Review

On the Timing of Signals in Multisensory Integration and Cross-modal Interactions: A Scoping Review

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Abstract

A scoping review was undertaken to explore research investigating early interactions and integration of auditory and visual stimuli in the human brain. The focus was on methods used to study low-level multisensory temporal processing using simple stimuli in humans, and how this research has informed our understanding of multisensory perception. The study of multisensory temporal processing probes how the relative timing between signals affects perception. Several tasks, illusions, computational models, and neuroimaging techniques were identified in the literature search. Research into early audiovisual temporal processing in special populations was also reviewed. Recent research has continued to provide support for early integration of cross-modal information. These early interactions can influence higher-level factors, and vice versa. Temporal relationships between auditory and visual stimuli influence multisensory perception, and likely play a substantial role in solving the 'correspondence problem' (how the brain determines which sensory signals belong together, and which should be segregated).

Keywords

Temporal principle, multisensory integration, cross-modal interactions, temporal ventriloquism, the correspondence problem

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Supplementary Material

Table S1.

Chart of studies that met the criteria for inclusion in the scoping review.

Authors (Year)	**Title**	**Aims/Concepts**	**Area of interest**	**Results**
Spence and Squire (2003)	Multisensory integration: maintaining the perception of synchrony.	Review studies examining how the perceptual system accounts for differences in the arrival time of inputs to different senses to produce the perception of synchrony.	Perception of synchrony.	A moving TBW and temporal ventriloquism may account for differences in the arrival time of inputs to different senses. Suggest more research is needed to examine the underlying causes of individual differences in the perception of multisensory synchrony.

Calvert and Thesen (2004)	Multisensory integration: methodological approaches and emerging principles in the human brain.	Briefly cover MSI concepts; Critically review neuroimaging techniques used in MSI research; Review research on attention and cross-modal binding.	MSI neuroimaging techniques. Redundant target effect.	Race models of the RTE largely replaced with co-activation models. Stimulus and task-related factors mediate crossmodal interactions. MSI at early and late stages of processing utilizes a parallel network of bidirectional connections. MSI cell responses in cerebral cortex are less studied than in SC. Response properties vary between these parts of the brain and may subserve different functions. Neuroimaging strategies to identify crossmodal interactions include matching tasks, superimposition of activity maps from similar tasks in different modalities, and tasks designed to tap crossmodal integration.

		Different networks underly different tasks. PET and fMRI are suitable for localization of multisensory regions. EEG and MEG are suitable for studying time courses of multisensory processes. Attention modulates multisensory processes. Suggest future research combine haemodynamic and EEG/MEG data to understand MS processes and take into account task-related effects and attention.

King (2005)	Multisensory integration: strategies for synchronization.	Examine processing strategies that allow the perception of synchrony from signals of various modalities that arrive, are tranduced, and are processed at different speeds in the sensory sytem.	TBW.	TBW varies depending on distance. Review evidence that this is based on reverb cues rather than intensity (loudness). As source distance increases, auditory stimulus must be delayed as a function of the additional sound travel time to bind with the visual stimulus. Temporal relationships between bound stimuli can be recalibrated with training. Suggests that this could be a way to investigate the adaptability of the brain.
Musacchia and Schroeder (2009)	Neuronal mechanisms, response dynamics and perceptual functions of	Describe the circuits that underlie multisensory convergence and	MSI in auditory cortex.	Multisensory integration occurs even at low levels of processing in the auditory system. This challenges the traditional hierarchical

	multisensory interactions in auditory cortex	physiologically feasible time windows of integration in auditory cortex.		view of processing.
Recanzone (2009)	Interactions of auditory and visual stimuli in space and time	Review studies that use illusions to examine multisensory processing of AV stimuli.	MSI and illusions.	A change in the spatial and/or temporal relationships between auditory and visual stimuli can produce illusions. The 3 key parameters that affect the strength of an illusion are compellingness, timing, and spatial disparity. Illusions and their after effects can be used to study perception and neural mechanisms underlying MS integration. The modality appropriateness hypothesis and bayesian probabilty models of MSI are both supported by illusion studies. Neuroimaging

				studies and single neuron studies reviewed were limited by technologies not yet equipped to directly link illusions to underlying mechanisms.
Vroomen and Keetels (2010)	Perception of intersensory synchrony: A tutorial review	Review studies that examined the perception of synchrony between the senses and key issues in intersensory timing.	Perception of synchrony.	Very similar to book chapter (Keetels & Vroomen 2012) below.
Fujisaki et al. (2012)	Multisensory timing	Review multisensory aspects in temporal perception, focusing on temporal judgements between	MSI aspects in temporal perception.	Review factors influencing temporal judgements such as attention, temporal structure, modality, implied causality, distance, and recalibration. Cross-modal

		modalities, and cross-modal influences on within-modality judgements.		temporal judgements appear to be result from complex processing at various stages. The authors suggest a multidisciplinary approach to understanding multisensory temporal perception.
Keetels and Vroomen (2012)	Perception of synchrony between the senses	Review studies that examined the perception of synchrony between the senses and key issues in intersensory timing.	Perception of synchrony.	TOJ and SJ tasks generally used for study of the perception of synchrony but produce different values for the TBW. PSS and JND measures are affected by other factors and each have their own pros and cons. The brain may deal with intersensory time differences by any or all of the following: TBW, compensation for external factors (e.g. distance), recalibration, and temporal

				ventriloquism. Debate as to whether perception of synchrony is automatic or not - authors think it is when stimuli are salient. Neural substrates not clear but most likely a network includng the SC and STS. Intersensory timing is flexible and adaptive.
Spence (2013)	Just how important is spatial coincidence to multisensory integration? Evaluating the spatial rule.	Assess when spatial coincidence of multimodal stimuli produces behavioural enhancements.	Spatial principle of MSI.	The spatial principle of MSI developed from electrophysiological studies on animal neurons. Translating this principle to human behaviour appears to be more complex. Support for the spatial rule comes from studies where the task requires an orienting or other spatial response, or spatial attention. Temporal judgement and target identification tasks

				generally do not support the spatial rule. Multisensory processing may include parallel "what" and "where" processing streams, similar to those described in unisensory research.
Van Atteveldt et al. (2014)	Multisensory integration: flexible use of general operations.	Review previous research to illustrate proposal that MSI is governed by the flexible use of a few general integrative operations.	Oscillatory phase resetting, divisive normalization.	Previous research suggests that the 3 principles of MSI are task, stimulus and/or context dependent. 2 canonical integrative operations, oscillatory phase resetting and divisive normalization, are proposed to work in concert to adaptively integrate multimodal stimuli.

Chan et al. (2016)	Temporal integration of multisensory stimuli in autism spectrum disorder: a predictive coding perspective.	Review studies that examine the role of MS temporal integration in ASD. Explain mixed results from different tasks/studies.	Multisensory temporal integration in ASD.	SJ and TOJ tasks produce similar TBW size estimates in ASD groups as in control groups. Studies using the SIFI report a wider TBW in ASD groups than in control groups. The authors suggest that predictive coding may be able to explain these different results.
Chen and Spence (2017)	Assessing the role of the 'unity assumption' on multisensory integration: a review,.	Review factors that may lead to the unity assumption.	The unity assumption. Priors.	The unity assumption describes when an observer considers that a number of different unimodal signals emanate from the same multisensory object or event. Paradigms used to investigate the unity assumption are discussed, including temporal ventriloquism. Whether the recent introduction of priors into computational models of MSI render the unity

		assumption obsolete is discussed. The conclusion is that the unity assumption is still a hotly debated topic in the MSI literature, and priors may help to explain how it comes about. The authors update the definition of the unity assumption.

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