

# Speech perception when the motor system is compromised

Stephen M. Wilson

Memory and Aging Center, Department of Neurology, 350 Parnassus Ave, Suite 905, University of California, San Francisco, CA 94143, USA

In a recent contribution, Lotto, Hickok and Holt [1] have made a compelling argument that findings on mirror neurons do not support a strong version of the motor theory of speech perception. However, they go further in arguing that there is 'little evidence that motor activity plays a necessary part in perception', a claim based primarily on the observation that speech production can be impaired in syndromes such as Broca's aphasia while leaving comprehension relatively intact [2]. Alternatively, this dissociation could reflect redundancy in the speech perception network, coupled with preserved access to top-down contextual information. So the dissociation does not rule out a role for the motor system in speech perception, a view supported by several lines of evidence.

In a striking demonstration of redundancy in the brain regions supporting speech perception, Hickok and colleagues [3] reported that in patients undergoing the Wada procedure, the right hemisphere alone made fewer than 10% phonemic errors. This apparent redundancy limits the extent to which speech perception deficits can be observed when any single region, such as speech motor cortex, is damaged. Second, all listeners, including patients with Broca's aphasia [4], make extensive use of contextual information in speech comprehension. For example, an altered phoneme midway between /d/ and /t/ is more often perceived as /d/ in the context *\_ash*, because *dash* is a word and *tash* isn't. This 'lexical effect' is actually larger than normal in Broca's aphasics, indicating that they rely more on top-down information and less on the phonetic detail of the input [5].

These observations imply that any specific role for the motor system in perception will be manifest only as a graded decrease in performance, and will emerge only in experimental settings which preclude reliance on contextual information. Several studies fit these criteria. First, Broca's aphasics showed poor auditory comprehension when stimuli were low-pass filtered and temporally compressed [6]. Degrading the acoustic input reveals the suboptimal functioning of the speech perception system. Second, Broca's aphasics performed worse at discriminating place of articulation than voicing, and made more errors when forced to rely on just one phonetic feature than on two [7]. Task-related processes [2] cannot account for differences between conditions determined by phonetic factors, so these data suggest a specifically phonetic impairment. Third, patients with Broca's aphasia showed reduced

priming when primes were acoustically altered to create poorer phonetic exemplars [8], suggesting involvement of the motor system in accounting for sub-phonemic variation.

Speech perception deficits in Broca's aphasia do not unambiguously implicate the speech motor system because lesions are typically extensive, and often impact attentional, executive and other processes [2]. Transcranial magnetic stimulation (TMS) studies in normal controls permit more anatomically specific investigations. Temporary inactivation of premotor cortex impaired phoneme discrimination in noise but not subtle color discrimination [9]. The phonetic and visual tasks were precisely matched in difficulty and task demands, indicating that the induced deficit was phonetic rather than attentional or executive. Another TMS study found that stimulation of motor areas for different articulators (e.g. tongue) selectively facilitated identification of phonemes relying on those articulators (e.g. alveolar consonants) [10]. This phoneme-specificity suggests that the role of the motor cortex relates to articulatory representations, and provides further evidence against a non-specific effect.

In summary, the speech motor system seems to have a crucial role in speech perception, which cannot be entirely supplanted by temporal regions. Speech production regions might instantiate top-down production-based models of the input, which are especially important under acoustically degraded conditions [11,12]. This functionality is important because in everyday language use, suboptimal auditory input is not the exception, but the norm.

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## Letters Response

# Response to Wilson: What does motor cortex contribute to speech perception?

Gregory Hickok<sup>1</sup>, Lori L. Holt<sup>2</sup> and Andrew J. Lotto<sup>3</sup>

<sup>1</sup>Cognitive Sciences, University of California, SSPA4109, Mail Code: 5100, Irvine, CA 92697, USA

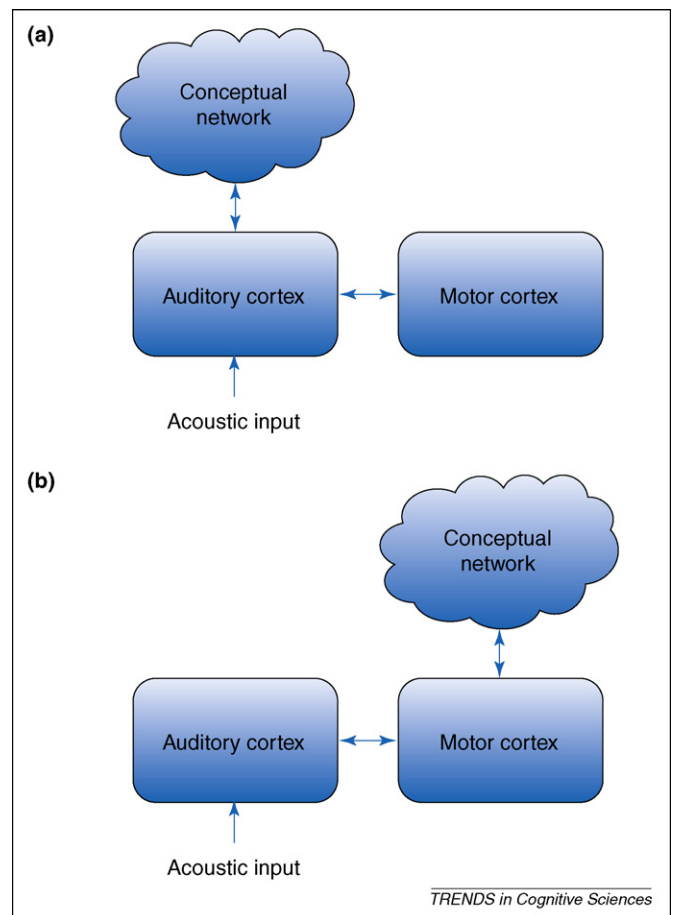
<sup>2</sup>Department of Psychology and Center for the Neural Basis of Cognition, 5000 Forbes Avenue, Pittsburgh, PA 15213, USA

<sup>3</sup>Speech, Language and Hearing Sciences, University of Arizona, 1131 E. 2nd Street, P.O. Box 210071, Tucson, AZ 85721-0071, USA

Although the main goal of our paper [1] was to argue against mirror neurons as a possible instantiation of the Motor Theory of speech, we also presented evidence in support for an alternative auditory theory of speech perception. That is, we promoted a model as in Figure 1a and against that represented in Figure 1b. Wilson [2] does not dispute this central position. Instead he argues that speech production regions could have a top-down influence on perception. We agree wholeheartedly and would add that speech production systems are not the only source of top-down information. As Wilson hints, lexical-semantic information can also influence perception, and visual speech information is known to have dramatic effects [3] – arguably to a much greater extent than motor information. Although some authors attribute the influence of visual speech entirely to motor activity [4], there is evidence that ‘direct’ cross-sensory integration (visual-to-auditory) is the more robust source of influence [5].

It seems that the only point of dispute raised by Wilson is one of terminology. We suggested that the motor system is not ‘necessary’ for speech perception; Wilson suggests that it is. By our use of the term we mean that it is possible, at least under some circumstances, for accurate speech perception to occur without the influence of the motor system. Evidence for this claim comes from the fact that even large left frontal lesions that reduce speech production to nil or stereotyped output do not produce considerable impairments in speech recognition [6]; that deactivating the entire left hemisphere in Wada procedures produces mutism yet results in only a 7.5% error rate in discriminating minimal phonemic pairs (hearing ‘bear’ and pointing to a matching picture among phonemic distractors [7]); that the failure to develop speech production does not preclude normal receptive speech development [8,9], and that infants as young as 1-month-old exhibit sophisticated speech perception ability including categorical perception well before they acquire the ability to speak [10].

It is a fair criticism that many studies demonstrating preserved auditory comprehension in Broca's aphasics do not implement tight controls on contextual information. However, (i) this indicates the auditory system in concert



**Figure 1.** Coarse schematic models of speech perception illustrating the fundamental difference between auditory and motor theories of speech perception. (a) Schematic of an auditory theory. Acoustic speech input activates auditory-phonological networks, which in turn activate lexical-conceptual networks. (b) Schematic of a motor theory. Acoustic speech input must make contact with motor speech systems to access lexical-conceptual networks.