

Supplemental Material:
Manuscript N-D-06-01343, fifth and final revision
Selective amplification of stimulus differences during
categorical processing of speech

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1 Supplemental discussion of estimating isolated-stimulus activation from the responses to stimulus pairs

In the main manuscript, we discussed a potential problem facing our claim to have demonstrated neural amplification: we are seeking to demonstrate that the neural response to an across-category pair is greater than the sum of the responses to its parts, but we did not directly measure the neural responses to the isolated individual stimuli that made up that pair. Instead, in order to avoid alerting or expectation-based effects, all the stimuli were presented in pairs. We must therefore try to make inferences about these isolated subparts, based on our measurements of the pairs' activation.

The main text discussed the "worst-case scenario" in which identical-pair stimuli such as 4&4 undergo 100% habituation, such that the response to the second stimulus in the pair is reduced to zero. In this situation, the total pair-elicited activity could never be less than the activity caused by one isolated stimulus. In shorthand: $4 \leq 4&4$. Therefore, $4 + 4 + 7 + 7 \leq 4&4 + 4&4 + 7&7 + 7&7 = 2 \times (4&4 + 7&7)$. This means that even the case of 100% habituation restricted exclusively to identical-pair stimuli would produce the appearance of amplification by at most a factor of two. For that reason, we present data in Supplemental Figures 3 and 4 showing that the across-category 3-step pairs produce more than twice as much activation as their corresponding identical-pairs. This result is stronger than any habituation-induced artifact could produce.

However, it could be argued that this discussion does not exhaust the full range of possibilities. In particular, it might be the case that the second stimulus in the pair could have its activation reduced not by

a passive adaptation process, which would reduce the activation level to zero but not below, but instead by an active inhibitory process, which could push the activation down to become negative. In such a circumstance, the brief argument above would be insufficient.

We therefore consider below the full range of possible scenarios in detail, and also discuss whether these hypothesised scenarios are consistent with empirical studies of auditory masking and suppression.

However, before discussing these various cases, and in particular the scenario, which turns out to be somewhat problematic, where the second stimulus is actively suppressed to become below zero, it is worth first considering whether such a circumstance has been found empirically to occur.

Is it empirically the case that pairs of auditory stimuli have been found to be actively suppressed, such that the second stimulus in the pair becomes negative?

In the discussion below, difficulties arise only in the hypothesised circumstance in which the second stimulus in an identical-pair such as 4&4 is suppressed to produce activation that is below zero. Even in this circumstance, we will argue, the resulting within-category active suppression is functionally equivalent to across-category active amplification.

However, such considerations are moot if it is empirically the case that pairs of auditory stimuli are not actively suppressed in this way. Our data cannot directly address that question, as we only measured the responses elicited by pairs of stimuli, as opposed to having access to the individual responses elicited by each of the stimuli within that pair. Other published studies, though, have examined this issue, using faster techniques than fMRI. Animal single-neuron neurophysiological recordings and human MEG and psychophysical studies can all provide relevant data, and indeed all three techniques show that the second stimulus within a pair produces attenuated but not actively suppressed signals. Moreover, they show that the attenuation of the second stimulus occurs only for much shorter ISIs than the 500ms interval that separated the two stimuli within each pair presented in our study.

Data from such studies are reproduced in Supplementary Figure 7. Figure 7A is the most directly comparable to design used in our study: using MEG, McEvoy et al. (1997) studied the neural responses to pairs of identical tones, presented with a between-tone ISI of 210ms. Because MEG has very high temporal resolution, they were able to measure the responses to each of the two tones separately. Moreover, they also recorded neural responses to single tones presented in isolation, and were able to compare them to the responses from the two stimuli presented in a pair. In contrast, our slow fMRI recordings can only measure the joint response to two stimuli within a pair together, despite the fact the two stimuli within our pairs were separated from each other by the longer ISI of 500ms.

Their results are shown in Supplementary Figure 7A, which is extracted from Figure 1 of their paper. The two panels correspond to recordings from left and right auditory cortex, respectively. In both hemispheres, it can be seen that the second tone within the pair produces a positive response that is somewhat attenuated in strength compared to the response to the first tone, but is nonetheless positive. Two responses to paired-presentations are shown: one in which the pairs are separated by 2.6s (the dotted line), and one in which the pairs are separated by 0.9s. In all cases, the *within-pair* ISI separating the two tones

was held fixed at 210ms.

From the McEvoy et al. (1997) study, we can conclude that when two sounds are presented in a pair 210ms apart, the second sound is not actively suppressed, but instead is only slightly weakened. At longer ISIs, even less weakening would take place. Thus, at the 500ms ISI used in our study, it can be concluded that it is extremely unlikely that the second stimulus in the pair would be suppressed not only to having zero activation, but indeed beyond that to have negative activation.

A different type of neural data is shown in Supplementary Figure 7B, which reproduces Fig.10 from the study of forward masking in cat auditory cortex by Brosch & Schreiner (1997). As with the study by McEvoy et al. (1997), they presented pairs of tones separated by a range of different ISIs. For each cortical single-unit and multi-unit recording that they made, they then calculated the maximum ISI at which suppression of the neural response to the second tone was observed. As can be seen from Supplementary Figure 7B, the majority of the neurons stopped showing any forward masking effects when the ISI was longer than around 200ms, and no neuron showed any masking for an ISI longer than 440ms. Again, this suggests that for the 500ms ISI used in our study, it is very unlikely that the second stimulus within our pair would be masked at all, let alone that it would be actively suppressed to produce negative activation.

Finally, human psychophysical studies of auditory forward and backward masking also reveal the range of ISIs for which masking occurs. For both forward and backward masking, the 500ms used in our study is outside of this range. Supplementary Figure 7C shows the degree of forward masking as a function of ISI. It is reproduced from Figure 10.17 in the book by Gelfand (2004), and plots the results from three separate studies on the same axes: the squares are from Wilson & Carhart (1971), the triangles are from Smiarowski & Carhart (1975), and the circles are from Weber & Moore (1981). Data showing the degree of backward masking are reproduced in Supplementary Figure 7D, from Kallman & Massaro (1983). As can be seen from these psychophysical data plots, the range of ISIs for which masking occurs is very similar to the range observed neurophysiologically in cat auditory cortex. In all cases, masking has completely disappeared by around 400ms. These converging and independent types of evidence together justify confidence that the 500ms interval separating the two stimuli within each pair in our study should be more than sufficient to prevent masking or any form of active suppression below baseline.

What must be shown in order to demonstrate neural amplification

In spite of the above empirical considerations, one may nonetheless consider the full range of hypothetical circumstances, including those which run contrary to published experimental studies. Such a discussion of all the different possible cases now follows.

The claim that we seek to demonstrate is the following: 3-step pairs that straddle the category boundary are neurally amplified, meaning that the neural response to the pair is greater than the sum of the responses to its constituent subparts.

Let us write the hypothesised isolated activation of the stimulus 4 presented on its own as 4_{iso} . What we recorded was the activation elicited by the pair 4&4. This activation can be written as $4_1 + 4_2$. These are the responses, which were not measured and are hence unknown, to the two stimuli in the pair.

If we had measured the responses to isolated stimuli, then the question of whether the 3-step pair response is greater than the sum of the responses to its constituent subparts could be addressed by directly testing the following: $4\&7 + 7\&4 > 4_{iso} + 4_{iso} + 7_{iso} + 7_{iso}$

However, because we measured the responses to the pairs 4&4 and 7&7, which in the terminology above we can write as $4_1 + 4_2$ and $7_1 + 7_2$, we therefore need to ask how these relate to the values of 4_{iso} and 7_{iso} .

The two stimuli within each pair were separated from each other by 500ms of silences. Auditory backward masking disappears after a 350ms inter-stimulus interval (see Supplementary Figure 7 and its associated text below), so this 500ms gap is more than enough to prevent it. Hence, the response to the first element of the pair, namely 4_1 , is no different from 4_{iso} .

The key question therefore becomes: what happens to 4_2 ? This neural response to the second element in the pair can be written as an unknown constant, k , multiplied by the response to the isolated stimulus: $4_2 = 4_{iso}k$

There are four possible cases, which we will now go through in detail.

Case 1: $k = 1$, so that 4_1 and 4_2 both behave just like 4_{iso}

This is the simplest and least problematic case. In this instance, $4\&4 = 4_{iso} + 4_{iso}$. Therefore, to demonstrate neural amplification, it is enough to show that $4\&7 + 7\&4 > 4\&4 + 7\&7$

In the terminology used in the manuscript, in this simple situation we merely need to show that $X > Y$, where $X = 4\&7 + 7\&4$ and $Y = 4\&4 + 7\&7$. Thus, in Case 1 we do not need to worry about demonstrating the stricter inequality $X > 2Y$ that is discussed in the manuscript, and also below.

In order to see that $4\&7 + 7\&4 > 4\&4 + 7\&7$, it is enough to observe in Figure 5 of the main text that the red line is higher than the blue line near the category boundary.

Case 2: $0 < k < 1$, so that 4_2 is reduced by neural adaptation, but is still greater than zero

This is the scenario discussed in the main text.

Recall from above, that we are defining 4_1 and 4_2 as the two unknown subparts of the response 4&4, i.e. $4\&4 = 4_1 + 4_2$. In the present case that we are considering: $4_2 > 0$. Therefore, $4_1 + 4_2 > 4_1$, which is equivalent to the statement that $4\&4 > 4_1$.

To summarise: because $4_2 > 0$, we are able to establish that the measured quantity 4&4 is an upper-bound for 4_1 , which we do not measure and which we must therefore estimate.

What we need to show is that $4\&7 + 7\&4 > 4_{iso} + 4_{iso} + 7_{iso} + 7_{iso}$. To be conservative, we will take the larger value, 4_1 , as our estimate of 4_{iso} . Similarly for 7_{iso} . Therefore, the inequality that we need to demonstrate becomes: $4\&7 + 7\&4 > 4_1 + 4_1 + 7_1 + 7_1$.

Because $4\&4 > 4_1$, it follows that $2 \times 4\&4 > 4_1 + 4_1$. Hence, we can establish the inequality $4\&7 + 7\&4 >$

$4_1 + 4_1 + 7_1 + 7_1$ if we can show that $4\&7 + 7\&4 > 2 \times (4\&4 + 7\&7)$. This is the $X > 2Y$ scenario discussed in the paper.

Case 3: $k > 1$, i.e. 4_2 increases due to some kind of neural facilitation, such that $4_2 > 4_1$

In this case, some unknown neural process increases the second element in the $4\&4$ pair such that it is actually stronger than 4_{iso} . Then the quantity that we measured, namely $4\&4$, is actually an *over-estimate* of $4_{iso} + 4_{iso}$, so by establishing that $4\&7 + 7\&4 > 4\&4 + 7\&7$ we have more than demonstrated the inequality with isolated stimuli.

Note that this follows purely from the inequality $4_2 > 4_1$, and is independent of whether these values are greater than or less than zero. Any “rising pair” of this sort results in an over-estimate of $4_{iso} + 4_{iso}$ and therefore meets our requirements, regardless of whether the pair rises from negative to positive, negative to less negative, or positive to even more positive.

Case 4: $k < 0$, so that 4_2 is reduced by neural adaptation or inhibition to become weaker than 4_1 , and indeed 4_2 becomes less than zero

In Case 2 above, our argument rested upon being able to establish a measurable upper-bound for 4_{iso} . This upper-bound allowed us to state conditions in which neural amplification could be shown to take place. However, that upper-bound estimate required that 4_2 be greater than zero, and in the present case we are considering the situation where $k < 0$, with the result that $4_2 < 0$.

Recall from above that $4\&4 = 4_1 + 4_2$. Given that $4_1 = 4_{iso}$ and $4_2 = 4_{iso}k$, this can be written as $4\&4 = 4_{iso} + 4_{iso}k = (1 + k)4_{iso}$.

In Case 2, we could show that $4\&4 > 4_{iso}$, but now in Case 4 the fact that $k < 1$ means that $4\&4 < 4_{iso}$. Therefore, the response to the pair $4\&4$, which we do measure, can no longer be used as an upper bound estimate of 4_{iso} , which we do not measure.

However, that does not mean that we lack any estimate of 4_{iso} . It means that our estimate must be a function of the unknown variable k , about which we only know that $k < 0$. From above, the estimate is: $4_{iso} = 4\&4/(1 + k)$. Similarly, $7_{iso} = 7\&7/(1 + k)$. Therefore, stated in terms of the responses that we measure and the unknown negative quantity k , the inequality that would demonstrate neural amplification becomes: $4\&7 + 7\&4 > (4\&4 + 7\&7) \times 2/(1 + k)$.

It can be seen that the “worst-case scenario” discussed in the main text, in which 100% neural adaptation reduces 4_2 to zero, can be described by setting $k = 0$. This yields the result described above of needing to show that $4\&7 + 7\&4 > 2 \times (4\&4 + 7\&7)$.

In the active-suppression scenario considered here, different values of k would require us to demonstrate different inequalities. For example, if stimuli are actively suppressed to become half as negative as they were formerly positive, i.e. if $k = -1/2$, then we would need to show that $4\&7 + 7\&4 > 4 \times (4\&4 + 7\&7)$.

However, an estimate that is a function of an unknown variable is of no use to us. We must therefore consider more closely the very situation that prevents us from making our upper-bound estimate: identical-pair stimuli such as 4&4 are suppressed so much that the second stimulus in the pair becomes negative. These identical-pair stimuli are, of course, all within-category pairs. Therefore, rather than demonstrating the amplification of between-category pairs, we would instead have a case of the suppression of within-category pairs.

The functional equivalence of across-category amplification and within-category suppression

We now present an argument seeking to show that, in terms of how the brain performs categorical processing, these two possibilities, namely across-category amplification and within-category suppression, are functionally equivalent. There are two key questions: whether the neurons are carrying out an active process, rather than merely a passive one, and what we can conclude about how categorical processing functions in the brain.

As was shown above, if $k > 0$, then our data demonstrate that, in across-category pairs, the whole is actively greater than the sum of its parts. In Case 4 above, we considered the hypothetical circumstance in which $k < 0$, i.e. such that, in within-category pairs, the whole is actively less than the sum of its parts.

In the former case, this active process involves pushing across-category pairs up, and in the latter case it actively pushes within-category pairs down. Thus, in terms of how the brain implements categorical processing, both cases describe the occurrence of an active process, rather than a passive one, and in both cases this active process differentiates across-category from within-category pairs. For every across-vs.-within category distinction made by the process in which $k > 0$, the same distinction is made by the process in which $k < 0$. In terms of how the brain processes information, the two statements are therefore functionally equivalent.

2 Supplemental discussion of possible edge-effects, and their relation to neural adaptation and amplification

In the main text of the paper, we argued that if “edge-effects” in our stimulus set were to cause additional neural adaptation to occur near the centre of the phonetic continuum, then this would in fact strengthen the evidence that neural amplification is taking place.

A specific example from the data may help to illustrate this point. Consider, for example, the plots in Fig. 4A in the main text, showing fMRI activation in the supramarginal gyrus. The blue curve of “position-responses” on the left shows that stimuli near the category boundary, in the middle of the 1-to-10 /ba/-/da/ continuum, tend to produce less activation when presented in identical pairs such as 4&4, 5&5 etc. than the stimuli near the ends of the continuum, such as 1&1 and 10&10. This gives rise to the upright-V shape of the blue curve. However, the red curve of “contrast responses” to pairs of stimuli separated by three steps along the continuum, such as 1&4, 3&6, 7&10 etc., shows precisely the opposite pattern,

namely an inverted-V shape. When the stimuli are combined together in these contrasting 3-step pairs, the pairs near the centre of the continuum, e.g. 4&7, produce the most activation, not the least.

Such a pair sits the peak of the red “contrast response” curve. The raw ingredients of this strongly-activating pair, in this case the stimulus 4 and the stimulus 7, are the very ingredients which when presented in the non-contrasting pairs 4&4 and 7&7 produce the weakest activation. The only difference is in how the stimuli are paired. When presented in identical pairs such as 4&4, only weak activation arises. When presented in contrasting 3-step pairs that straddle the category boundary, neural amplification boosts these weak ingredients into a strong neural response. If an edge-effect is occurring, causing additional adaptation of the stimuli near the continuum centre to be even weaker than otherwise, then the amplification required to generate the strong observed 4&7 activation must be even more powerful than otherwise. Thus, if such edge-effect adaptation is occurring, then it strengthens the evidence that neural amplification is taking place.

In order to directly examine any possible consequences of the continuum-centre stimuli being presented more frequently than the edge stimuli, we replotted the “position-response” neurometric curves of Figs. 4 and 5 in the main text, but now without aligning them with respect to each subject’s perceptual category boundary. Thus, the x-axis in these curves is simply the raw phonetic continuum, from 1 to 10. This makes it easier to see whether there is any sudden drop-off in activity when transitioning from the edge-stimuli 1, 2, 3, 8, 9 and 10 to the centre-stimuli 4, 5, 6 and 7, which participate in twice as many 3-step pairs. These replotted neurometric curves are shown in Supplemental Figures 5 and 6. As can be seen from these figures, there is no such sudden drop-off at the 3-to-4 and 7-to-8 transition points, but instead a gradual reduction in activity from the edges to the centre. Such a gradual reduction could not be caused by the sudden switch in the number of 3-step pairs in which a stimulus participates.

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Supplemental Figure captions

Caption to Supplemental Figure 1:

Data illustrating that the six categorically processing regions respond more to the 3-step pairs that are perceived as different than to the 3-step pairs that are perceived as the same, i.e. that they regions respond more to across-category than to within-category pairs. **Panel (A):** The individual subjects' neural responses to the 3-step pairs that they perceive as the same, and those that they perceive as different. Each line plots the data for one subject in one ROI, with the left end of the line being the response to perceived-as-same pairs, and the right end the response to perceived-as-different. Thus, ascending lines indicate subjects for whom the perceived-as-different pairs elicited greater neural activity. It can be seen that a large majority of subjects exhibited this pattern, with at most three subjects showing less activity for perceived-as-different 3-step pairs, in any given ROI. The letters labeling the ROIs are as follows: (a): Left supramarginal gyrus (b): Right cerebellum (c): Anterior cingulate (d): Left parietal cortex (e): Left middle frontal cortex (f): Right prefrontal cortex. **Panel (B):** The group-average different-minus-same activity, in each of the six categorically processing regions. Error bars show across-subjects standard error of the mean. The ROI labels are as above.

Caption to Supplemental Figure 2:

Overlaid neurometric curves, as in Figure 5 of the main text, but now for the anatomically-defined ROIs of lower-level auditory areas. In these overlaid plots, the red curves of responses to 3-step pairs are the same as in Figure 6 from the main text, but the blue curves now show the average neural responses to the identical-pairs made out of the corresponding constituent subparts. For example, where a red 3-step curve shows the average of the responses to 4&7 and 7&4, the blue curve at the same x-position shows the average of the responses to 4&4 and 7&7. Error bars show across-subjects standard error of the mean.

Caption to Supplemental Figure 3:

Plots illustrating a strict test of whether amplification is taking place, in the "worst-case scenario" extreme case of 100% habituation making the identical pairs appear artifactually weak. These plots show the value of $X - 2Y$, where X is equal to a voxel's average activation at a given position along the continuum of 3-step pairs, e.g. the average activation elicited by the stimuli 4&7 and 7&4, and Y is equal to the voxel's average activation elicited by the corresponding identical pair stimuli, in this case 4&4 and 7&7. Error bars show across-subjects standard error of the mean. When the black $X - 2Y$ curve is greater than zero, shown by the red dotted line, then neural amplification is taking place even in this hypothesised worst-case scenario. It can be seen that such amplification does take place near the category boundary, for all six of the categorically processing regions.

Caption to Supplemental Figure 4:

"Worst-case scenario" plots of the neural amplification value $X - 2Y$, as in Supplemental Figure 3, but now showing the values for the four anatomically-defined ROIs of lower-level auditory areas.

Caption to Supplemental Figure 5:

Neurometric curves for the six categorically processing regions, plotted without any realignment to the subjects' perceptual thresholds. These plots allow a more direct inspection of whether there is any sudden drop-off in neural activity at the 3-to-4 and 7-to-8 transition points of the blue "position-response" curves, corresponding to the change from stimuli that participate in only one 3-step pair to stimuli that participate in two. It can be seen that there is no such sudden drop-off in activation; instead, many of the regions show a relatively smooth reduction in activity at the edges of the continuum. This reduction starts already at the very outermost edges of the continuum, at stimuli 1 and 10, even though there is no change in how frequently the stimuli are presented until stimulus 4, from the left, and stimulus 7, from the right. Whatever the cause of this reduction might be, it cannot therefore be the change in how many 3-step pairs the stimuli are part of. **(A):** Left supramarginal gyrus **(B):** Right cerebellum **(C):** Anterior cingulate **(D):**

Left parietal cortex **(E)**: Left middle frontal cortex **(F)**: Right prefrontal cortex

Caption to Supplemental Figure 6:

The neurometric curves for the anatomically defined ROIs, showing the same data as Fig.6 from the main text, but now without aligning the curves to each subject's perceptual category boundary. As with the neurometric curves shown in Supplemental Fig.5, no sudden drop-off occurs at the 3-to-4 and 7-to-8 transition points.

Caption to Supplemental Figure 7:

(A): MEG data from McEvoy et al. (1997), showing that two tone stimuli separated by an ISI of 210ms both produce positive neural responses. The two panels correspond to recordings from left and right auditory cortex, respectively. **(B)**: Neurophysiological data from the study of forward masking in cat auditory cortex by Brosch & Schreiner (1997). The majority of the neurons stopped showing any forward masking effects when the ISI was longer than around 200ms, and no neuron showed any masking for an ISI longer than 440ms. **(C)**: Human psychophysical data showing the degree of forward masking as a function of ISI. It is reproduced from Figure 10.17 in the book by Gelfand (2004), and plots the results from three separate studies on the same axes: the squares are from Wilson & Carhart (1971), the triangles are from Smiarowski & Carhart (1975), and the circles are from Weber & Moore (1981). **(D)**: Data showing the degree of backward masking as a function of ISI, from Kallman & Massaro (1983).

Supplemental Figures

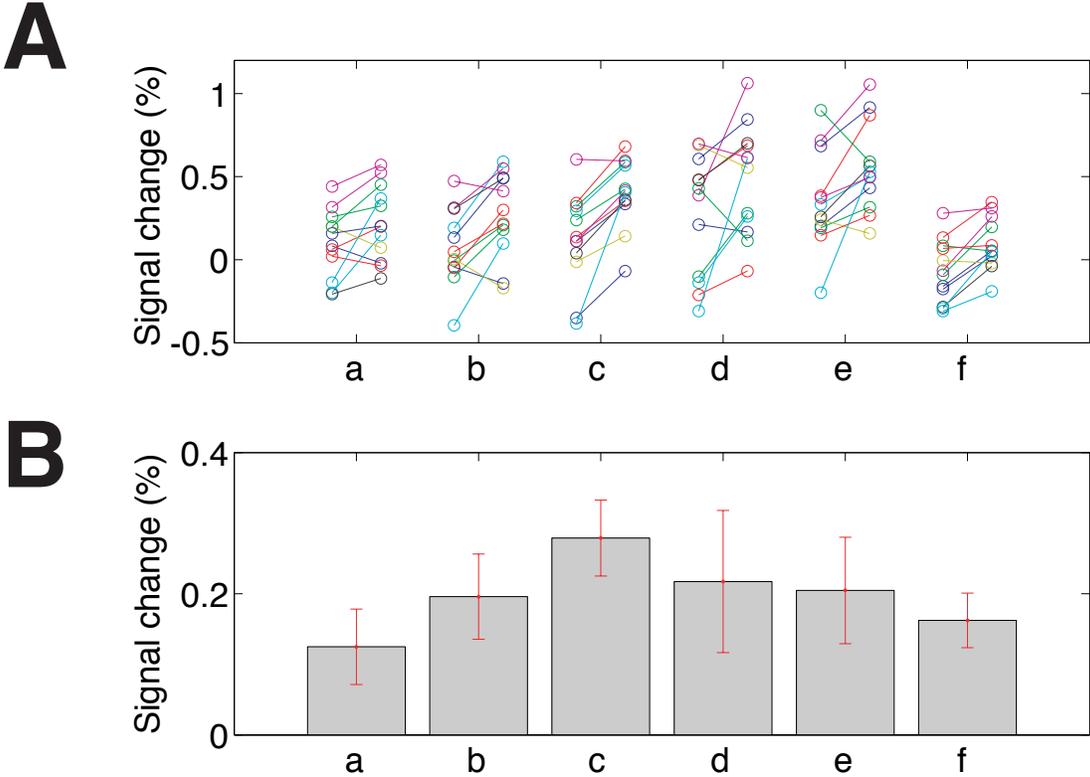


Figure 1:

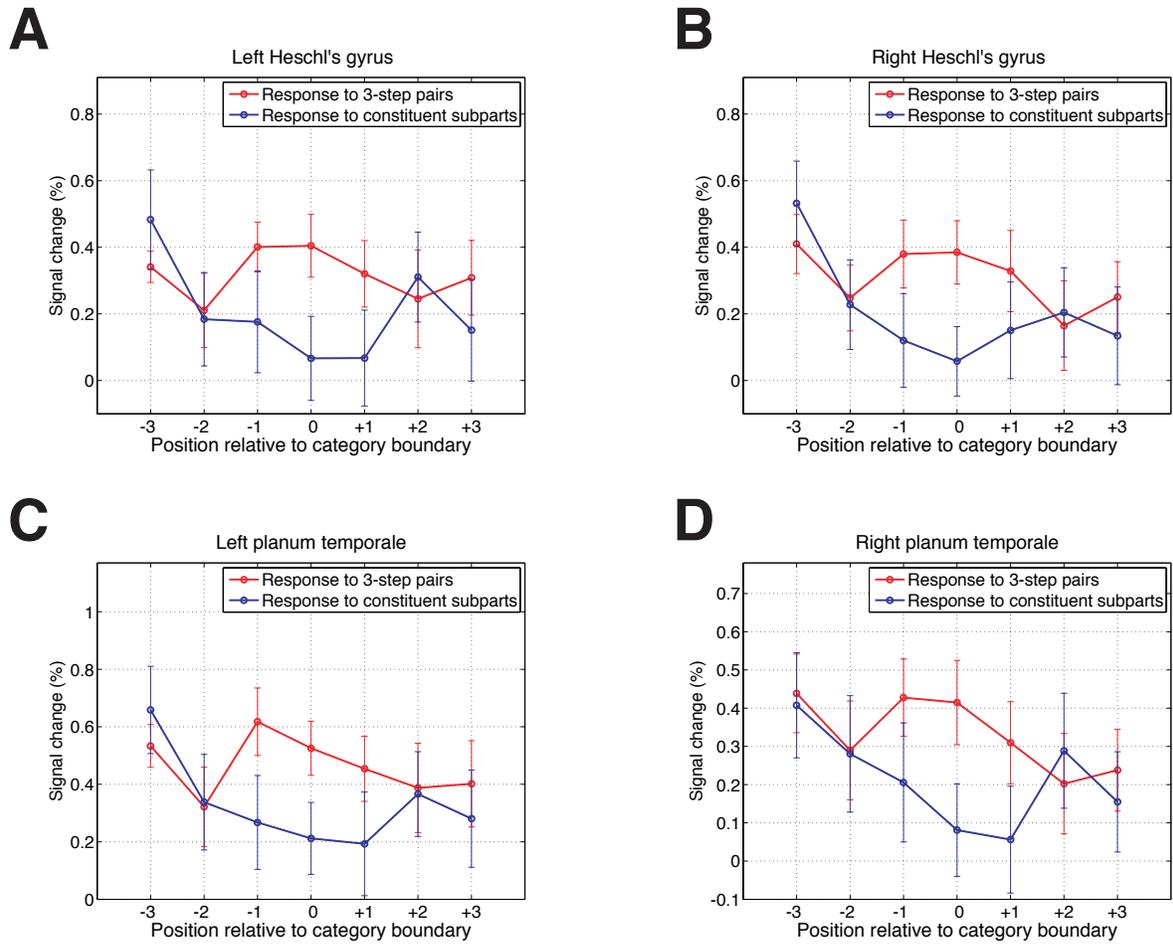


Figure 2:

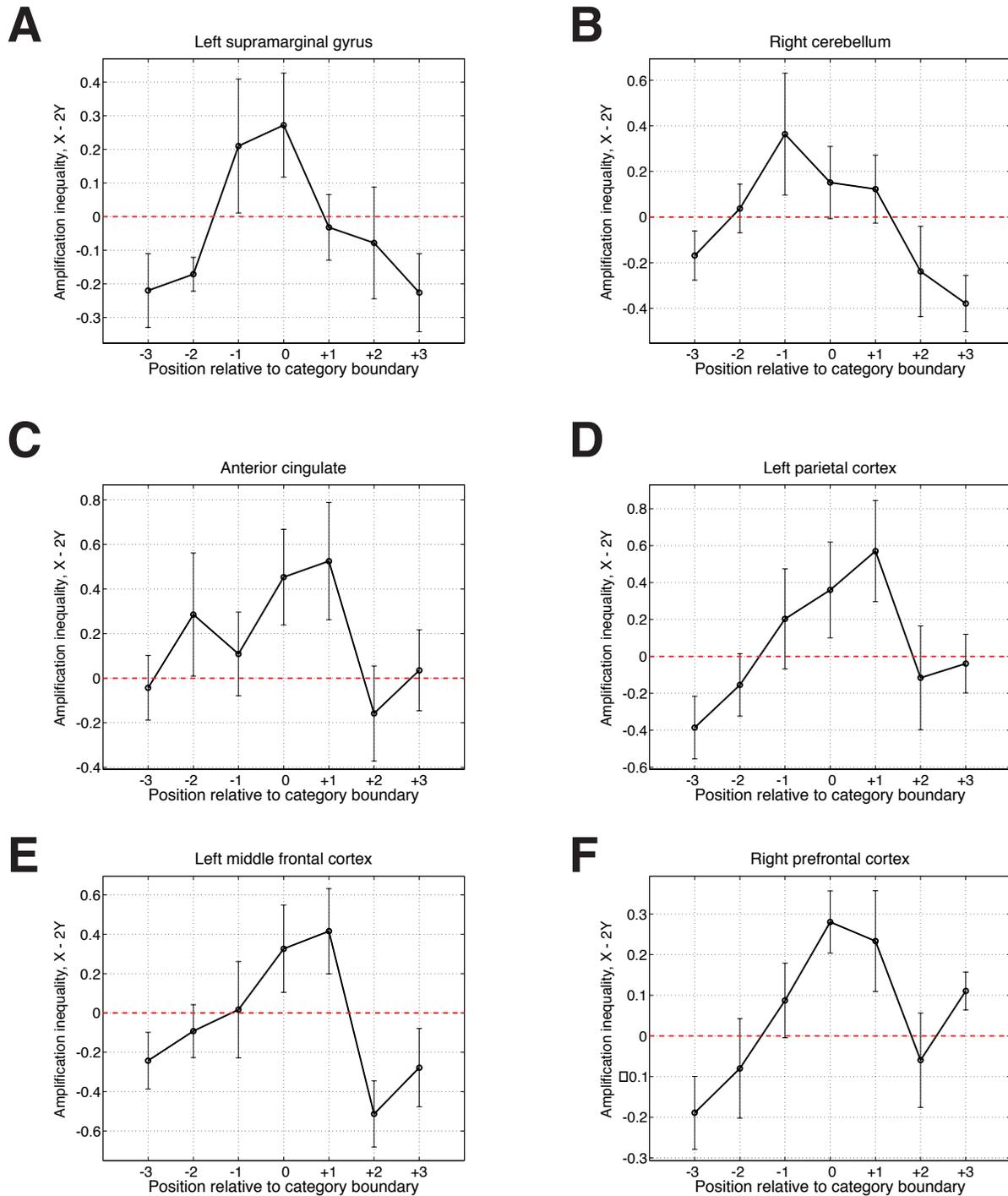


Figure 3:

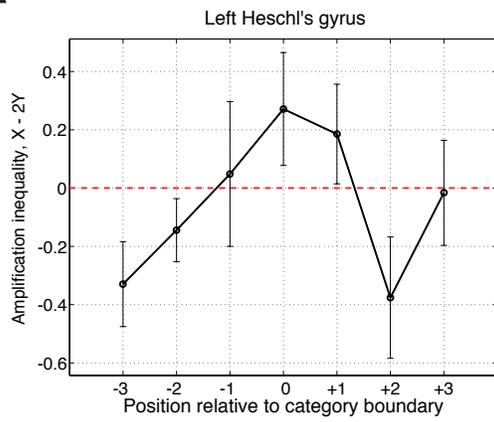
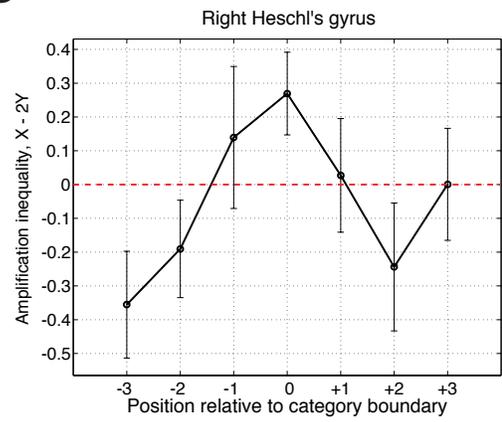
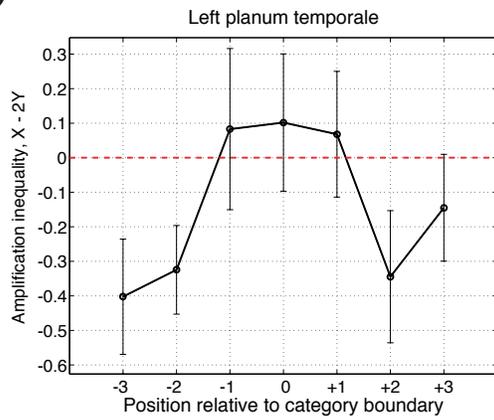
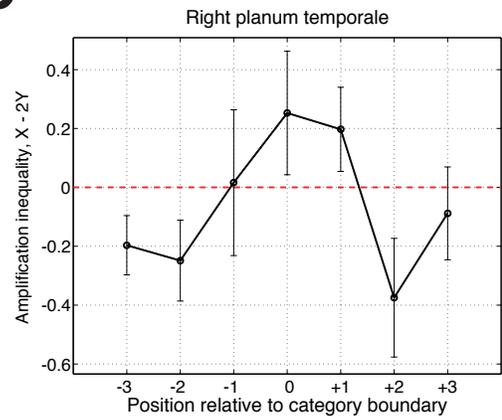
A**B****C****D**

Figure 4:

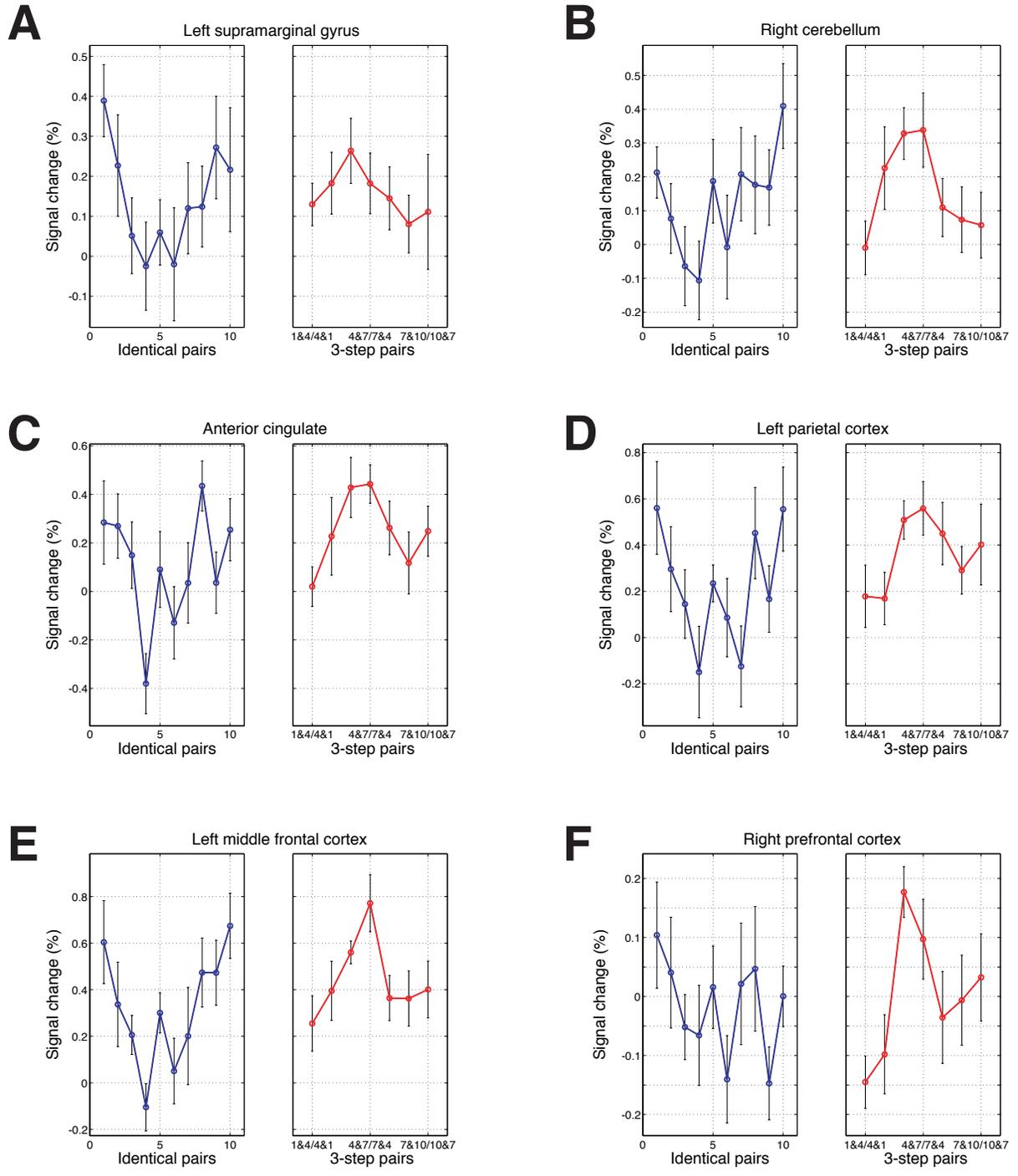


Figure 5:

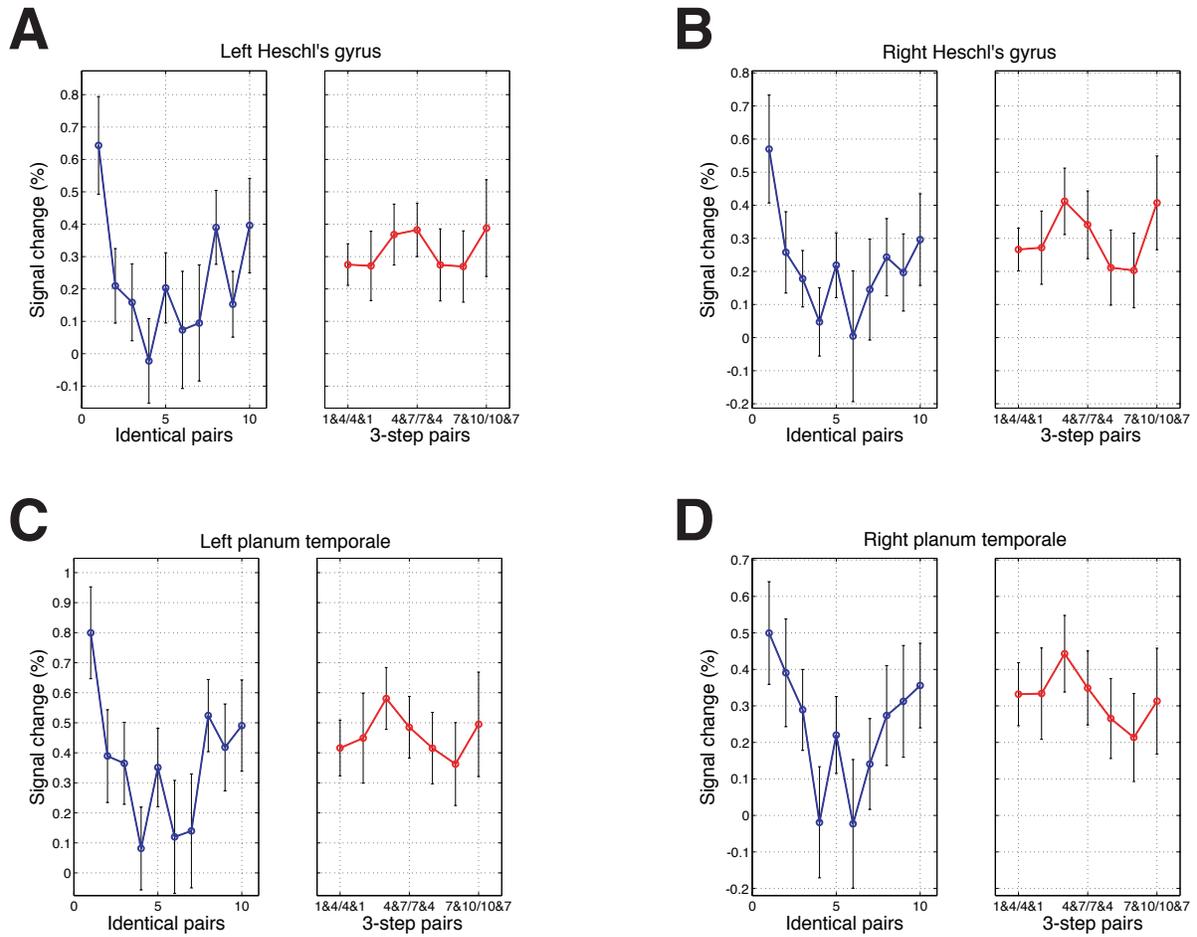


Figure 6:

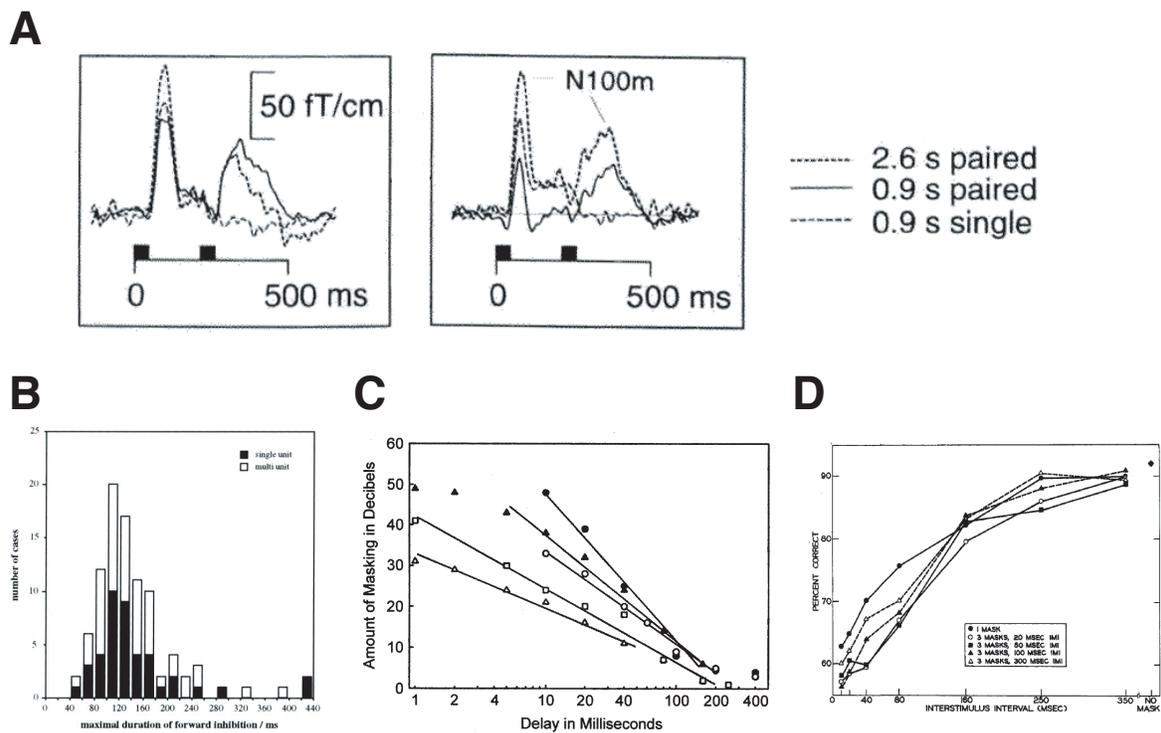


Figure 7: