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Is Listening in Noise Worth It? The Neurobiology of Speech Recognition in Challenging Listening Conditions

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Abstract

This review examines findings from functional neuroimaging studies of speech recognition in noise to provide a neural systems level explanation for the effort and fatigue that can be experienced during speech recognition in challenging listening conditions. Neuroimaging studies of speech recognition consistently demonstrate that challenging listening conditions engage neural systems that are used to monitor and optimize performance across a wide range of tasks. These systems appear to improve speech recognition in younger and older adults, but sustained engagement of these systems also appears to produce an experience of effort and fatigue that may affect the value of communication. When considered in the broader context of the neuroimaging and decision making literature, the speech recognition findings from functional imaging studies indicate that the expected value, or expected level of speech recognition given the difficulty of listening conditions, should be considered when measuring effort and fatigue. We propose that the behavioral economics and/or neuroeconomics of listening can provide a conceptual and experimental framework for understanding effort and fatigue that may have clinical significance.

A strikingly consistent observation from neuroimaging studies of speech recognition in challenging listening conditions (e.g., degraded and speeded speech or background noise) is the engagement of non-auditory systems that support performance monitoring and attention (Davis & Johnsrude 2003; Rodd et al. 2005; Wong et al. 2008; Adank & Devlin 2010; Adank et al. 2012; Hervais-Adelman et al. 2012; Wild et al. 2012; Golestani et al. 2013; Vaden et al. 2013). These findings are important because they highlight which neural systems are critical for supporting speech recognition in challenging listening conditions and can perhaps be leveraged to enhance speech recognition. Moreover, the finding that additional non-auditory systems support speech recognition offers insight into the effortful demands of speech recognition for many older adults.

The definition of effort used in this manuscript relates closely to the concept of cognitive load (Lemke & Besser, this issue, pp. XXXX). An important subtlety to our definition is that effort is experienced when understanding speech is necessary to perform a task, which is consistent with the definition in the consensus paper in this issue that the experience of effort occurs when there is a need to overcome an obstacle. It is for this reason that we describe

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neural systems that are important for attention to stimuli and the intention to understand and perform some action with speech information (e.g., overt report of the words presented, button pressing, working memory tasks). In the context of challenging and changing listening conditions that affect speech recognition, we further consider effort as being dependent on adaptive control or the adjustment of behavior to optimize performance (Vaden et al. 2013, 2015). We view fatigue as the consequence of using adaptive control systems over an extended period of time. In particular, we view fatigue from speech recognition as the brain's mechanism for providing feedback that there is diminishing value from using intention and attention neural systems for the listening task compared to alternative behavioral opportunities (Hornsby et al., this issue, pp. XXXX).

Our review of functional MRI studies on speech recognition focuses on cingulo-opercular and fronto-parietal systems that appear to be upregulated in challenging listening conditions. A large body of literature strongly suggests that cingulo-opercular and fronto-parietal regions constitute intention and attention systems (Dosenbach et al. 2008), which provides a conceptual framework for considering how these systems support speech recognition and a neurobiologically-grounded definition of effort. We then present findings that engagement of these systems supports or predicts speech recognition on a subsequent trial (activity measured ~ 8 seconds before the trial), which is consistent with our premise that listeners engage an adaptive control mechanism to optimize performance in challenging listening conditions.

The use of adaptive control appears to have an effort-related cost. It is in this context that we consider neuroeconomic studies demonstrating that systems supporting adaptive control are upregulated when the outcomes of goal-directed behavior have value, such as achieving higher performance levels or receiving an overt reward (Kouneiher et al. 2009) and avoiding loss (Paulus et al. 2003). In other words, supporting neural systems are used during listening when the value from listening outweighs the relative cost of using these systems. Based on our review of the literature, we emphasize below why clinical approaches to understanding effort and fatigue should incorporate an evaluation of the *relative value* from listening (Matthen, this issue, pp. XXXX).

Functional Imaging Studies of Speech Recognition

fMRI studies of speech recognition using vocoding, background noise, accented speech, time compressed speech, and frequency filtering manipulations of listening difficulty all demonstrate similar patterns of brain activation in fMRI studies. Increasing speech intelligibility typically produces increasingly higher activity in the anterior and posterior superior temporal gyrus and sulcus regions (Scott et al. 2000; Davis & Johnsrude 2003; Narain et al. 2003; Friederici et al. 2010; Abrams et al. 2012; Kuchinsky et al. 2012; McGettigan et al. 2012; Evans et al. 2014; Kyong et al. 2014; Zekveld et al. 2014). This perceptual response in temporal cortex typically occurs independently of task demands. In contrast, declining speech intelligibility typically produces increasingly higher activity in cingulo-opercular and fronto-parietal cortex (Davis & Johnsrude 2003; Rodd et al. 2005; Wong et al. 2008; Adank & Devlin 2010; Adank et al. 2012; Hervais-Adelman et al. 2012; Wild et al. 2012; Golestani et al. 2013; Vaden et al. 2013).

An Activation Likelihood Estimation (ALE) meta-analysis of coordinates from 10 speech recognition experiments (Davis & Johnsrude 2003; Rodd et al. 2005; Wong et al. 2008; Adank & Devlin 2010; Adank et al. 2012; Hervais-Adelman et al. 2012; Wild et al. 2012; Golestani et al. 2013; Vaden et al. 2013) was performed to demonstrate the brain regions that exhibit consistently elevated activity during challenging compared to easier listening conditions. These studies included specific comparisons of a harder compared to an easier listening condition and the authors reported coordinates for significant differences in activation for these comparisons. An ALE meta-analysis integrates coordinates that were reported to be activated by a task across multiple studies. This is possible when researchers use the same coordinate space for describing the location of functional imaging findings in the brain. Sixty-eight coordinates were reported for brain regions that exhibited elevated activity during the challenging listening condition compared to a control condition across these normative samples (please see the Figure 1 caption for additional methodological details). Importantly, this analysis was not restricted to particular brain regions. Nonetheless, Figure 1 shows that cingulo-opercular regions exhibited consistently elevated activity during the challenging listening conditions used in these studies.

Increased activity occurs in cingulo-opercular regions when participants generate a response to indicate recognition of a stimulus rather than when the task involves passive listening (Fiez et al. 1995) or directing attention to a secondary task or stimulus (Wild et al. 2012). These observations appear to be dependent on the ability of participants to perform a task and do not simply reflect performance errors during a hard task. For example, cingulo-opercular activity is relatively low when a task is so difficult that participants demonstrate “floor” performance (Poldrack et al. 2001; Zekveld et al. 2006, 2012). This is important because it indicates that frontal activity is not an obligatory response to challenging listening conditions, but instead reflects the intention to optimize speech recognition when there is value from using attention (Shenhav et al. 2013).

Description of Key Intention and Attention Systems

Cingulo-opercular Intention System

The cingulo-opercular system is composed of bilateral dorsal cingulate, inferior frontal, and anterior insula regions (Figure 1) that exhibit elevated activity when performance declines and/or task difficulty increases for different cognitive and perceptual tasks (Dosenbach et al. 2006; Eckert et al. 2009). Functional connectivity and graph theoretic studies demonstrate that activity in these regions covaries or is coordinated over time, particularly when people perform a task compared to a resting or non-task condition (Seeley et al. 2007; Dosenbach et al. 2008; Vaden et al. 2013). This functional system comes online across a wide range of tasks when cognitive control is needed to optimize performance (Carter et al. 1998; Botvinick et al. 1999, 2004; Durston et al. 2003; Kerns et al. 2004; Crone et al. 2006; Kerns 2006; Luks et al. 2007; Sridharan et al. 2008; Menon & Uddin 2010). While there is likely a specific mapping of sensory representations within cingulate cortex, the relatively gross resolution of typical functional imaging group experiments suggests that similar regions of cingulo-opercular cortex are responsive across tasks involving different sensory systems (Barch et al. 2001; Eckert et al. 2009).

The activity between cingulo-opercular regions can be coordinated through a recently described frontal aslant tract that provides direct connections between cingulate and inferior frontal cortex (Catani et al. 2012; Figure 1). This connectivity would therefore allow cingulo-opercular cortex to share information about performance outcomes, task difficulty, and the value in exerting control (cingulate: Carter et al. 1998, 2000; Botvinick et al. 1999, 2004; Kerns et al. 2004; Kerns 2006; Shenhav et al. 2013) in order to increase arousal through autonomic function (anterior insula: Hoffman & Rasmussen 1953; Meyer et al. 2004; Cechetto 2014), increase response cautiousness or response inhibition (right inferior frontal cortex: Wager et al. 2005; Chambers et al. 2007; Goghari & MacDonald 2009; Hughes et al. 2013; Aron et al. 2014), and guide controlled retrieval or response selection (left inferior frontal cortex: Thompson-Schill et al. 1997; D'Esposito et al. 1999; Sohn et al. 2003; Moss et al. 2005; Goghari & MacDonald 2009; Davey et al. 2015).

A prominent hypothesis regarding the cingulo-opercular system states that cingulo-opercular activity reflects the establishment of stable performance over time (Dosenbach et al. 2006, 2008). Much like autopilot, cingulo-opercular cortex is thought to detect when there is uncertainty about how to respond or perform a task (response uncertainty) and related performance decline so that control can be implemented to set performance back on track. In this context, cingulo-opercular activity is important for maintaining optimal performance even for the easiest of tasks. Indeed, declines in cingulo-opercular activity precede declines in performance for simple and choice reaction time experiments when subjects identify a visual symbols presented with competing information (Weissman et al. 2006; Eichele et al. 2008), as well as for a speech recognition in noise task described below. Thus, cingulo-opercular activity can indicate an intention to optimize performance.

A hypothetical example of cingulo-opercular function is presented in Figure 2 to show how and why cingulo-opercular activity may vary over time. The figure shows (1) a pronounced rise in activity that we (Vaden et al. 2013) and others (Dosenbach et al. 2006) have observed at the onset of transitions between tasks or conditions. This response has been described as the engagement of a ventral attention system to salient stimuli (Sridharan et al. 2007). The figure also shows (2) sustained elevated activity over the course of an experiment that is hypothesized to reflect the maintenance of task parameters in the service of performance monitoring (Dosenbach et al. 2006, 2008). This response can vary in magnitude based on the demands or effort required to perform the task (horizontal straight lines in Figure 2). Finally, (3) greater fluctuation in cingulo-opercular activity (hatched lines in Figure 2) corresponds to heightened adaptive control when we would predict increased signaling to fronto-parietal cortex with the goal of implementing inhibitory control. It is possible that this activity reflects minor fluctuations in task difficulty and/or tonic vigilance that affect response uncertainty and performance (Sadaghiani & D'Esposito 2015). We show below that variation around the mean on a trial-by-trial basis is a strong predictor of subsequent speech recognition. These and similar findings from the decision making literature support the premise that the cingulo-opercular system acts as an adaptive control mechanism to enhance speech recognition.

Interestingly, older adults with and without hearing loss are more likely to exhibit elevated cingulo-opercular activity compared to younger adults across a variety of tasks, including

language tasks (Sharp et al. 2006; Eckert et al. 2008; Harris et al. 2009; Erb & Obleser 2013). This observation has led to the hypothesis that cingulo-opercular activity reflects a compensatory mechanism to support performance when age-related sensory, perceptual, and cognitive declines increase the relative difficulty of a task (Wingfield & Grossman 2006; Reuter-Lorenz & Cappell 2008; Reuter-Lorenz & Park 2010). This view is supported by neuroimaging evidence that older adults with elevated cingulo-opercular activity perform better in challenging speech recognition tasks (Wingfield & Grossman 2006; Harris et al. 2009; Peelle et al. 2010; Erb & Obleser 2013; Vaden et al. 2015; c.f. Meinzer et al. 2012). These findings are important because they indicate that cingulo-opercular activity is a normal response to improve performance and because increased cingulo-opercular activity has been associated with increased effort (Botvinick et al. 2009; Burke et al. 2013), as we discuss below.

Fronto-parietal Attention System

A separate neural system appears to be upregulated when task difficulty increases and there is competing information that might interfere with word recognition (Obleser et al. 2007; Brownsett et al. 2014). This fronto-parietal system includes inferior frontal sulcus/precentral sulcus (Figure 1A), dorsolateral prefrontal cortex/middle frontal gyrus, intraparietal sulcus, and inferior parietal lobule regions (Dosenbach et al. 2008). Fronto-parietal activity appears critical for implementing control to focus attention on relevant information, suppress irrelevant information, and select a task-appropriate response (Durstun et al. 2003; Kerns et al. 2004; Kerns 2006; Wager et al. 2005; Luks et al. 2007) by monitoring the responsiveness of other cortical regions. The fronto-parietal system exhibits greater connectivity with other neural systems compared to any other major functional system and its pattern of connectivity can significantly predict the particular task being performed (Cole et al. 2013). Thus, the fronto-parietal network may instantiate task-specific control by modulating the responsiveness of cortex that is necessary to recognize target speech, perhaps by suppressing the activity in other cortical regions that might interfere with speech recognition [Also see studies on EEG alpha rhythms and suppression (e.g., Strauß et al. 2014) that have relevance to hearing loss (e.g., Petersen et al. 2015)].

Fronto-parietal mediated inhibitory control appears to be crucial for recognizing speech in challenging listening conditions. The need to selectively focus attention on target speech and suppress distracting stimuli, including similar sounding lexical alternatives, increases as interference from background noise increases. Both younger and older adults recruit right dorsolateral prefrontal cortex to a greater extent when speech is degraded versus clear (Sharp et al. 2006). This fronto-parietal recruitment increases over the course of a task in older but not younger adults, which suggests that older adults increasingly engage fronto-parietal control to offset speech recognition decrements that are due to declines in the auditory system (Sharp et al. 2006; This effect could also reflect age-group differences in learning about the tasks over the course of the scanning session). Moreover, older adults with lower inhibitory control abilities have worse speech recognition in noise than those with higher control, especially for words with many phonological competitors (Taler et al. 2010; Janse 2012). These results suggest that inhibitory control helps older adults to suppress incorrect lexical alternatives during speech recognition.

Although the necessity for inhibitory control may increase with age-related sensory declines, the ability to implement control does not. Aging is accompanied by decrements in inhibitory control that are hypothesized to underlie the apparent decline of many cognitive functions in older adults (Hasher & Zacks 1988; Lustig et al. 2007). Thus, dysfunction of the fronto-parietal network is a candidate mechanism for older adults' difficulty recognizing speech. Whereas younger adults exhibit increased activation of the left dorsolateral prefrontal cortex as speech intelligibility decreases, older adults exhibit the opposite pattern (Eckert et al. 2008). This may indicate that older adults recruit fronto-parietal control in relatively easy listening conditions, with limited use of control when the task becomes too difficult (Eckert et al. 2008). In these cases, applying additional control may have limited value relative to the effort required to implement control.

Coordination of Intention and Attention Systems

Listeners must have both the intention to optimize speech recognition and the attentional focus to prevent distraction and interference from irrelevant information in order to perform well in challenging listening conditions. Monitoring performance will not help those who are unable to apply inhibitory control and having good inhibitory control will not help those who fail to monitor performance. Thus, communication between the cingulo-opercular and fronto-parietal systems is essential for coordinating the implementation of control during demanding tasks, such as recognizing speech in challenging listening conditions.

Studies examining fluctuations in activity from trial to trial demonstrate that anterior cingulate activity positively predicts the extent of activity in the fronto-parietal network on a subsequent trial (Kerns et al. 2004; Kerns 2006; Walsh et al. 2011). Moreover, greater preceding activity in the anterior cingulate and elevated ongoing fronto-parietal activity is associated with faster and more accurate responding on the current trial (Kerns et al. 2004; Kerns 2006; Walsh et al. 2011). The idea that the cingulo-opercular system evaluates the value of control and signals to fronto-parietal regions to flexibly adjust top-down control is further supported by evidence of connectivity between these networks. Anterior cingulate cortex and dorsolateral prefrontal cortex demonstrate functional connectivity at rest (Taren et al. 2011) that appears to be supported by fiber tracts between anterior cingulate and dorsolateral prefrontal cortex (Beckmann et al. 2009). Declines in this connectivity could result in lapses in attention (Prado et al. 2011), including when older adults fail to detect target stimuli in a noisy background (visual continuous performance task; Mani et al. 2005).

The failure of these two systems to coordinate activity may further impair listening by decoupling the intention to perform from the implementation of inhibitory control. Functional connectivity between the right anterior insula of the cingulo-opercular network and fronto-parietal regions declines with age (He et al. 2013). This could produce a negative feedback loop by which a failure to engage inhibitory control decreases performance and reduces or discounts the value of trying to improve performance. We expand on this discounting idea below.

Summary of Adaptive Control

Adaptive control, or the adjustment of behavior to optimize performance during challenging tasks, can be implemented with a cingulo-opercular attention system that exhibits both sustained engagement during task execution and fluctuations in activity that track changes in task difficulty and performance. This system then appears to signal a fronto-parietal attention system to implement inhibitory control with the goal of directing attention to task-relevant information by suppressing responses to irrelevant information. Adaptive control appears to help older adults to achieve similar performance as younger adults (Reuter-Lorenz & Park 2010). We now turn to evidence that adaptive control is employed to facilitate word recognition in challenging listening conditions and the degree to which adaptive control improves speech recognition in older adults with and without hearing loss.

Evidence of Adaptive Control during Speech Recognition

The adaptive control framework described above predicts that cingulo-opercular cortex initiates changes in attention to optimize speech recognition in challenging listening conditions. The experimental design required to test this prediction involves measuring brain activity before the presentation of a speech stimulus (Figure 3A). We used this approach to examine if and when cingulo-opercular activity predicted subsequent performance on a trial-by-trial basis for each listener. The results from a study of healthy younger adults demonstrated that elevated cingulo-opercular activity predicted word recognition on a subsequent trial for each listener (Vaden et al. 2013). Although this experimental framework is correlational, activity preceding word recognition suggests that cingulo-opercular activity supports or improves word recognition. Interestingly, cingulo-opercular regions exhibited patterns of activity that were coordinated over time (Figure 1B) and the magnitude of this functional connectivity increased from silent rest to task trials. Moreover, the likelihood of correct word recognition on a subsequent trial was greatest with increasing co-activity across cingulo-opercular regions. Thus, performance was higher when cingulo-opercular regions functioned as an engaged system prior to the presentation of a word.

Evidence for cingulo-opercular support of speech recognition was also predicted for older adults based on the results above and prominent frontal compensation theories of aging (Wingfield & Grossman 2006; Reuter-Lorenz & Cappell 2008). Indeed, fluctuations in cingulo-opercular activity were associated with the likelihood of correct word recognition in noise on the subsequent trial in a group of middle-aged to older adults (Figure 3B; Vaden et al. 2015). However, the relationship between cingulo-opercular activity and trial-level word recognition was significantly lower compared to the younger adults from Vaden et al. (2013). Thus, the cingulo-opercular results are generally consistent with frontal compensation theories of cognitive aging (Reuter-Lorenz & Cappell 2008; Grady 2012), but there appears to be relatively less contribution from cingulo-opercular activity in predicting word recognition for older compared to younger adults.

A greater likelihood of word recognition following elevated cingulo-opercular activity was also observed for listeners with mild to moderate hearing loss (HL). During performance of the speech recognition in noise task from Vaden et al. (2013, 2015), middle-aged and older participants with less HL ($N = 12$, mean pure tone thresholds, PTA = 19.2 ± 4.8 dB HL, 0.25

to 8 kHz, both ears) and more HL ($N = 12$, $PTA = 38.4 \pm 4.5$ dB HL) demonstrated significant but relatively low magnitude effects of cingulo-opercular activity on trial-level word recognition (Vaden et al. 2016). These results indicate that aging, rather than hearing loss, determines the extent to which the cingulo-opercular system significantly predicts speech recognition, at least when sufficient speech audibility is provided.

Unexpectedly, visual cortex activity in older adults was a strong predictor of word recognition across trials for the worst performing cases, which appeared to be a consequence of age-related changes in attention (Vaden et al. 2015). Older adults were more likely to exhibit reduced visual cortex activity before they failed to recognize an aurally presented word. Our interpretation of this result was that older adults were more likely to make an error when their attention drifted from a visual cue that provided information about the timing of each trial and when to respond with the word that they heard. This interpretation was supported by evidence of age-related changes in a fiber tract connecting frontal and visual cortex, which also predicted the visual cortex association with word recognition (Vaden et al. 2015). These results suggested that while older adults demonstrated intention to recognize speech, task-directed attention was not sustained. The need to maintain inhibitory control despite faulty architecture for implementing control may increase speech recognition effort and perhaps contribute to fatigability from implementing adaptive control, as described below.

Linking the Neurobiology of Decision Making to Speech Recognition in Noise

The use of adaptive control in challenging task conditions has been hypothesized to indicate that the value of correct performance outweighs the cost of implementing control (Shenhav et al. 2013; Botvinick & Braver 2015). As discussed throughout this issue, the cost of listening in noise has been defined as fatigue resulting from sustained effort for extended periods, particularly for older adults with and without hearing loss (Gosselin & Gagné 2011; van Esch et al. 2013). We propose that adaptive control is worth the cost when a listener anticipates that there is relatively high value in speech understanding. We also predict that task-related fatigue occurs when the costs of listening effort are greater than the value from listening. Indeed, cingulate cortex appears to track performance and reward over time to guide decision making (Jocham et al. 2009). Trial-by-trial activations in cingulo-opercular cortex may therefore reflect the automatic calculation that performing a listening task is possible and that the speech is worth trying to understand.

Cingulate neurons weigh the value from performance against the effort-related costs of performance (Holroyd & McClure 2015). For example, rodents with anterior cingulate lesions will decide not to work to overcome physical barriers that limit access to a high reward and will instead choose a low reward option that requires less physical work (Holec et al. 2014). A roughly similar observation has been made from patients who received cingulectomies for treatment of mental disorders in the mid-20th century. These patients reported evidence of increased afternoon tiredness and a post-operative decrease in rewarding but effortful activities like reading, gardening, or carpentry. (“There seems also

less energy available for these activities.” Tow & Whitty 1953, p. 192). These types of animal and patient findings are consistent with the interpretation of fMRI findings from normative samples that dorsal cingulate activity in humans reflects the need for and decision to allocate effort during a challenging task (Botvinick et al. 2009; Burke et al. 2013). Indeed, midline frontal EEG theta power increases with effort ratings in response to relatively low speech signal to noise ratios (Wisniewski et al. 2015). Moreover, results from our lab suggest that the strength of relation between cingulate activity and word recognition on the next trial can be explained in part by individual differences in a measure of cognitive persistence (Teubner-Rhodes et al. 2015) or conation (Phillips, this issue, pp. XXXX). Together, these findings support the premise that cingulate cortex calculates the value of speech recognition relative to the expected difficulty of the listening condition.

We have emphasized throughout the present paper that elevated cingulo-opercular activity supports speech recognition, but there is strong evidence that upregulated cingulo-opercular activity has a cost. This is important because elevated dorsal cingulate activity, reflecting increased effort, can result in the devaluation of reward (e.g. understanding). In other words, people may decide that the reward is not worth the required listening effort (For an example, see the Furness and William sections in Matthen, this issue, pp. XXXX). This is a foundational idea in the study of effort discounting or the loss in value for achieving a goal because of the effort required to achieve the goal. In addition, people appear to decide whether to allocate cognitive control based on the expected value of a reward (Botvinick et al. 2009; Prévost et al. 2010). Recall that cingulo-opercular activity is maximal when speech recognition is possible but challenging because of low intelligibility and/or competing stimuli (an inverted U shaped response; as in Poldrack et al. 2001; Zekveld et al. 2006). Changes in the relative value of reward (e.g. understanding) and changes in effort-related barriers (e.g. listening condition) would be expected to affect speech recognition because effort discounting should reduce engagement in the listening task. This premise is supported by evidence that 1) older adults are more likely than younger adults to exhibit elevated frontal activity across a wide range of tasks (Reuter-Lorenz & Cappell 2008) and 2) older adults are more likely to demonstrate cognitive effort discounting (at least for a monetary reward; Westbrook et al. 2013).

One indication of effort discounting during listening is the fatigue that people experience when trying to recognize speech in noise for an extended period of time. The studies reviewed above suggest that cingulo-opercular activity relates to effort, but measuring this activity as well as fronto-parietal activity may be critical for understanding when and why older adults with hearing loss will experience fatigue. Again, the cingulo-opercular system is thought to signal the fronto-parietal system to implement control. Left inferior frontal sulcus/precentral sulcus (IFS/PCS) regions, a part of the fronto-parietal system, appeared to be critical for implementing control when younger adults performed a challenging cognitive task that they reported a preference to avoid (McGuire & Botvinick 2010), even after controlling for varied reaction times and errors that were associated with elevated cingulo-opercular activity. Moreover, this IFS/PCS effect was most pronounced in participants with the highest avoidance ratings. While cingulo-opercular regions were also associated with avoidance ratings, these regions were not significantly associated with avoidance after controlling for reaction time and errors (McGuire & Botvinick 2010). Thus, cingulo-

opercular regions appear to signal when effort or control is necessary and the sustained engagement of the fronto-parietal system is predicted to underlie the perception of fatigue (Lim et al. 2010; McGuire & Botvinick 2010).

As we noted above, IFS/PCS regions have been related to inhibitory control or selective attention (Sylvester et al. 2008; Bharadwaj et al. 2014; Kong et al. 2014). Inhibitory control therefore appears to be associated with a perceived cost and a desire to avoid the task. Importantly, Gatehouse and Noble (2004) reported that items from the Speech, Spatial and Qualities of Hearing Scale questionnaire involving selective attention, which requires inhibitory control, were most strongly associated with reported hearing handicap. These findings guide the prediction that sustained activity of IFS/PCS regions, especially in the absence of improved speech recognition, could negatively affect the value of implementing control during speech recognition. Clinically, we might predict that older adults with hearing loss experience social withdrawal and depression (Strawbridge et al. 2000; Gates & Mills 2005) when they feel there are limited options to implement control or ability to adapt to their hearing loss. From a more positive perspective, interventions that reduce dependence on or increase the efficiency of IFS/PCS inhibitory control would be predicted to increase the relative value of listening because less effort is required, perhaps as demonstrated by lower effort ratings following from acclimatization to hearing aids (Dawes et al. 2014).

The Neuroeconomics of Listening

We have summarized and integrated a wide ranging literature showing that cingulo-opercular activity is: 1) up-regulated when listening conditions are challenging but sufficient for speech recognition; 2) up-regulated for older adults even when they are performing as well as younger adults; and 3) associated with speech recognition on a subsequent trial for younger and older adults (adaptive control), although to a lesser extent for older adults with and without hearing loss. We have also emphasized that elevated cingulo-opercular activity appears to reflect a decision to act because there is value in performing a task. However, the need for sustained adaptive control may diminish the value of listening in ways that could have clinical implications.

To our knowledge, there has been no assessment of the hypothesis that prolonged effort (adaptive control or cingulo-opercular activity) in challenging listening conditions diminishes the value of listening to speech or effort discounting. This idea is consistent with the experience that many of us have in a noisy restaurant, for example, when we decide to disengage from conversation after a period of effortful listening. The time point and/or signal to noise ratio at which people decide to disengage could be useful for understanding the effort-related difficulties that hearing loss patients experience and in considering interventions.

Behavioral economics, the study of choice relative to the value of options, provide a conceptual and experimental framework for measuring when and why people decide not to listen. As we have tried to emphasize, value can be relative and dependent on cost or effort. For example, you may decide that it is worth the effort to get up off of your couch to get some ice cream from your refrigerator if the couch is close to the refrigerator, but not if you

have to climb some stairs to get to the refrigerator. The cost of climbing the stairs reduces the value of the ice cream, as measured by the decision not to get the ice cream. Figure 4 presents an example of how hard you might work to understand a speaker across varied listening conditions depending on the content of the information. We also provide with this figure a detailed summary of how effort can be modeled for two different listening scenarios that would likely have different value to a listener; having a conversation with a loved one and listening to a lint brush commercial. For each of these listening scenarios, we model how the value from listening would diminish with increasing listening difficulty. Note that the curves for a change in value are steeper for the lint brush example for which we would predict there is less value. In this example we could measure this loss of value as the amount of time one might listen for a given degree of noise or barriers to speech understanding.

The simple examples above demonstrate the inter-dependence between effort and value, which means that interventions that affect effort or value could affect hearing health behaviors. Speech training is one mechanism for reducing listening effort. Kuchinsky et al. (2014) showed that speech training improved word recognition for hearing aid candidates and reduced effort as measured by a pupillometry metric. The onset of the pupil response was faster for correctly recognized words after training compared to before training. Trainees were able to make decisions about the word they heard more quickly after training. This is important because by reducing effort, we may be able to delay the onset of fatigue and increase the time that people with hearing loss (and ideally hearing aid users) will choose to listen.

Conversely, enhancing the value from listening should also affect hearing health behaviors. Reward sharpens representations in the brain during perceptual learning and this effect appears to be mediated through ventral-striatal brain regions that would enhance the responsiveness of cingulo-opercular and fronto-parietal regions (Krebs et al. 2012) to high reward outcomes (Jocham et al. 2009). The inclusion of high value training stimuli (e.g., voices of loved ones) may speed speech training and therefore more quickly reduce the degree of inhibitory control that is necessary to listen in challenging conditions.

Finally, the relation between value and effort may also be useful in guiding hearing aid dispensing and counseling. We predict that hearing aid satisfaction and usage depends on the cost (effort and price) relative to the expected value from using the hearing aid. For example, potential hearing aid users who are willing to pay more for a hearing aid that provides the best possible audibility, particularly when hearing benefit from the aid meets expectations (Saunders et al. 2009; Meyer et al. 2014), may be more likely to use their hearing aids to a greater extent than potential users who discount the value of the hearing aid. This prediction is consistent with evidence that hearing aid counseling increases the value and use of hearing aids (Saunders & Forsline 2012). Effective counseling may increase self-efficacy for using hearing aids (West & Smith 2007; Hickson et al. 2014), which may correlate with cingulo-opercular function that signals effective hearing aid use is possible for people who find listening valuable.

In closing, functional imaging studies of speech recognition in noise highlight the importance of non-auditory systems that support speech recognition. These systems reflect

the need for effort and contribute to decision making about whether control is valuable. Given evidence that motivation and barriers affect hearing health behavior (Abdellaoui & Huy 2013; Salonen et al. 2013; Saunders et al. 2013), there is an opportunity to model and objectively quantify the effort that older adults with hearing loss experience relative to the value of listening.

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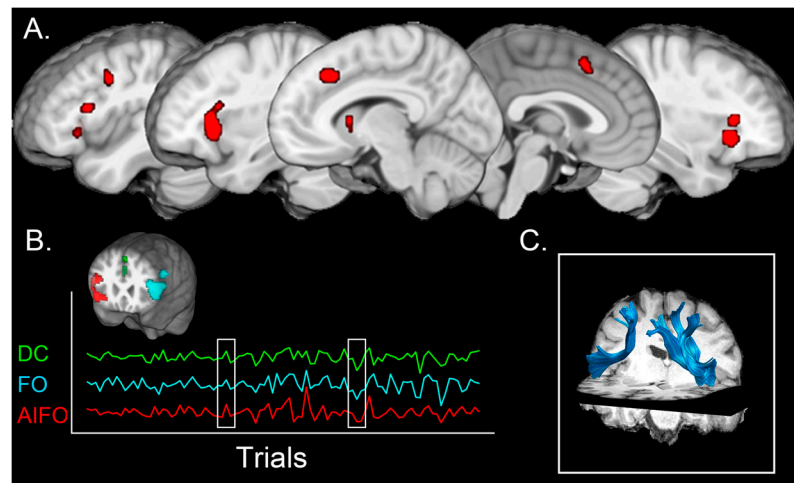


Figure 1.

The cingulo-opercular system. A. Meta-analysis results showing that investigators consistently report elevated brain activity, or increased blood-oxygen-level-dependent (BOLD) response, for challenging compared to easier listening conditions (Meta-analysis software: GingerAle v2.3; False Discovery Rate $p < 0.05$, min. cluster volume = 200 mm; 68 coordinates representing the peak effect within activated regions across 10 normative experiments: Davis & Johnsrude 2003; Adank & Devlin 2010; Hervais-Adelman et al. 2012; Golestani et al. 2013; Adank et al. 2012; Vaden et al. 2013; Wong et al. 2008; Wild et al. 2012; Rodd et al. 2005). A left posterior superior temporal sulcus region also exhibited elevated activity for the harder versus easier listening conditions (not shown). B. Cingulo-opercular activity time-series are correlated across regions during speech recognition (Vaden et al. 2013). DC: Dorsal Cingulate (green); FO: left Frontal Operculum (blue); AIFO: right Anterior Insula/Frontal Operculum (red). C. These regions are connected by callosal fibers, as well as the frontal aslant tract (blue fibers) that connects medial and inferior frontal regions.

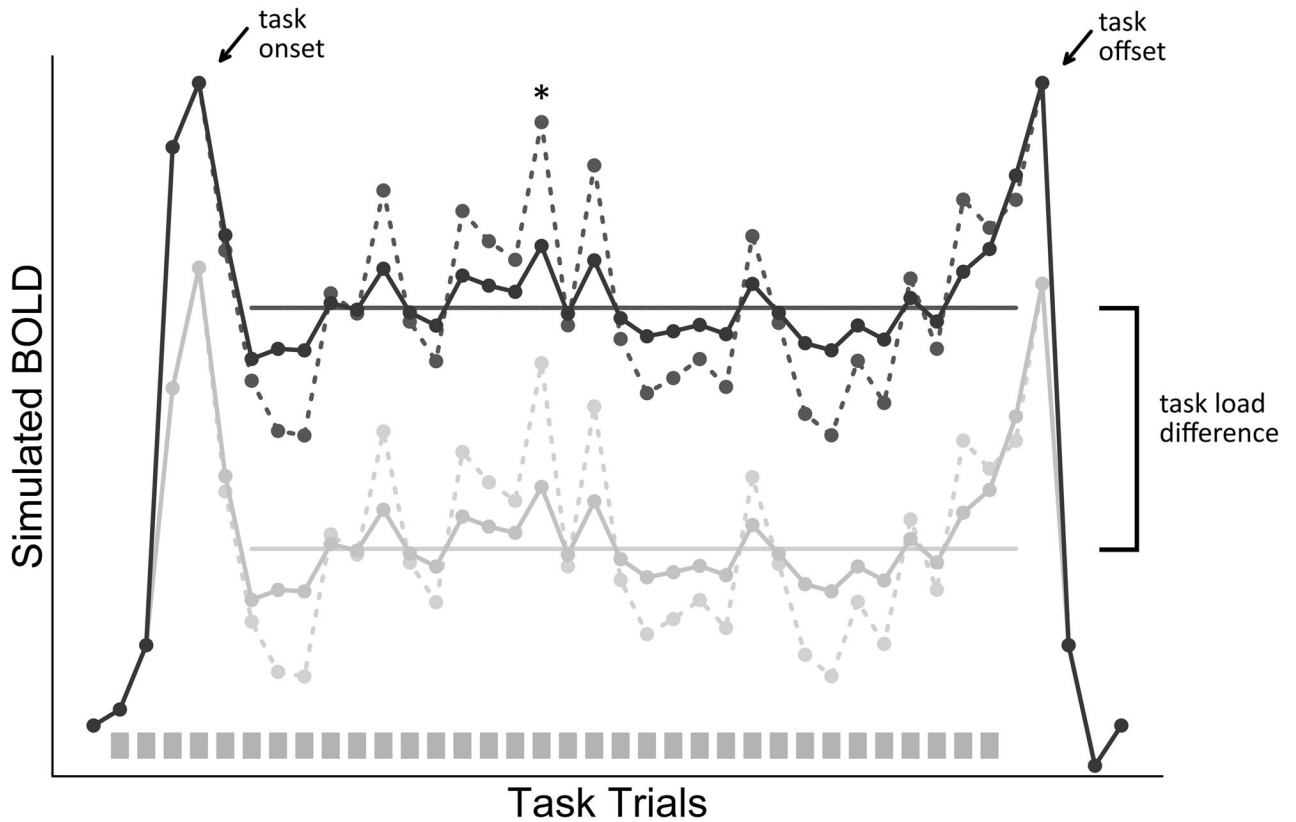


Figure 2.

Simulated BOLD contrast or activity time series that are characteristic of cingulo-opercular cortex activity during a task (adapted from Dosenbach et al. 2006). The large activity spikes reflect a cingulo-opercular response to salient events, in this example the onset and offset of a word recognition task. Mean activity levels during word recognition are represented by the horizontal straight lines to indicate the difficulty of two different signal-to-noise-ratio (SNR) conditions, assuming relatively stable task demand and motivation. Trial-level variation in the BOLD contrast (fluctuating lines) is thought to reflect response uncertainty and performance monitoring that is impacted by variation in word recognition difficulty within an SNR condition. (*) Hatched lines indicate increased trial-level variability in BOLD contrast that we have observed predict word recognition on a subsequent trial.

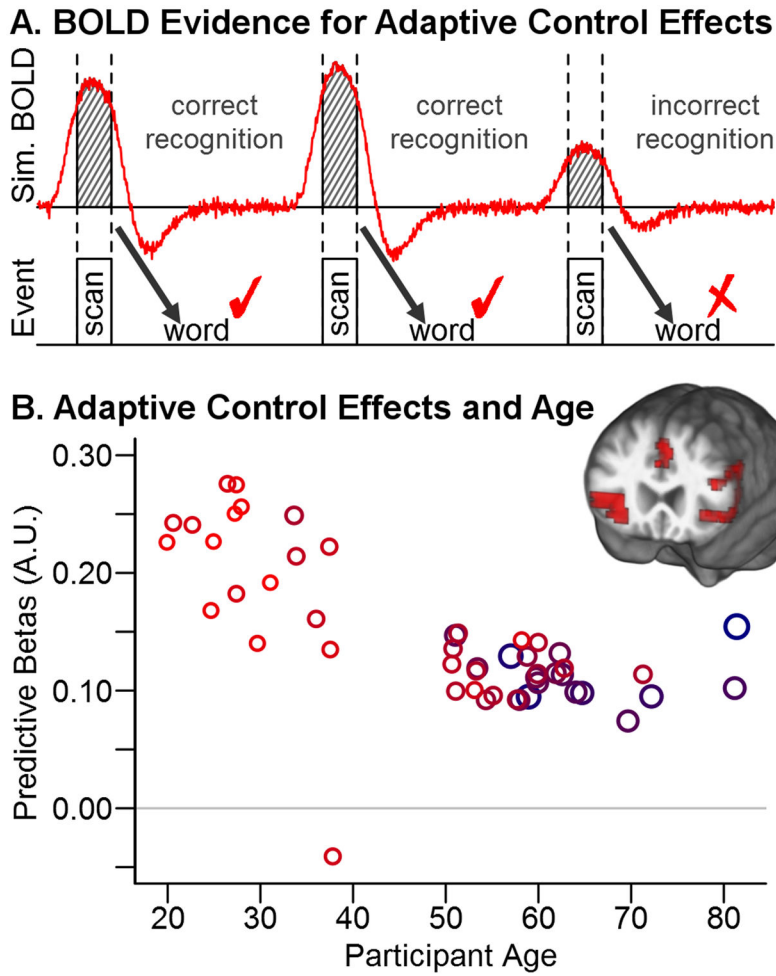


Figure 3. A. Simulated cingulo-opercular BOLD contrast (red line) illustrating changes immediately prior to correct or incorrect word recognition with a sparse sampling fMRI design. Note the lower amplitude of the BOLD response prior to an error. B. Adaptive control effects were pooled within significant regions that overlapped across the younger and older adult study samples, shown in red (Vaden et al., 2013; 2015). Adaptive control effects were lower when a sample of middle-aged and older adults (N = 31) was compared directly to a sample of younger adults (N = 18), although these effects did not change with participant age or hearing loss within the older sample (Vaden et al., 2015). The size and shading of each circle indicates the extent of hearing loss (range = -1.88 to 25 dB HL, 0.25 to 8 kHz, best ear; small red circles = less hearing loss; large blue circles = more hearing loss) to show that elevated pure tone thresholds did not diminish the effects in this sample of older adults.

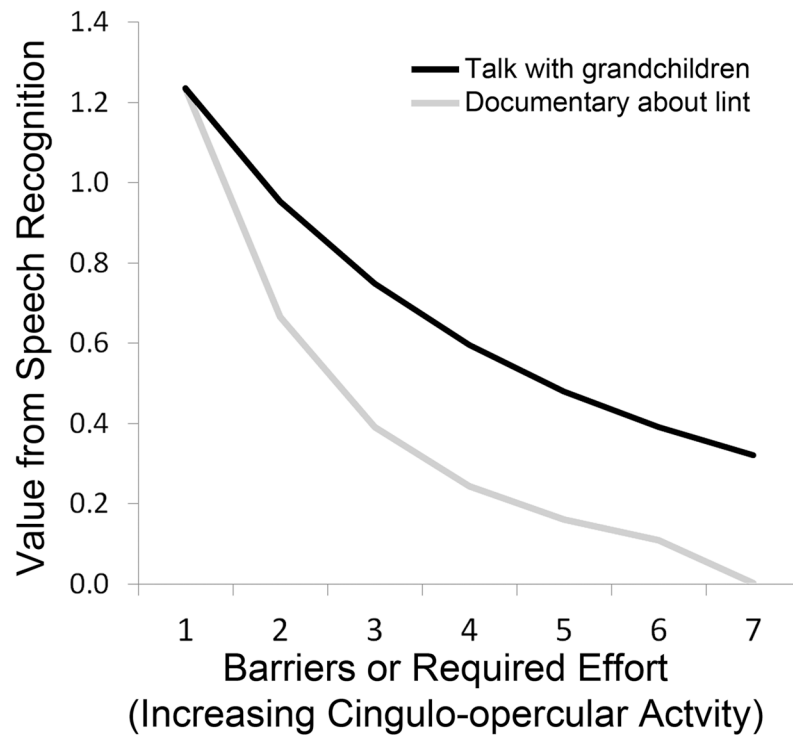


Figure 4. Hypothetical listening effort discounting curves for speech content with different value to an older adult listener. Note that the value of communication would decline more quickly for a less interesting topic assuming equivalent recognition across conditions (modeled hyperbolic function: value of listening = constant level of recognition/(1+listening difficulty)^S; where S is a scaling factor). Listening difficulty would then equate with increasing cingulo-opercular activity. This approach could then be used to measure the time to fatigue (based on ratings or performance) given a listening condition, which is predicted to be reflect the degree of sustained inferior frontal sulcus/pre-central sulcus activity.