



Auditory-visual interactions in spatial scene analysis: development and neural bases

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Abstract

The interactions observed in the ventriloquism situation suggest that visual and auditory signals are not processed as independently as the notion of separate senses would imply. A review of the conditions for pairing, the hypothetical mechanism underlying these interactions, argue for cognitive impenetrability and computational autonomy, the pairing rules being the Gestalt principles of common fate and proximity. There is much evidence in support of the view that auditory-visual integration is present early in life. Data from studies of the perinatal period, such as those on neonatal synesthesia, sensory deprivation, and sensory sur-stimulation as well as neuroanatomical evidence for transitory intersensory connections in the brain support the view that sensory modalities are bound together at birth and differentiate later, consistent with experience-expectant development. The discovery in the superior colliculus of different species of bimodal neurons governed by spatial and temporal rules similar to those underlying ventriloquism suggests a possible neural substrate. Differences between ventriloquism and speechreading are discussed.

1. Ventriloquism and recalibration

One of the crossmodal interactions that are sometimes observed in situations of spatial conflict between visual and auditory signals is the ventriloquism phenomenon. This is the illusion that the speech produced by the ventriloquist comes from the mouth of his puppet. Such a situation not only gives rise to immediate fusion but also to aftereffects, showing that true perceptual recalibration occurs. Aftereffects were observed after exposure to synchronous series of sound pulses and light flashes coming from positions separated by 15° to 20° (Radeau & Bertelson, 1974). After exposure, auditory pointing with the light off were shifted some degrees in the direction previously occupied by the flashing light and, in some conditions, a small shift of opposite direction was also observed in visual pointing tests with the sound off.

The criteria used by the perceptual system for pairing light flashes and sound trains coming

from different positions, that is to register the signals as related to a single event and not to different events, seem to be structural or sensory criteria present in non familiar situations. Cognitive factors like instructions or a context evoking a situation known to produce correlated sensory data do not play any role. A context simulating a real-life situation like seeing the face of a speaker while hearing the voice displaced or seeing the hands of a man playing bongos while hearing the music displaced did not increase adaptation above the level reached in non real-life situations like when diffuse light modulated by the sounds was presented on the screen (Radeau & Bertelson, 1977).

The sensory factors that are critical for pairing seem to be the principles of common fate and proximity that Gestalt Psychologists have applied to visual scene analysis. Indeed, pairing is affected both by the timing of the signals and by the distance between them. As regards the timing of the signals, delaying the sound 350 ms relative to the visual signal did not suppress but significantly reduced the size of the aftereffect in comparison to a synchronous condition (Radeau & Bertelson, 1977). Plasticity is also limited to spatial conflict of restricted extent. One of best demonstrations for the operation of the principle of proximity was provided by Knudsen & Knudsen (1989) who raised barn owls from birth to adulthood with prisms. For 11° and 23° visual displacements, recalibration was almost complete (8.5° and 18.1° , respectively) but for a larger displacement (34°), it was smaller in size (13.9°), this even after extended practice with the prismatic device.

The possibility that synchronization and proximity influence pairing indirectly by strengthening the unity assumption (Welch & Warren, 1980) was examined, using a test of cognitive penetrability (Pylyshyn, 1980). The comparison of two situations involving mainly sensory or conceptual factors showed that conceptual factors alone in the absence of sensory factors was completely inefficient (Radeau, 1992). In the conceptual condition, the same sound pulses as in the sensory condition were produced while the subjects, instead of seeing flashes of light, looked at a small dummy loudspeaker from which the sound was told to emanate. No effects

were found in this conceptual condition arguing for the cognitive impenetrability of the pairing system. Since the notion of cognitive impenetrability is at the core of modular theories of the mind (Marr, 1982; Fodor, 1983), the system underlying ventriloquism has been considered as being computationally autonomous (Radeau, 1994a). The computations in this system could be based on primal knowledge of the Gestalt principles of common fate and proximity used not only in visual grouping but also in "auditory scene analysis" (Bregman, 1990).

2. Development

What about the development of multisensory integration? Does it result from amodal representations that would be functional early in life or is it learned from experience of co-occurrent unimodal informations, as assumed by traditional integrative theories (Piaget, 1952)? There is much behavioral evidence to indicate that there are links between the different modalities at birth, the sensory systems becoming gradually differentiated during development (Bower, 1974; Marks, 1978). In this regard, the data on facial imitation in human neonates some hours after birth provide especially strong evidence for links between the visual and haptic senses (Meltzoff, 1993). For vision and audition, one of the first pieces of evidence for early connections is Wertheimer's (1961) report of oculomotor responses toward a noise in a human newborn a few minutes old.

Further support for a primitive unity of the senses is the finding of intensity-based responses without distinction of modality in neonates from different species. Responses to variations of intensity of a visual stimulation are influenced by quantitative variations of an auditory stimulation in both humans (Lewkowicz & Turkewitz, 1980) and rats (Spear & McKinzie, 1994) a few weeks old but not in adults. Intersensory equivalence based on intensity is probably a consequence of the large number of intersensory connections present in the young organism but whose a great deal are transient. The process of elimination of inappropriate connections through development has been accounted for by epigenetic theories of brain organization based on selective stabilization (Changeux, 1983; Edelman, 1987).

Other arguments for the poor differentiation between the senses at birth come from neonatal synesthesia in humans. Synesthesia means joined sensation. It is very important in the first month of life (Maurer, 1993) and decreases during development, being two to three times more

frequent in infants than in adults. In adults, synesthesia is defined as occurring when stimulation in one modality automatically triggers a perception in another unstimulated modality. One of the most commonly reported experience is colored-hearing and consists in consistent associations between sounds (especially, vowels or music) and colors (Marks, 1975). Developmental synesthesia in adults has to be distinguished from pseudosynesthesia or acquired synesthesia (for instance, induced by the use of psychoactive drugs). It seems to be heritable with a female-biased pattern of inheritance (Bailey & Johnson, 1997) and it begins to be manifest in childhood. This is consistent with a genetic view of synesthesia based on neuronal pruning (Harrison & Baron-Cohen, 1997) by which neonatal intersensory connections which are normally transitory persist during development (but see Cytowic, 1993, for a theory involving the limbic system).

Data from studies on perinatal sensory sur-stimulation or sensory deprivation have provided additional support for early auditory-visual interactions. Unusually early experience in a late-developing system has been shown to interfere with sensory functioning in earlier-developing systems. In vertebrates, the auditory system develops before the visual one. Exposure of bird embryos to visual stimulation several days prior to hatching resulted in an auditory deficit, ducklings (Gottlieb, Tomlinson & Radell, 1989) and quail chicks (Lickliter & Banker, 1994) failing to learn the maternal call. Thus, normal limitations of functioning in one modality facilitate the functional organization in an earlier developing modality. On the other hand, perinatal deprivation in a sensory system can affect functioning in the remaining modalities. In naturally blind rodents like the mole rat and in mice completely deprived of visual stimulations from birth, auditory neurons have been found in the region normally occupied by the visual cortex (King & Carlile, 1993). Deprivation of patterned visual stimulation by binocular eyelid suture in ferrets (King & Carlile, 1993) and barn owls (Knudsen, Esterly & Du Lac, 1991) resulted in anomalous responses of auditory neurons. Electrophysiological studies using the event-related potential (ERP) method in congenitally deaf cats (Rebillard, Rebillard & Pujol, 1980) and humans (Neville, 1990) have shown responses to visual stimulations in temporal brain areas which, in the hearing subject, contain the auditory cortex. No changes, however, were recorded in humans who have had four years of auditory experience. Thus, the observed compensatory changes can reflect stabilization of transitory connections in one modality in the

absence of competing input from another modality.

There is some neuro-anatomical evidence for transient intersensory connections around birth. Auditory to visual cortex connections which disappear in the fourth week of age have been reported in the kitten (Innocenti & Clark, 1984) and in another carnivore, the ferret (Kennedy & Dehay, 1993). Connections have also been found between the retinas and the somatosensory and auditory nuclei of the thalamus in the hamster less than a week old (Frost, 1990). For the time being, intersensory connections have not been described in primate newborns. However, auditory ERPs have been recorded over the occipital visual cortex of human 6-month-old babies but not in older children (Neville, 1995). All these results suggest that there is some unity of the senses at birth and that development is associated with increased differentiation between the sensory modalities.

3. Neural bases

As regards the brain bases of crossmodal interactions, the discovery of multimodal cells is of crucial importance since sensory convergence on individual neurons may well be the neural mechanism underlying this kind of interaction. Multisensory neurons which receive inputs from different sensory modalities have been found in many parts of the central nervous system and in many species. An important center of sensory integration involved in locating and orienting relative to sensory stimuli is the superior colliculus in mammals (or, its homologue in non-mammals, the optic tectum). Although the superficial layers are essentially visual, the deep layers of the superior colliculus receive projections from different sensory modalities and contain neurons related to eye and head movement. Cells receiving inputs from two or three sensory modalities have been described, the predominant pattern of sensory convergence depending on the species and probably reflecting ecological differences. Especially relevant here are the auditory-visual cells found in cats (Wickelgren, 1971).

Each sensory modality in the superior colliculus or the optic tectum is organized spatiotopically and in register with one another and with motor representations, though the size of the maps may be different. As a consequence, in the case of auditory-visual cells, stimuli coming from a same location (the image and song of a bird) activate the same region of the superior colliculus (of the cat) and this results in upward movements of the eyes and head. The alignment of the sensory

maps is obviously critical for efficient multisensory functioning. At what time is the alignment realized is still unknown. There are, however, several arguments for postnatal plasticity in the auditory modality. Barn owls raised from birth with a plug occluding one of the ears develop bimodal cells with receptive fields in spatial register with one another (Knudsen, 1983). Such plasticity is restricted to a short period after birth. It is also restricted to small deviations. So, it occurs in owls wearing weak ocular prisms (Knudsen, & Knudsen, 1989) or in ferrets after small ocular deviation (15° to 20°) but not after a 180° artificial rotation of the eye (King, Hutchings, Moore & Blakemore, 1988).

Stein & Meredith (1993) compared the responses of the cat auditory-visual cells under unimodal and bimodal stimulation. They found cells exhibiting response enhancement to bimodal stimulation, that is, cells which often failed to respond to unimodal stimulation but exhibited a vigorous response when both stimulations were presented simultaneously. The opposite, response depression, was found in other cells. Multisensory enhancement is multiplicative and thus especially efficient for weaker stimuli. The interplay of response enhancement and depression allows the organism to detect a prey or a predator despite minimal cues from each modality, and also to distinguish stimuli related to different objects or events.

The interactions in the superior colliculus are governed by spatial and temporal rules (Stein, Meredith & Wallace, 1993). The spatial rule means that the greatest response enhancement occurs for bimodal stimuli which coincide in space. Spatially disparate stimulations produced no response or response depression. This pattern of responses was linked to the existence of receptive fields with an excitatory center and an inhibitory surrounding, response enhancement occurring when the two stimuli fell in the excitatory region. Behavioral studies in which cats were trained to move to a visual or auditory stimulus confirmed the results of the neurophysiological studies. There was a significant enhancement of correct responses when the visual and auditory stimuli were presented together at the same spatial location. However, when the same bimodal stimuli were spatially disparate, the number of correct responses to the trained stimulus dramatically decreased. Interestingly, the degree of spatial disparity at which enhancement was eliminated was around 15°, a separation that has proved to be optimum in the resolution of the auditory-visual spatial conflict. Temporal disparity is another

critical factor of bimodal cell responses, the size of response enhancement being inversely related to temporal disparity. Response enhancement, however, while being maximum for temporally coincident stimulations, was still observed during a temporal window as long as several hundred ms. This has an adaptive value since the visual and auditory systems are specialized for the detection of distant events for which arrival times are very different. It is worth noting that although synchronization was shown to favor recalibration in the ventriloquism situation, it was not a critical condition. A 350 ms delay of the sound relative to the light reduced but did not eliminate recalibration.

The rules that govern responses of auditory-visual cells in the superior colliculus are reminiscent of the Gestalt principles of common fate and proximity. This is highly adaptive since stimuli that are close in space and time are likely to originate from a common event. Multisensory integration enhances the salience of the stimulus and helps detection. Because these rules also underly ventriloquism interactions, bimodal cells of the superior colliculus could well constitute one of the neural substrate of these interactions. Recently, polymodal cells with the same integrative rules have been recorded in other sites, especially in the polysensory cortex of cat and monkey (Stein, Wallace & Meredith, 1994). No projections were found between these multisensory cortical neurons and those of the superior colliculus, these latter receiving inputs from unimodal regions of cortex, suggesting that multisensory integration may be carried out by separate systems.

4. Speechreading

As proposed previously (Radeau, 1994b), the integration of auditory and visual information that plays a role in the perception and understanding of speech (Sumby & Pollack, 1954) and whose a striking demonstration is the McGurk illusion (McGurk & McDonald, 1976) is probably not subserved by the same system as that underlying ventriloquism. Although the available neural data (Campbell, 1998) do not help distinguishing the two kinds of interactions, some differences can be pointed out. On the one hand, the two interactions concern different domains. While ventriloquism concerns spatial scene analysis and localization, the McGurk illusion concerns identification of speech events. In the visual modality, there is neurophysiological evidence for the "what" and "where" problems being subserved by different pathways (Ungerleider & Mishkin, 1982). Identification was considered to be mediated by a

ventral or occipito-temporal channel and localization by a dorsal or occipito-parietal channel including also inputs from the superior colliculus. Refining this division of labour, Livingstone & Hubel (1988) proposed that the ventral pathway represented the parvocellular system projection while the dorsal pathway was an extension of the magnocellular system. Recently, the role of the two systems has also been accounted for in terms of an output distinction between perception and action, the control of action being more primitive in the phylogenetic history than the formation of perceptual representation (Milner & Goodale, 1995). It is worth noting that recent data argue for a "what" vs "where" distinction in the auditory modality as well (Binder et al., 1997). On the other hand, audiovisual integration does not follow the same rules in speech as in ventriloquism. While spatial proximity is critical for ventriloquism, increasing the spatial separation between the visual and auditory sources has little influence on the McGurk illusion (Bertelson, Vroomen, Wiegeraard & de Gelder, 1994).

5. Conclusions

The data presented here support the view that interactions of the ventriloquist type are performed in a computationally autonomous way, start early in life and are mediated by specific neural mechanisms. Ventriloquism is better accounted for in terms of primal or experience-expectant development than in terms of learned or experience-dependent development. As support for this view, it is worth remembering that the adjustments in localization realized by barn owls raised from birth to adulthood with prisms are of limited extent. The neural circuitry for these interactions is present at birth and constrains the range of possible adjustments. The adjustments which normally occur during development being small in size mean the capacity for larger changes has not evolved. According to Smith (1994), the discovery of different multisensory integration sites in the brain provides additional evidence against integrative theories because integration through learning would be expected to implicate high levels of cognitive processing (association areas of the cortex).

Because many objects or events are specified by two or more modalities, multimodal integration provides many advantages. In being operative early in life in a way consistent with the Gestalt grouping principles, it allows the young organism to analyze the spatial scene and to begin learning. Recently, Proust (1997) came to the conclusion that the ability to detect and compensate spatial

discordances in animals was a prerequisite for elaborating representations and for developing mind.

References

- Bailey, M. & Johnson, K. (1997). Synesthesia: is a genetic analysis feasible? In S. Baron-Cohen & J. Harrisson (Eds.). *Synesthesia* (pp. 182-207). Oxford, UK: Blackwell .
- Bertelson, P., Vroomen, J., Wiegendaard, G. & de Gelder, B. (1994). Exploring the relation between McGurk interference and ventriloquism. *Proceedings of the International Conference on Spoken Language processing, 2*, 559-562, Yokohama
- Binder, J.R., Frost, J.A., Hammeke, T.A., Springer, J.A., Bellgowan, P.S.F. & Rao, S.M. (1997). "What" vs. "where" in the auditory cortex: A functional MRI study. *Society for Neurosciences Abstracts*, 1032, New Orleans.
- Bower, T.G.R. (1974). *Development in infancy*. San Francisco: W.H. Freeman
- Bregman, A.S. (1990). *Auditory scene analysis*. Cambridge, MA: The MIT Press.
- Changeux, J.P. (1983). *L'homme neuronal*. Paris: Fayard.
- Campbell, R. (1998). How brains see speech: the cortical localisation of speechreading in hearing people. In: R. Campbell, B. Dodd & D. Burnam (Eds) *Hearing by eye II* (pp. 177-194). Hove, U.K.: Psychology Press.
- Cytowic, R.E. (1993). *The man who tasted shapes*. London: Abacus.
- Edelman, G. (1987). *Neural Darwinism*. New York: Basic Books.
- Fodor, J.A. (1983). *The modularity of mind*. Cambridge, MA: The MIT Press.
- Frost, D.O. (1990). Sensory processing in novel, experimentally induced crossmodal circuits. In A. Diamond (Ed.), *The Development and neural bases of higher cognitive functions*. *Annals of the New York Academy of Sciences*, 608, 92-112.
- Gottlieb, G., Tomlinson, W.T. & Radell, P.L. (1989). Developmental intersensory interference: Premature visual experience suppresses auditory learning in ducklings. *Infant Behavior and Development*, 12, 1-12.
- Greenough, W.T., Black, J. & Wallace, C.S. (1987). Experience and brain development. *Child development*, 58, 539-559.
- Harrison, J. & Baron-Cohen, S. (1997). Synesthesia: a review of psychological theories. In S. Baron-Cohen & J. Harrisson (Eds.). *Synesthesia* (pp. 109-122). Oxford, UK: Blackwell.
- Innocenti, G.M. & Clarke, S. (1984). Bilateral transitory projection to visual areas from auditory cortex in kittens. *Developmental Brain Research*, 14, 143-148.
- Johnson, M.H. (1997). *Developmental Cognitive Neuroscience*. Oxford, UK: Blackwell.
- Kennedy, H. & Dehay, C. (1993). The relevance of primate corticogenesis for understanding the emergence of cognitive abilities in man. In: B. de Boysson-Bardies, S. de Schonen, P. Juszczyk, P. McNeilage & J. Morton (Eds.). *Developmental neurocognition: Speech and face processing in the first year of life* (pp. 17-30). Dordrecht: Kluwer.
- King, A.J., & Carlile, S. (1993). Changes induced in the representation of auditory space in the superior colliculus by rearing ferrets with binocular eyelid suture. *Experimental Brain Research*, 94, 444-455.
- King, A.J., Hutchings, M.E., Moore, D.R. & Blakemore, C. (1988). Developmental plasticity in the visual and auditory representations in the mammalian superior colliculus. *Nature*, 332, 73-76.
- Knudsen, E.I. (1983). Early auditory experience aligns the auditory map of space in the optic tectum of the barn owl. *Science*, 222, 939-942.
- Knudsen, E.I., Esterly, S.D. & du Lac S. (1991). Stretched and upside-down maps of auditory space in the optic tectum of blind-reared owls; Acoustic basis and behavioral correlates. *The Journal of Neuroscience*, 11, 1727-1747.
- Knudsen, E.I. & Knudsen, P.F. (1989). Vision calibrates sound in developing barn owls. *The Journal of Neuroscience*, 9, 3306-3313.
- Lewkowicz, D.J. & Turkewitz, G. (1980). Cross-modal equivalence in early infancy: Auditory-visual intensity matching. *Developmental Psychology*, 16, 597-607.
- Lickliter, R. & Banker, H. (1994). Prenatal components of intersensory development in precocial birds. In: D.J. Lewkowicz and R. Lickliter (Eds.), *The Development of Intersensory Perception* (pp.: 59-80). Hillsdale, NJ: Lawrence Erlbaum Ass.
- Livingstone, M. & Hubel, D. (1988). Segregation of form, color, movement and depth: Anatomy, physiology, and perception. *Science*, 240, 740-749.
- Milner, A.D. & Goodale, M.A. (1995). *The visual brain in action*. New York: Oxford University Press.
- Marks, L. (1975). On colored-hearing synesthesia: Cross-modal translations of sensory dimensions. *Psychological Bulletin*, 82, 303-331.
- Marks, L. (1978). *The unity of the Senses*. New York: Academic Press.
- Marr, D. (1982). *Vision*. New York: W.H. Freeman and Co.

- Maurer, D. (1993). Neonatal synesthesia: Implications for the processing of speech and faces. In: B. de Boysson-Bardies, S. de Schonen, P. Jusczyk, P. McNeilage & J. Morton (Eds.). *Developmental neurocognition: Speech and face processing in the first year of life* (pp. 109-124). Dordrecht: Kluwer.
- McGurk, H. & McDonald, J. (1976). Hearing lips and seeing voices. *Nature*, 264, 746-748.
- Melzoff, A.N. (1993). Molyneux's babies: Cross-modal perception, imitation and the mind of the preverbal infant. In: N. Eilan, R. McCarthy and B. Brewer (Eds.), *Spatial representation. Problems in Philosophy and Psychology* (pp.: 219-235). Cambridge, MA: Blackwell.
- Neville, H.J. (1990). Intermodal Competition and Compensation in Development. Evidence from studies of the visual system in congenitally deaf adults. In A. Diamond (Ed.), *The Development and neural bases of higher cognitive functions. Annals of the New York Academy of Sciences*, 608, 71-91.
- Neville, H.J. (1995). Developmental specificity in neurocognitive development in humans. In M. Gazzaniga (Ed.), *The cognitive Neurosciences* (pp.: 219-236). Cambridge, MA: The MIT Press.
- Piaget, J. (1952). *The origins of intelligence in children*. New York: International Universities Press.
- Proust, J. (1997). *Comment l'esprit vient aux bêtes. Essai sur la représentation*. Paris: Gallimard
- Pylyshyn, Z.W. (1980). Computation and cognition: issues in the foundations of cognitive science. *The Behavioral and Brain Sciences*, 3, 111-169.
- Radeau, M. (1992). Cognitive impenetrability in auditory-visual interaction. In: J. Alegria, D. Holender, J. Morais, & M. Radeau (Eds.), *Analytic Approaches to Human Cognition*. (pp. 41-55). Amsterdam: Elsevier Science Publishers.
- Radeau, M. (1994a). Auditory-visual spatial interaction and modularity. *Cahiers de Psychologie Cognitive*, 13, 1-51.
- Radeau, M. (1994b). Ventriloquism against audio-visual speech: Or, where Japanese speaking barn owls might help. *Cahiers de Psychologie Cognitive*, 13, 124-140.
- Radeau, M. & Bertelson, P. (1974). The aftereffects of ventriloquism. *Quarterly Journal of Experimental Psychology*, 26, 63-71.
- Radeau, M. & Bertelson, P. (1977). Adaptation to auditory-visual discordance and ventriloquism in semirealistic situations. *Perception and Psychophysics*, 22, 137-146.
- Rebillard, G., Rebillard, M. & Pujol, R. (1980). Factors affecting the recording of visual-evoked potentials from the deaf cat primary auditory cortex (AI). *Brain Research*, 188, 252-254.
- Smith, L.B. (1994). Foreword. In: D.J. Lewkowicz and R. Lickliter (Eds.), *The Development of Intersensory Perception* (pp.: ix-ix). Hillsdale, NJ: Lawrence Erlbaum Ass.
- Spear, N.E. & McKinzie, D.L. (1994). Intersensory integration in the infant rat. In: D.J. Lewkowicz and R. Lickliter (Eds.), *The Development of Intersensory Perception* (pp.: 133-161). Hillsdale, NJ: Lawrence Erlbaum Ass.
- Stein, B.E. & Meredith, M.A. (1993). *The merging of the sense*. Cambridge, MA: The MIT Press.
- Stein, B.E., Meredith, M.A. & Wallace, M.T. (1993). Nonvisual responses of visually-responsive neurons. In: T.P. Hicks, S. Molotchnikoff and T. Ono (Eds.), *Progress in Brain Research* (95), *The visually Responsive Neuron: From Basic Neurophysiology to Behavior* (pp.: 79-90). Amsterdam: Elsevier.
- Stein, B.E., Wallace, M.T. & Meredith, M.A. (1994). Neural mechanisms mediating attention and orientation to multisensory cues. In: M. Gazzaniga (Ed.), *The cognitive Neurosciences* (pp.: 683-702). Cambridge, MA: The MIT Press.
- Sumby, W.H. & Pollack, I. (1954). Visual contributions to speech intelligibility in noise. *Journal of the Acoustical Society of America*, 26, 212-215.
- Ungerleider, L.G. & Mishkin, M. (1982). Two cortical visual systems. In: D.J. Ingle, M.A. Goodale & R.J. Mansfield (Eds.), *The analysis of visual behaviour* (pp.: 549-586). Cambridge, MA: The MIT Press.
- Welch, R.B. & Warren, D.H. (1980). Immediate perceptual response to intersensory discrepancy. *Psychological Bulletin*, 88, 638-667.
- Wertheimer, M. (1961). Psychomotor coordination of auditory-visual space at birth. *Science*, 134, 1692.
- Wickelgren, B.G. (1971). Superior colliculus: Some receptive field properties of bimodally responsive cells. *Science*, 173, 69-72.
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