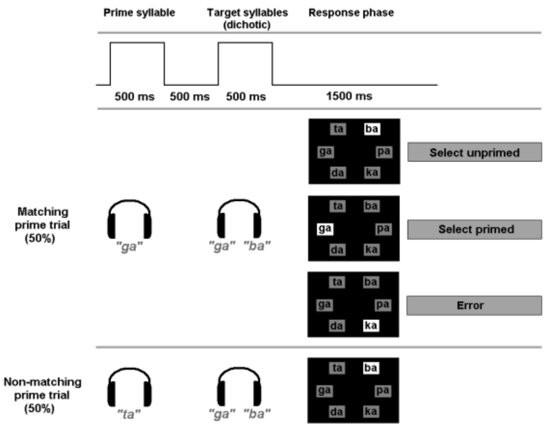

Figure 1: For each trial, a 450-500 ms single syllable was presented equally to both ears, and after a 500 ms inter-stimulus interval the dichotic stimuli were presented, which consisted of one 450-500 ms syllable presented in each ear. There was 1500 ms for response collection after the offset of the dichotic syllables. For ”matching prime condition”, the prime was the same as one of the syllables in the subsequent dichotic pair. For ”non-matching prime condition”, the prime was one of the four syllables not used in the dichotic pair.

There were a total of 396 trials. Of these, 132 trials were null-events, where the visual display remained on screen, but no prime or dichotic syllables were presented. Of the remaining trials, there were 132 ”matching prime condition” trials, where the prime syllable was the same as the left or right syllable in the subsequent dichotic pair, and 132 ”non-matching prime condition” trials, where the prime syllable was one of the four syllables not part of the subsequent dichotic target pair. The dichotic syllable pair thus had one primed syllable and one unprimed syllable in the ”matching prime condition”, while both

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[2] The pre-test consisted of the following tasks: Twelve trials presenting single binaural syllables with the task “report the syllable you heard”; 60 trials presenting dichotic syllables with the task “report the syllable you heard most clearly”; and 120 trials presenting two dichotic syllable pairs with the task “ignore the first pair and report the syllable you heard most clearly from the second pair”.

of the dichotic syllables were unprimed in the ”non-matching prime condition”. Examples of stimuli conditions are shown in Figure 1. Responses were scored according to whether the subjects reported the primed or the unprimed stimulus on the “matching prime condition” trials. Based on previous studies it was predicted that the unprimed syllable would be selected more often than the primed syllable. Examples of the scoring of trials according to responses can be seen in Figure 1. Response time (RT) was measured from the onset of the dichotic syllables.

fMRI data acquisition and statistical analysis: BOLD image acquisition was done on a 3.0T GE Tesla Signa Excite MR scanner. Initial 3D anatomy scanning was done with a T1-weighted MPRAGE sequence. Thereafter 402 BOLD-sensitive echo-planar image (EPI) volumes were acquired (first three scans were dummy scans that were discarded) with an acquisition time (TA) of 1.5 s and a repetition time (TR) of 3 s, thus allowing a 1.5 s silent gap between volume acquisitions for stimulus presentations. An EPI volume consisted of 25 slices based on a 64 x 64 voxel matrix, with 3 x 3 x 5 mm voxels. The DICOM images were converted to the ANALYZE image format using the nICE software (NordicNeuroLab). The EPI images were further pre-processed and analyzed using the Statistical Parametric Mapping software (SPM5, Wellcome Department of Cognitive Neurology, London, UK, www.fil.ion.ac.uk), running in MatLab version 6.5.1. (Mathworks Inc., Natick, MA, USA, www.mathworks.com). The pre-processing steps involved realignment and unwarping of all subsequent EPI volumes to the first volume of the time series to correct for head movements, normalization to the Montreal Neurological Institute (MNI) stereotaxic space, resampling to a voxel size of 2 x 2 x 2 mm, and smoothing with an 8 mm full-width-at-half-maximum kernel. Single subject analyses were performed, in which the “matching prime” and “non-matching prime” condition were modeled as separate conditions, and for “matching prime” condition an additional parameter was used in order to model trials where the primed or unprimed syllable was selected. For each subject, t-test contrasts were estimated for “matching prime condition” versus “non-matching prime condition”, and “matching prime” trials where the primed target was selected versus “matching prime” trials where the unprimed target was selected. The resulting individual contrast images served as input for subsequent random-effects analyses, where one-sample t-tests were used to explore group effects for the contrasts of interest. To evaluate the a priori hypothesis of pMFC and right-sided IFG involvement in the primed dichotic listening task, an uncorrected p-value of < .001 with an extend threshold of at least 10 voxels per cluster was used. The MRIcroN software (www.sph.sc.edu/comd/rorden/mricron) was used for anatomical localization and visualization of the fMRI results.

Results

Behavioral results: In the ”matching prime condition” there were significantly more responses selected the unprimed syllable than selected the primed syllable ($t(17) = 5.66$, $p < .001$, $M = 69.5$, $SD = 7.43$ vs. $M = 50.22$, $SD = 8.45$, Cohen’s $d = 2.42$). To illustrate with the ”matching prime condition” trial example shown in Figure 1, where the prime was */ga/* and the dichotic target syllables pair was */ga-ba/*, the results indicated that participants were more likely to respond */ba/* and less likely to respond /*ga*/. There was a low number of mistakes for both the ”matching prime condition” and the ”non-matching prime condition” ($M = 9.06$, $SD = 5.96$ and $M = 7.39$, $SD = 4.64$, respectively, $d = 0.31$), and no significant difference in number of errors between the two conditions.[3] There was a borderline significant trend ($t(17) = 2.04$, $p = .058$) for longer RTs for ”matching prime condition” compared to ”non-matching prime condition” ($M = 1241$ ms, $SD = 86$ vs. $M = 1220$ ms, $SD = 81$, $d = 0.25$). Within the ”matching prime condition”, responses selecting the unprimed syllable were significantly faster ($t(17) = -2.62$, $p < .05$) than responses selecting the primed syllable ($M = 1234$ ms, $SD = 94$ vs. $M = 1273$ ms, $SD = 112$, $d = 0.36$).

fMRI results: Contrasting ”matching prime condition” with ”non-matching prime condition” showed that two clusters in pMFC (one cluster in supplementary motor area and one cluster in medial superior frontal gyrus, border of rostral cingulate zone) and one cluster in right lateral IFG were significantly more activated when the prime matched one of the targets. The reverse contrast (”non-matching prime condition” > ”matching prime condition”) did not show any significantly activated voxels. Within the “matching prime condition”, contrasting trials where the unprimed syllable was selected with trials where the primed syllable was selected showed one cluster in the right IFG (orbital surface), two clusters in bilateral superior frontal gyrus, and two bilateral parietal clusters. The reverse contrast (“select primed syllable” > “select unprimed syllable”) showed three activated clusters in pMFC (one cluster involving pre-supplementary motor area and middle cingulate cortex, stretching into anterior cingulate cortex and two bilateral superior frontal gyrus clusters) and one cluster in left IFG and insula. Please see Table 1 and Figure 2 for detailed descriptions of activations, including the Brodmann areas involved.[4]

Discussion

When the ignored prime syllable was the same as one of the subsequent dichotic target syllables (”matching prime condition”), the unprimed target was more likely to be selected than the primed target was. This replicates previous findings (Sætrevik & Hugdahl, 2007a, 2007b) and is compatible with the interpretation that conflict increases when task-irrelevant information overlaps with task-relevant information, and that the response selection is influenced by the inhibited task-irrelevant information. The tendency for longer RT for ”matching prime condition” than for ”non-matching prime condition” also supports the proposition that repetition of the inhibited prime as target increases cognitive conflict, and that resolving the conflict constitutes additional effort for the cognitive system. The significantly shorter RT for ”matching prime" trials where the unprimed syllable was selected compared to ”matching prime" trials where the primed syllable was selected, indicates that responses selecting unprimed syllables were more efficient, possibly because resolving cognitive conflict through inhibition of the prime information is an adaptive solution of the conflict, or that responses selecting the primed syllable need additional time to overcome the inhibition.

”Matching prime condition” trials yielded increased activation in pMFC and right IFG compared to ”non-matching prime condition” trials (see Figure 2a). According to the proposed theoretical model, trials where the task-irrelevant prime syllable was repeated as one of the task-relevant dichotic syllables would induce higher levels of cognitive conflict than trials where task-irrelevant information was not repeated as the task-relevant information, and would thus require additional cognitive control resources. According to Botvinick and colleagues (2001), a cognitive control function requires a mechanism for detecting and registering cognitive conflict and another mechanism for resolving the conflict. From this perspective, the increase in pMFC activation for ”matching prime condition” may represent the increase in cognitive conflict (c.f. Ridderinkhof, Ullsperger et al., 2004; Ridderinkhof, van den Wildenberg et al., 2004), while the increase in right IFG activation may represent the increase in inhibitory resources necessary for resolving the

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[3] The behavioural data was also analyzed according to whether the location of prime match influenced which of the dichotic targets was selected. This is an alternative way to measure the priming effect on response selection, and is similar to the analyses done in previous studies (Sætrevik & Hugdahl, 2007a, 2007b). For "non-matching prime" trials, there were on average 13.1 ($SD = 9.7$) left syllable responses and 47.5 ($SD = 11.3$) right ear responses, thus showing a right ear advantage , when prime matched left target there were on average 9.7 ($SD = 9.3$) left syllable responses and 50.8 ($SD = 12$) right ear responses, and when prime matched right target there were on average 18.7 ($SD = 12.2$) left syllable responses and 47.06 ($SD = 14.2$) right ear responses. A 3x2 ANOVA (prime match left target / prime match right target / prime match neither target, response match left target / response match right target) showed a main effect and an interaction effect ($p < .001$), indicating that the right ear syllable was reported more often than the left ear syllable, and that the ratio of left and right ear responses varied with the priming match. Tukey post-hoc testing showed the number of left and right ear responses to be different for “prime match left target” and “prime match right target” trials ($p < .01$).

[4] Contrasting the activation on "prime match left target" trials with the activation on "prime match right target" trials did not yield any significant voxels.

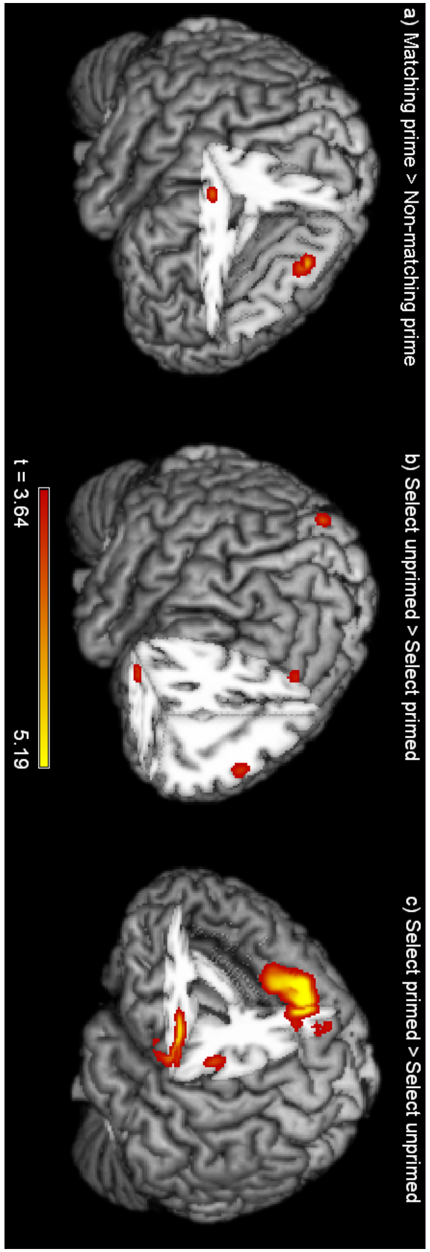

Figure 2: The figure shows some of the clusters activated above threshold (a) for the contrasts "matching prime condition" > "non-matching prime condition", (b) for "matching prime" trials where the unprimed syllable was selected > "matching prime" trials where the primed syllable was selected, and (c) for "matching prime"trials where the primed syllable was selected > "matching prime" trials where the unprimed syllable was selected.

a)

Coordinates X	Y	Z	t-value	z-value	Cluster size	Anatomical localization	Brodmann area
0	20	58	43586	35125	59	Supplementary motor area	6, 8
44	6	22	19450	22706	33	Right inferior frontal gyrus (opercular part)	6, 44, 48
-8	32	42	46844	17593	10	Medial superior frontal gyrus	8, 32

b)

Coordinates X	Y	Z	t-value	z-value	Cluster size	Anatomical localization	Brodmann area
42	34	-12	20911	23437	14	Right inferior frontal gyrus (orbital part)	47
36	-54	66	18719	22341	11	Right superior parietal gyrus	7
24	28	62	42461	15036	17	Right superior frontal gyrus	8
-40	-64	26	40121	13940	12	Left middle occipital gyrus	39
-12	58	30	40029	13210	20	Left superior frontal gyrus	9, 10

c)

Coordinates X	Y	Z	t-value	z-value	Cluster size	Anatomical localization	Brodmann area
-2	14	56	40034	15097	939	Supplementary motor area, middle cingulum and anterior cingulum	6, 8, 32, dorsal 24
4	18	46	40061	33298			
-10	25	35	39818	31837			
-40	18	6	13667	17989	330	Left insula and left opercular part of inferior frontal gyrus	47, 48
-46	12	2	35886	31107			
-46	8	24	44652	16132	64	Left opercular part of inferior frontal gyrus	6. 44, 48
20	10	54	44287	16132	10	Right superior frontal gyrus	8
-14	6	70	39998	13210	19	Left superior frontal gyrus	6

Table 1: Coordinates for significantly activated clusters (p < .001, uncorrected, clusters extend over ten voxels) in contrasts (a) between "matching prime condition" > "non-matching prime condition", (b) between "matching prime" trials where unprimed syllable was selected > "matching prime" trials where primed syllable was selected, and (c) between "matching prime" trials where primed syllable was selected > "matching prime" trials where unprimed syllable was selected.

conflict (in line with neuroimaging, lesion and perturbation findings from various tasks that require response inhibition and suppression, for a review, see Aron et al., 2004). By contrast, no voxels were significantly more activated for ”non-matching prime condition” than for ”matching prime condition”, as would have been expected from alternative bottom-up explanations, such as habituation, (c. f. Pfleiderer, Ostermann, Michael, & Heindel, 2002).

A cognitive control mechanism may resolve the cognitive conflict with varying degrees of efficiency across trials, and this variation may be reflected in the behavioral responses. One may thus attempt to decompose the pMFC and right IFG activation seen in the “matching prime > non-matching prime” comparison to distinguish areas involved in conflict detection from areas involved in conflict resolution through inhibition. Contrasting "matching prime" trials where the primed syllable was selected with "matching prime" trials where the unprimed syllable was selected should show which areas correlate with efficient cognitive control through involvement of inhibition. Three clusters in frontal cortex were more activated when selecting the unprimed syllable (see Figure 2b); two clusters in the superior frontal gyrus and one cluster in the orbital surface of right IFG. The two superior frontal gyrus clusters were positioned more dorsally and laterally than the pMFC activation seen in the “matching prime” > “non-matching prime” comparison. It has been proposed (MacDonald, Cohen, Stenger, & Carter, 2000; Ridderinkhof, van den Wildenberg et al., 2004) that while medial frontal cortex represents cognitive conflict, dorsolateral frontal cortex activation represents top-down maintenance and manipulation of information according to context, and is thus involved in the implementation and adjustment of cognitive control. As argued above, the activation in the right IFG may serve to implement an inhibition process. The fact that the right IFG activation was more ventral for the “select unprimed syllable” > “select primed syllable” contrast than it was for the ”matching prime condition” > “non-matching prime condition” contrast, may indicate that the IFG areas found in the two contrasts reflect different aspects of inhibition, or inhibition applied at different cognitive levels (e.g. stimulus discrimination vs. response selection). The activation seen in the bilateral parietal clusters may indicate the involvement of working memory (for a review, see Cabeza & Nyberg, 2000).

In "matching prime" trials where the predominant response pattern of selecting the unprimed syllable was not seen, response selection was to less extent determined by inhibition of the prime information. These trials would have higher levels of cognitive conflict compared to when the syllables were of unequal salience due to the recent inhibition biasing the selection. The RTs showed that these responses were indeed slower than responses selecting the unprimed syllable. Activation data for these trials (“select primed syllable > select unprimed syllable”) showed additional activations in pMFC and in left IFG. As can be seen in Figure 2c, the pMFC activation is more extensive than for the previous contrasts, which may indicate a higher level of cognitive conflict on these trials. An fMRI study (Thomsen et al., 2004) that compared dichotic listening (without priming) to binaural listening across attention instruction conditions found more activation in left than in right frontal cortex. Other studies where the response selection has not been biased by recent inhibition have also indicated left IFG activation (e. g. Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). The activation of left IFG in the current experiment may thus express some attention mechanism that selects between two stimuli of roughly equal salience.

To summarize, it has been proposed that the previously observed effect of selecting the unprimed rather than the primed syllable in the primed dichotic listening situation can be explained through the concepts of conflict and inhibition. When the task-irrelevant prime matches one of the targets, conflict increases, which is registered by mechanisms located in pMFC. Additional inhibitory mechanisms located in right IFG are recruited to resolve the conflict. Trials where the response was determined by inhibition of the prime showed right IFG and additional dorsolateral prefrontal cortex activation, representing inhibition and cognitive control, and had faster responses. In contrast, trials where the selection was not determined by inhibition would have more conflict, and showed increased RT, activation in left IFG and more extensive pMFC activations than in previous contrasts. The primed dichotic listening task has relatively simple instructions, uses natural stimuli with ecologically valid presentation mode, and demonstrates effects both in terms of response selection, RT and neuroimaging. The present task may thus be an interesting alternative for testing functions of cognitive control and inhibition in both healthy and clinical populations.

References

Aron, A. R. (2007). The neural basis of inhibition in cognitive control. *Neuroscientist, 13*(3), 214-228.

Aron, A. R., Fletcher, P. C., Bullmore, E. T., Sahakian, B. J., & Robbins, T. W. (2003). Stop-signal inhibition disrupted by damage to right inferior frontal gyrus in humans. *Nature: Neuroscience, 6*(2), 115-116.

Aron, A. R., & Poldrack, R. A. (2006). Cortical and subcortical contributions to stop signal response inhibition: role of the subthalamic nucleus. *Journal of Neuroscience, 26*(9), 2424-2433.

Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences, 8*(4), 170-177.

Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and cognitive control. *Psychological Review, 108*(3), 624-652.

Botvinick, M. M., Nystrom, L. E., Fissell, K., Carter, C. S., & Cohen, J. D. (1999). Conflict monitoring versus selection-for-action in anterior cingulate cortex. *Nature, 402*(6758), 179.

Braver, T. S., & Barch, D. M. (2006). Extracting core components of cognitive control. *Trends in Cognitive Sciences, 10*(12), 529-532.

Broadbent, D. E. (1954). The role of auditory localization in attention and memory span. *Journal of Experimental Psychology, 47*(3), 191-196.

Bryden, M. P., Munhall, K., & Allard, F. (1983). Attentional biases and the right-ear effect in dichotic listening. *Brain and Language*, *18*(2), 236-248.

Cabeza, R., & Nyberg, L. (2000). Imaging cognition II: An empirical review of 275 PET and fMRI studies. *Journal of Cognitive Neuroscience*, *12*(1), 1-47.

Chambers, C. D., Bellgrove, M. A., Stokes, M. G., Henderson, T. R., Garavan, H., Robertson, I. H., et al. (2006). Executive "brake failure" following deactivation of human frontal lobe. *Journal of Cognitive Neuroscience, 18*(3), 444-455.

Chikazoe, J., Konishi, S., Asari, T., Jimura, K., & Miyashita, Y. (2007). Activation of right inferior frontal gyrus during response inhibition across response modalities. *Journal of Cognitive Neuroscience, 19*(1), 69-80.

Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature: Neuroscience, 8*(12), 1784-1790.

Houghton, G., & Tipper, S. P. (1996). Inhibitory mechanisms of neural and cognitive control: applications to selective attention and sequential action. *Brain and Cognition, 30*(1), 20-43.

Hugdahl, K. (2000). Lateralization of cognitive processes in the brain. *Acta Psychologica, 105*(2-3), 211-235.

Hugdahl, K., & Andersson, L. (1986). The "forced-attention paradigm" in dichotic listening to CV-syllables: a comparison between adults and children. *Cortex, 22*(3), 417-432.

Hugdahl, K., Bronnick, K., Kyllingsbaek, S., Law, I., Gade, A., & Paulson, O. B. (1999). Brain activation during dichotic presentations of consonant-vowel and musical instrument stimuli: a 15O-PET study. *Neuropsychologia, 37*(4), 431-440.

Hugdahl, K., Law, I., Kyllingsbaek, S., Bronnick, K., Gade, A., & Paulson, O. B. (2000). Effects of attention on dichotic listening: an 15O-PET study. *Human Brain Mapping, 10*(2), 87-97.

Hund-Georgiadis, M., Lex, U., Friederici, A. D., & von Cramon, D. Y. (2002). Non-invasive regime for language lateralization in right- and left-handers by means of functional MRI and dichotic listening. *Experimental Brain Research, 145*(2), 166-176.

Jäncke, L., Buchanan, T. W., Lutz, K., & Shah, N. J. (2001). Focused and nonfocused attention in verbal and emotional dichotic listening: an FMRI study. *Brain and Language, 78*(3), 349-363.

Jäncke, L., & Shah, N. J. (2002). Does dichotic listening probe temporal lobe functions? *Neurology, 58*(5), 736-743.

Jäncke, L., Specht, K., Shah, J. N., & Hugdahl, K. (2003). Focused attention in a simple dichotic listening task: an fMRI experiment. *Brain Research Cognitive Brain Research, 16*(2), 257-266.

Kimura, D. (1967). Functional asymmetry of the brain in dichotic listening. *Cortex, 3*, 163-178.

Lipschutz, B., Kolinsky, R., Damhaut, P., Wikler, D., & Goldman, S. (2002). Attention-dependent changes of activation and connectivity in dichotic listening. *Neuroimage, 17*(2), 643-656.

MacDonald, A. W., 3rd, Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science, 288*(5472), 1835-1838.

May, C. P., Kane, M. J., & Hasher, L. (1995). Determinants of negative priming. *Psychological Bulletin, 118*(1), 35-54.

Metzler, C., & Parkin, A. J. (2000). Reversed negative priming following frontal lobe lesions. *Neuropsychologia, 38*(4), 363-379.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*, 167-202.

Milliken, B., Joordens, S., Merikle, P. M., & Seiffert, A. E. (1998). Selective attention: a reevaluation of the implications of negative priming. *Psychological Review, 105*(2), 203-229.

Neill, W. T., Valdes, L. A., Terry, K. M., & Gorfein, D. S. (1992). Persistence of negative priming: II. Evidence for episodic trace retrieval. *Journal of Experimental Psychology: Learning, Memory and Cognition, 18*(5), 993-1000.

O'Leary, D. S., Andreason, N. C., Hurtig, R. R., Hichwa, R. D., Watkins, G. L., Ponto, L. L., et al. (1996). A positron emission tomography study of binaurally and dichotically presented stimuli: effects of level of language and directed attention. *Brain and Language, 53*(1), 20-39.

Oldfield, R. (1971). The assessment and analysis of handedness: The Edinburg Inventory. *Neuropsychologia, 9*, 97-113.

Pfleiderer, B., Ostermann, J., Michael, N., & Heindel, W. (2002). Visualization of auditory habituation by fMRI. *Neuroimage, 17*(4), 1705-1710.

Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science, 306*(5695), 443-447.

Ridderinkhof, K. R., van den Wildenberg, W. P., Segalowitz, S. J., & Carter, C. S. (2004). Neurocognitive mechanisms of cognitive control: the role of prefrontal cortex in action selection, response inhibition, performance monitoring, and reward-based learning. *Brain Cognition, 56*(2), 129-140.

Rubia, K., Smith, A. B., Brammer, M. J., & Taylor, E. (2003). Right inferior prefrontal cortex mediates response inhibition while mesial prefrontal cortex is responsible for error detection. *Neuroimage, 20*(1), 351-358.

Sommer, I. E., Ramsey, N. F., & Kahn, R. S. (2001). Language lateralization in schizophrenia, an fMRI study. *Schizophrenia Research, 52*(1-2), 57-67.

Stuss, D. T., Toth, J. P., Franchi, D., Alexander, M. P., Tipper, S. P., & Craik, F. I. (1999). Dissociation of attentional processes in patients with focal frontal and posterior lesions. *Neuropsychologia, 37*(9), 1005-1027.

Sætrevik, B., & Hugdahl, K. (2007a). Endogenous and exogenous control of attention in dichotic listening. *Neuropsychology, 21*(3), 285-290.

Sætrevik, B., & Hugdahl, K. (2007b). Priming inhibits the right ear advantage in dichotic listening. *Neuropsychologia, 45*(2), 282-287.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci U S A, 94*(26), 14792-14797.

Thomsen, T., Rimol, L. M., Ersland, L., & Hugdahl, K. (2004). Dichotic listening reveals functional specificity in prefrontal cortex: an fMRI study. *Neuroimage, 21*(1), 211-218.

Tipper, S. P. (1985). The negative priming effect: inhibitory priming by ignored objects. *The Quarterly Journal of Experimental Psychology Section A, 37*(4), 571-590.

Tipper, S. P. (2001). Does negative priming reflect inhibitory mechanisms? A review and integration of conflicting views. *The Quarterly Journal of Experimental Psychology Section A, 54*(2), 321-343.