

Perceptual-Training Induced Narrowing of the Multisensory Binding Window

Albert R. Powers III* and Mark T. Wallace§

While it has long been understood that accurate perception of events in the environment requires the successful combination of information from all senses, researchers have only recently begun to uncover the powerful perceptual and behavioral benefits arising from this combination. The study of how multisensory information shapes our view of the world around us has exploded in recent years (see ¹⁻² for reviews), and current investigation has begun to focus upon the neural substrates underlying these multisensory interactions.

INTRODUCTION: MULTISENSORY INTERACTIONS

Examples of multisensory interactions fill nearly every aspect of our lives. One common everyday example is the increase in speech intelligibility experienced when a speaker is visible³. Psychophysical research involving human subjects has provided numerous other examples of how multisensory interactions influence perception and behavior. The most basic of these include the speeding of responses⁴⁻⁶ and the improved detection of targets when information from two sensory modalities is presented⁷⁻⁹. The interactions behind these two examples clearly confer an adaptive benefit. Multisensory illusions, although unlikely to have such benefits, further illustrate the power of multisensory interactions to shape our perceptions and behaviors in the absence of our conscious knowledge. In the Flash-Beep Illusion¹⁰⁻¹¹, participants frequently perceive multiple flashes of light when two sounds are presented, even when only a single flash actually occurred. In the ventriloquist effect, perception of the location of a sound source can be shifted by the presence of a temporally coincident but spatially disparate visual cue¹²⁻¹⁴. In the realm of speech, the McGurk Effect uses simultaneous presentation of visual /ga/ and auditory /ba/ to produce a fused percept that reflects a synthesis of the visual and auditory channels (/da/ or /tha/)¹⁵⁻¹⁶. These multisensory interactions are not unique to the audiovisual realm. One of the more entertaining multisensory illusions, for example, is the somewhat alarming “parchment skin illusion” wherein changing the frequency of the sound of one’s fingers rubbing together alters the tactile perception of that action from “like rubbing against glass” to “like rubbing

against sandpaper”¹⁷⁻¹⁸. Many other tasks of daily life are inherently multisensory in nature, from tasting food to reading. Purposeful manipulation of the processes underlying multisensory interactions, then, carries potential to alter our most basic experiences in very profound ways.

PRINCIPLES OF MULTISENSORY INTEGRATION AND THE TEMPORAL BINDING WINDOW

Conventional knowledge of multisensory integration in both humans and animal models indicates that multisensory interactions are guided by a set of principles that ultimately relate to the nature of the stimuli that are being that multisensory neurons (*i.e.*, those neurons that respond to or are influenced by multiple sensory modalities) are likely to show the largest multimodal response gains when the stimuli presented are spatially proximate¹⁹⁻²⁰. The second is the rule of inverse effectiveness, stating that the largest gains are seen when stimuli that are only weakly effective on their own are paired²¹. Most germane to the current work, the temporal principle posits that close temporal pairing of multisensory stimuli results in the most significantly enhanced behavioral or electrophysiological responses²². Instances of this rule’s application in perception and behavior abound²³⁻²⁵, and examples of its validity in non-invasive human electrophysiology are also plentiful²⁶⁻²⁸. Although these examples indicate that the greatest response gains are seen when there is a close temporal relationship between stimuli of different sensory modalities, there appears to be a window of time within which the pairing of multisensory stimuli results in a significantly enhanced behavioral or electrophysiological response.

*Neuroscience
Graduate Program,
Vanderbilt University
Medical School, U1205
Medical Center North,
Nashville, TN 37232,
USA.

§Vanderbilt Brain
Institute, Vanderbilt
University, Nashville,
TN 37232, USA.
Correspondence to
A.R.P. e-mail:
albert.powers@vanderbilt.edu
ilt.edu

We refer to this interval in a general sense as the temporal window of multisensory integration (**Figure 1**).

Several studies have focused upon this concept of a multisensory temporal binding window and have begun to define its boundaries in human behavioral studies^{25,29-34}. The boundaries of the temporal window of multisensory integration can be delineated psychophysically by identifying the range of audiovisual asynchronies over which a multisensory interaction (e.g., a change in performance or perception) is observed. Dixon and Spitz³⁵ first defined the window in just this way, and their findings have been replicated on other psychophysical tasks³⁶⁻³⁷. However, though the window's boundaries have been well established using several different psychophysical tasks, the literature have surprisingly little to say about the permanence of these boundaries and their ability to be manipulated in time.

SENSORY PLASTICITY AND THE TEMPORAL WINDOW

The brain's ability to alter its structure and function based upon input from the environment ranks among its most evolutionarily valuable traits. Seminal early developmental studies showed that this plasticity can be driven in a bottom-up fashion by exposure to a constrained set of sensory stimuli³⁸⁻⁴⁰ and that passive exposure to these stimuli becomes less likely to drive behavioral change and neural reorganization as an animal reaches the end of a critical period of development⁴¹. Later, electrophysiological studies revealed that both the behavioral and anatomical changes typically elicited in developing animals by passive exposure can indeed take place in adults via top-down perceptual training, wherein stimuli are paired with either reward or punishment⁴²⁻⁴⁴.

In humans, perceptual training studies have

highlighted the ability of the individual sensory systems to exhibit plastic change. For example, it has been demonstrated that adults with amblyopia exhibit improvement in Vernier acuity judgments following training⁴⁵⁻⁴⁶, and in the auditory realm, that adults demonstrate accuracy gains on synchronicity judgments and temporal order judgment tasks following practice⁴⁷⁻⁴⁸. In these studies, while subjects showed improvement in the task on which they were trained, training effects did not generalize to a separate, albeit related, task.

Indeed, lack of transfer between tasks in perceptual training paradigms is common⁴⁹⁻⁵⁰, especially in perceptual training studies focusing upon a unimodal task. The extent to which perceptual training generalizes across stimuli⁵¹ and across tasks⁴⁸ has been hypothesized to vary according to the level of specialization exhibited by the neural circuitry involved in training; a training paradigm that produces alterations in performance on other, unrelated tasks are likely to have altered circuits common to both tasks. Thus, the amount of generalization a perceptual training paradigm elicits provides invaluable information to the researcher regarding the circuits that have been altered by said training, with circuits responsible for processing a range of stimuli exhibiting cross-stimulus generalization and circuits essential for processing a number of related tasks showing cross-task generalization.

It is unclear from the literature whether temporally-based multisensory training paradigms should be expected to show generalization across tasks. Some task generalization has been seen in multisensory short-term passive exposure studies^{34,52-55}. Fujisaki and colleagues⁵² assessed participants' likelihood of perceiving a range of asynchronous audiovisual pairs as simultaneous and then repeatedly exposed participants to an audiovisual stimulus pair separated by a fixed onset asynchrony for a period of minutes. Re-assessment revealed short-term shifts in participants' perception of simultaneity, and these shifts extended to a pair of audiovisual illusions; notably, these two illusions—the Flash-Beep Illusion¹⁰⁻¹¹ and the Stream-Bounce Illusion⁵⁶—while unrelated to the exposure task, have a strong basis in multisensory temporal processing, showing a monotonic decline in effect size with deviation from simultaneity. Thus, the authors may be said to have temporarily altered some aspect of multisensory processing underlying all three of the tasks used. In a similar vein, Virsu and colleagues recently reported lasting improvements in accuracy of unisensory and multisensory simultaneity judgments and decreases in mean simultaneity thresholds following practice, but failed to see transfer of training effects across modalities⁵⁷. None of these studies, however, have

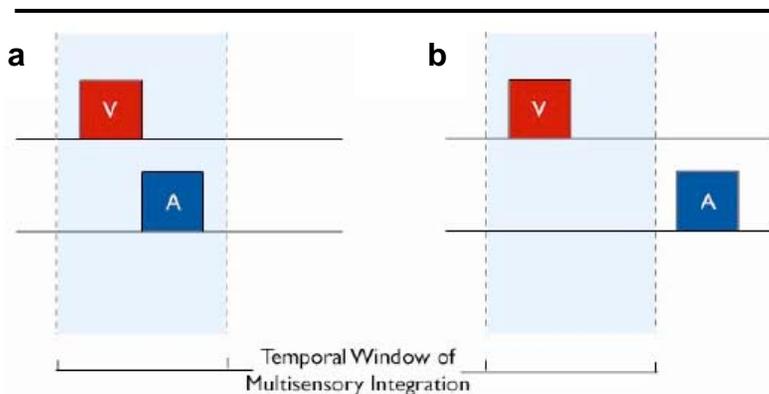


Figure 1 | The temporal window of multisensory integration. The dashed lines and light blue shading delimit the temporal window of multisensory integration, in which visual (V) and auditory (A) stimuli are bound into a unified perceptual entity (a). When visual and auditory stimuli are sufficiently separated in time, they are processed as independent events (b).

attempted to specifically alter the temporal window of multisensory integration by perceptual training.

As described above, the degree to which perceptual training effects generalize across stimuli and across tasks provides important information about the circuits involved in these tasks. In conjunction with these behavioral measures, neuroimaging measures such as fMRI are capable of identifying those brain regions most likely to underlie perceptual phenomena like those described above. As of yet, no neuroimaging data have been produced identifying brain regions altered by perceptual training in a temporally-based multisensory task. It may be hypothesized, however, that the brain regions altered by said training may be the same regions underlying multisensory processing in general and multisensory temporal processing in particular. The literature regarding these brain areas is outlined below.

MULTISENSORY BRAIN NETWORKS

Traditional views of sensory cortical organization posit that sensory information is routed from the thalamus to the primary sensory cortices and then to association cortices where it may be combined with information from other modalities. The focus of much multisensory research has been on these cortical association areas; indeed, the earliest of these have been described as possible loci for the initial binding of multisensory information⁵⁸⁻⁶⁰. This early multisensory cortical network appears to be located at the borders between temporal, occipital, and parietal lobes, and includes Brodmann's areas (BA) 39/40 and the posterior superior temporal sulcus (PSTS) as major nodes. These areas have been shown to respond to multisensory stimulation in a variety of different tasks and contexts^{26,61-64}, which, in conjunction with preliminary data from our lab^{30,65} and others^{33,66}, make them the focus of the current proposal.

The network defined above has been further refined by studies examining the temporal aspects of multisensory processing, which are most germane to the current review. A number of other studies⁶⁷⁻⁶⁸ have described an expanded network, identifying the multisensory areas above in addition to insula/frontal operculum, dorsolateral medial prefrontal cortex, posteriorparietal cortex, posterior thalamus, superior colliculus, and posterior cerebellar vermis as being involved with multisensory processing in the temporal realm. Because the experiments proposed here will specifically involve measures of multisensory temporal processing, our own analysis will focus on both general multisensory areas and those areas described above that are known to be involved specifically in multisensory temporal function.

Increasing evidence is pointing to early sensory cortices (i.e., unisensory regions) as possible sites for multisensory interactions in addition to these

canonically defined multisensory areas⁶⁹⁻⁷⁷. While it is unclear whether these interactions are the result of feed-forward, feed-back or lateral connectivity, it seems wise at this juncture to include these areas in any analysis of multisensory processing via neuroimaging.

A thorough description of the plasticity of brain networks involved in multisensory temporal processing is of obvious importance in understanding the characteristics and flexibility of these networks from a basic science perspective. However, as outlined below in the final section of this review, emerging evidence suggests that these questions may also be of utmost importance in establishing the pathophysiology of clinical disorders that have multisensory temporal processing as their basis. Thus, outlining the effects of perceptual training upon these networks brings the hope that training-induced alteration may represent a step toward remediation of these disorders.

CLINICAL IMPLICATIONS

While the study at hand proposes to fill gaps in our knowledge of how multisensory systems react dynamically to changes in the external environment, the conclusions drawn from this research may ultimately extend to the diagnosis and treatment of several disorders. Our lab and others^{30,57,78-82} have identified altered multisensory temporal processing in dyslexic readers. Specifically, our lab has described an extended temporal window of multisensory integration in these readers when compared with typical readers. Correspondingly, imaging studies have shown that areas that lie at the borders between occipital, temporal and parietal cortices exhibit significant activation differences in dyslexic readers when compared with typical readers⁸³⁻⁸⁸. The areas that have been identified in these studies share many similarities with those that make up the early multisensory regions outlined above. Thus, the successful completion of the study proposed here may provide the basis for the investigation of multisensory perceptual training as a viable strategy in the remediation of developmental dyslexia.

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FURTHER INFORMATION:

Mark Wallace's Lab: <http://kc.vanderbilt.edu/multisensory/index.html>