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Spatial characteristics of visual-auditory summation in human saccades

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Abstract

Bimodal (auditory + visual) stimuli reduce saccade latencies in human observers to a degree that exceeds levels predictable by probabilistic summation between parallel, independent unimodal pathways. These interactions have been interpreted in terms of converging visual and auditory afferents within the oculomotor pathways, specifically within the superior colliculus (SC). The present work describes the spatial tuning of auditory-visual summation in human saccades, using diagnostics derived from stochastic models of information processing. Consistent with expectations based on the electrophysiology of the SC, the magnitude of facilitation varied with the degree of spatial correspondence, and the spatial tuning was quite coarse. © 1998 Elsevier Science Ltd. All rights reserved.

Keywords: Auditory-visual; Convergence; Saccade latencies

1. Introduction

The purpose of saccadic eye movements is to align the high-resolution fovea with peripheral events. These events are often multimodal in character, so it is perhaps not surprising to find a considerable diversity of sensory inputs which can serve to initiate saccades. In addition to visual inputs, vestibular, somesthetic, and auditory afferents access saccade-generating mechanisms. Indeed, the oculomotor system has become something of a model system for the analysis of polymodal integration.

One important oculomotor structure, the superior colliculus (SC), receives convergent visual, auditory, and somesthetic inputs [1–6]. The colliculus lies at an interface between sensory and motor processing, and plays an important role in initiating saccades [7–12]. Some collicular neurons appear to be entirely sensory in nature while others discharge prior to saccadic eye movements [13–15]. The presaccadic discharge depends upon the particular movement vector, which, in analogy to sensory receptive fields, is called the cell's 'movement field'. The orderly distribution of these fields in the SC creates a topographically organised map of saccade movement vectors. The receptive field locations of visually responsive cells are also arranged in an orderly way within the colliculus, and the receptive fields of visual cells are in spatiotopic register with the movement fields of the pre-saccadic discharge neurons [3,16–18]. Thus, the neural circuitry in the SC appears well-suited to perform the task of foveating eccentric visual events.

A similar topographic arrangement within the SC has been discovered for the representation of auditory space [1–3,17,19–21] and the body surface [3,5,6,22,23]. Indeed, polymodal convergence occurs at the cellular level, and polymodal cells within the SC display distinct patterns of spatial correspondence between the locations of their visual, auditory, and/or somesthetic receptive fields [3,5,6,17,21,22,24–29]. These cells integrate afferent activity conveyed over different modality-specific pathways, and their responses to a polymodal signal are often substantially greater than their responses to the individual unimodal components [3,4,27,28,30].

This paper describes a psychophysical analog of polymodal integration in the human saccadic control system. We begin by describing a method for ascertaining the rules by which signals carried over initially

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separable pathways might be combined. We then apply this method to an analysis of visual-auditory interactions in the generation of saccadic eye movements. In view of the spatial correspondence between the auditory and visual receptive field locations observed in polymodal neurons in the superior colliculus, we predicted that summation effects should depend on the degree of spatial alignment between the auditory and visual targets. This prediction was confirmed. We also describe the accuracy of saccades generated under these different stimulus conditions.

2. Method

2.1. Recording

Eye position was recorded (with a resolution of at least 10 min arc) using the scleral search coil technique. The large induction coils used in this experiment (2 × 2 m) produced a magnetic field of sufficient uniformity, so that eye position could be recorded independent of head motions. Head rotation was recorded via a second coil placed on the forehead, but only the eye movements are reported in this paper.

Eye and head position were digitized using 16 bit digital-to-analog converters at a sampling rate of 250 Hz. The records were converted from voltage signals to angular deviations based on calibration records taken at the beginning of each experimental session. As suggested by the manufacturer of the search coils (Skalar Medical), experimental sessions were confined to 30 min duration. Data were obtained on alternate days. The eye records were then analyzed off-line. Saccades were automatically detected using a velocity criterion, and their latencies were defined as the temporal interval between the onset of the target and the initiation of the saccade. In some bimodal conditions (described below) targets were presented with a temporal onset asynchrony. In these cases the latencies were measured relative to the onset of the first stimulus in the pair.

2.2. Subjects

There were three subjects. Two were authors (HH and DA) and the other (RT) was an undergraduate and was paid for her participation. All observers had normal acuity or wore corrective eyeglasses. Each subject was informed about the nature of the recording procedures and the general goals of the experiment and each signed an informed consent document. All experimental procedures were approved by the Dartmouth College Committee for the Protection of human subjects.

2.3. Procedure

A discrete trial procedure was used in which each trial began with the onset of a central fixation point. After a variable interval (750–1250 ms), a saccade target appeared. Subjects were instructed to look at these targets as quickly as possible. They were told that they could move both their heads and eyes, and they should perform these gaze shifts using whatever combination of head and eye movements that seemed natural for them. Both eye and head position were recorded relative to the frame of reference provided by the field inducing coils.

Red light-emitting diodes (LEDS) served as visual targets. Small speakers located directly beneath each LED provided the auditory targets. There were six possible target locations, located at eccentricities of ± 5.0, 15.0 and 25.0° along the horizontal meridian. Visual targets consisted of 5 ms flashes of 500.0 cd m^{-2}. The auditory targets were brief clicks (5 ms, 72 d Bspl). The experiments were conducted in an isolated, completely darkened room.

There were two types of experimental sessions. During single modality sessions, subjects were presented with either visual or auditory targets. There were no bimodal targets during these sessions. Visual and auditory targets occurred in a random sequence and were equally likely. Position varied randomly as well, and each position was sampled with equal frequency. These sessions were required in order to estimate the distribution functions for latencies to each possible unimodal target. We describe the actual analysis below.

The second type of experimental session contained bimodal targets. In this condition, half of the trials presented visual targets, and the other half presented bimodal (visual + auditory) targets. Unimodal visual trials were included in the bimodal condition in order to encourage responses to the visual targets in general. Bimodal stimuli were presented with either synchronous onsets, or with a temporal onset asynchrony (SOA). The SOA was introduced in an attempt to compensate for any differences that might occur in the saccadic latencies to the unimodal visual and auditory targets. Although the intensities selected were intended to match the saccade latencies for each target modality, the SOA manipulation provided some additional insurance that matched latencies would be obtained under each condition. Since previous experience suggested that auditory stimuli tend to produce saccades with shorter latencies, the visual stimulus lead the auditory in all non-zero SOA conditions.

Subjects were told that some trials would present auditory as well as visual stimuli, and that these auditory signals might or might not be aligned with the visual targets. In all cases they were instructed to direct their saccades to the visual targets. We refer to the auditory stimulus as an accessory stimulus, since the subject's intent was to fixate the visual target on bimodal trials. For each of the six visual target locations, there were four possible locations for the accessory auditory stimuli: the three locations within the same hemifield (5.0, 15.0 and 25.0°) and the 5° location in the contralateral hemifield. Each of these four auditory locations was sampled with equal frequency in a randomized order.

The experiment consisted of multiple, interleaved replications of these two experimental conditions. All events were controlled by computer, and data were collected in repeated blocks of 100 trials (typically two to three blocks/day). The single modality and bimodal sessions were interleaved with a ratio of 3 to 1 (bimodal to unimodal). The combined data base from all three subjects consists of 16 000 saccades (12 000 trials from the bimodal condition (6000 of which actually had bimodal targets) and 4000 trials from the unimodal condition).

2.4. Method of analysis: The race model inequality

We now turn to a description of the logical foundations of the analytic method. We begin with the assumption that visual and auditory stimuli selectively activate different afferent pathways, at least early in sensory processing. The issue then, is to determine whether the activity conveyed over these pathways remains independent or becomes integrated. If processing of the unimodal signals occurs independently and in parallel, bimodal detection is optimized by use of an OR decision rule. That is, processing should continue until either unimodal channel has obtained sufficient information to elicit the correct response. In the reaction time (RT) literature, models of parallel processing using this OR decision rule are often called 'race models', since the first channel to complete processing determines the timing of the response [31]. The processing times (i.e. times needed to reach the independent criteria for detection of the visual and auditory targets) on each channel are assumed to be random variables. Race models predict that processing times are reduced by presenting redundant (bimodal) signals because the OR decision rule effectively selects the minimum of two random variables, and the distribution mean for the minimum of two random variables is smaller than the mean of either of the marginal distributions, i.e. $E(\min[T_\mathrm{a}, T_\mathrm{v}]) \leq \min[E(T_\mathrm{a}), E(T_\mathrm{v})]$ where T_a is the random variable representing the detection time for the auditory target, T_v represents the corresponding visual detection time, min[ ] is an operator that selects the first process to complete processing (the OR decision rule) and E is the expected value. Thus, parallel channels can remain completely separate, and therefore the activities conveyed within them can remain statistically independent, and we would still expect redundant auditory and visual signals to reduce the mean latency of saccades; at least when the targets are aligned in space (so the same saccade serves to foveate either target). This is often termed probability summation [31–34]. It is a purely statistical effect and does not rely on interactions between the two afferent channels.

On the other hand, various sorts of interactions and/or statistical dependencies could occur [32,33,35,36]. In the global sense, dependence between parallel sensory channels could be mutually inhibitory or faciliatory. This type of dependence might result from interactions between auditory and visual pathways, which of course, appears to occur at several levels of neural processing, including the cortex [30,37] and the SC [3,4,17,27,28,30]. One issue that is especially important to the present experimental situation concerns the possibility that signals might be combined prior to being evaluated by a single decision mechanism. In general, such a model is termed a channel summation model. All other things being equal, the redundant signals effect produced by a channel summation architecture is greater than that attributable to probability summation [31,36].

In the absence of mutually excitatory or inhibitory interactions, the cumulative distribution function (CDF) of the detection times in one channel remains invariant whether or not the other channel is active. This effect is termed 'context independence' (CI), and amounts to an assumption that the effects of multimodal stimuli can be assessed via an analysis based upon latency distributions obtained from unimodal signals presented in isolation.

To see how can these notions be applied to actual experimental results, we turn to a mathematical inequality that has received considerable experimental [32,33,36,38–42] and theoretical attention [31,34]. Consider the latency of a saccade when an observer is presented with auditory and visual targets that occupy the same spatial location. The task is to execute a saccade towards the target(s). Whether or not any statistical dependencies are present, any parallel model of bimodal processing using the OR decision rule states that the probability that the observer detects either the visual or the auditory stimulus by time t is given by the probability that the visual stimulus was detected by time t, plus the corresponding probability for the auditory stimulus, minus the probability that both stimuli were detected by time t. This can be expressed in terms of cumulative distribution functions as follows:

$$\begin{aligned} P(\min[T_\mathrm{a}, T_\mathrm{v}] \leq t \mid A\&V) \\ = P(T_\mathrm{a} \leq t \mid A\&V) + P(T_\mathrm{v} \leq t \mid V\&A) \\ - P(T_\mathrm{a} \leq t \cap T_v \leq t \mid A\&V) \end{aligned}$$

The last term on the right side of this equality is the joint probability (the probability that both stimuli are detected by t). According to the elementary laws of probability theory, the joint probability of the co-occurrence of two statistically independent events equals the product of the probabilities of each individual event. If context independence is in force, the above formula is identical to one where the probabilities can be taken from the unimodal stimulation conditions:

$$P(\min[T_a, T_v] \leq t|A\&V) = P(T_a \leq t|A\&\bar{V}) + P(T_v \leq t|V\&\bar{A}) - \{P(T_a \leq t|A\&\bar{V}) \times P(T_v \leq t|V\&\bar{A})\}$$

Even if statistical independence does not hold, the term representing the joint event is still a positive quantity (on the interval between 0.0 and 1.0) subtracted from the summed single channel probabilities. Hence, if our assumption that each modality selectively activates a modality-specific input channel is satisfied, we can permit any degree of statistical dependency and it still follows that race models predict that:

$$P(T_a \text{ OR } T_v \leq t|A\&V) \leq P(T_a \leq t|A) + P(T_v \leq t|V) \tag{1}$$

Cast in terms of saccade latencies, we rewrite Eq. (1) as:

$$P(\text{Lat}_{\text{saccade}} \leq t|A\&V) \leq P(\text{Lat}_{\text{saccade}} \leq t|A) + (P\ \text{Lat}_{\text{saccade}} \leq t|V) \tag{2}$$

The above expression is known as the race model inequality [31–34]. It represents a performance boundary for separate parallel processing that is terminated according to the OR decision rule.

We now can state how these notions of the probabilistic nature of neural information processing can be applied to actual human performance. Violations of the race model inequality falsify race processing between parallel channels that conform to context independence, and therefore indicate channel summation, or at least parallel processing of channels that display a massive form of mutual facilitation. Thus, strong evidence of sensory convergence is provided any time the cumulative distribution function (CDF) for saccade latencies obtained using bimodal targets exceeds the sum of the unimodal CDFs.

In order to simplify the presentation of results, we evaluated the race model inequality by subtracting the sum of the CDFs for saccade latencies to visual and auditory targets from the obtained CDF for bimodal targets consisting of each of these component stimuli presented either simultaneously or with a stimulus onset asynchrony (SOA) of 50 or 100 ms (visual leading). This difference is evaluated as a function of time, and is positive if the inequality has been violated at that point in time. The systematic combination of six different visual targets (±5, 15 and 25° along the horizontal meridian), with different acoustic sources produced 24 different bimodal stimulus conditions with varying degrees of spatial (mis)alignment. The race model inequality was evaluated for each of these stimulus conditions, for at least two SOAs in each of three observers. The results presented include only the SOAs that produced the best latency match for each observer. For observer RT, we present the results at 0 ms SOA, and for HH and DA we present the results for the 50 ms (visual-leading) SOA condition.

3. Results

3.1. Saccades to bimodal targets consistently violate the race model inequality

Fig. 1 illustrates an example of a robust violation of the race model inequality for spatially aligned visual and auditory targets. Included in the figure are the CDFs for the unimodal visual and the unimodal auditory targets, the race model boundary (the unimodal CDFs summed and truncated at 1.0) and the obtained

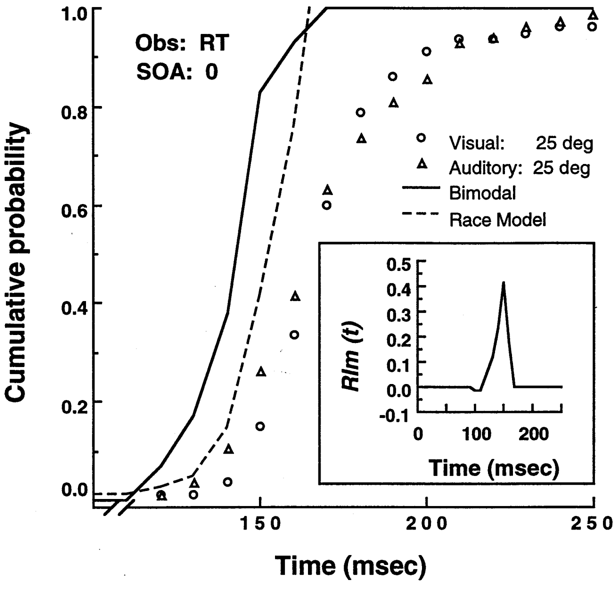

Fig. 1. Illustration of the diagnostic method used to evaluate polymodal summation. All cumulative distribution functions (CDFs) are estimated from latency distributions with a bin width of 10 ms. For clarity, the data points for the bimodal and race model CDFs and the lines for the unimodal CDFs have been omitted. The sum of the unimodal CDFs represents an upper performance limit for probability summation, which is indicated by the dotted line. The obtained bimodal CDF (solid line) lies above the boundary, providing strong evidence of bimodal neural summation. The inset shows the difference between the obtained bimodal CDF and the upper bound of the race model.

CDF for bimodal targets. Given the assumption of context independence (that activity in a visual channel is not influenced by activity in an auditory channel), the race model inequality defines a performance limitation on parallel processing using the OR decision rule. It can be seen that the cumulative densities for the bimodal targets consistently violate this boundary (the obtained CDF is greater than the upper limit predictable on the basis of probability summation). This provides strong evidence for channel summation (convergence of auditory and visual inputs prior to response execution). In the inset of Fig. 1, we plot the difference between the obtained bimodal CDF and the summed unimodal CDFs. For convenience we call this the race inequality measure, or RIm. Positive values of RIm result from violations of the inequality, providing evidence for channel summation.

Notice that the shortest latency saccades to bimodal targets were faster than any of the saccades to either type of unimodal target. This clearly disconfirms the race model, since the OR operator cannot produce saccades to bimodal targets with latencies shorter than the shortest latency unimodal saccades. Notice too, how the observed performance exceeds the race boundary throughout the entire range of latencies. This result is actually fairly unusual. Typically, violations of the race model boundary occur early in time, but because of the skewed nature of latency distributions, usually do not occur later in time. Like any boundary condition, the race model bound is asymmetric in that violations are diagnostic, whereas an absence of violations need not be. We therefore focus on the violations of the race model inequality, or the positive values of RIm(t). In order to look for patterns in the magnitude of the violations that might relate to the degree of spatial coincidence between the visual and auditory targets, it is necessary to condense the RIm(t) curves into some meaningfully small set of data points. This was accomplished by computing the areas under the positive portions of the measure. These areas provide some reflection of the magnitude of the violations, and permit comparisons between the different bimodal conditions (degrees of spatial alignment). If summation is greatest when the unimodal targets are aligned, then that should be reflected in a greater positive area in the RIm(t) curve for that condition.

3.2. Coarse spatial tuning of bimodal summation for saccades

Figure 2 illustrates the patterns of these arial calculations for each bimodal stimulus condition. Each data point represents the calculated positive area of RIm(t) for a given pair of visual and auditory targets, averaged across the three observers. Each curve illustrates data for visual targets at either 5, 15 or 25°, and the abscissa represents the spatial location of the auditory component of the pair. The data for leftward and rightward saccades have been combined. The curves are generally concave downward, indicating a degree of spatial tuning for the summation effect. However, the tuning is obviously fairly coarse, as auditory stimuli as much as 30° from the visual target can still reduce latencies to an extent that suggests bimodal convergence rather than a 'race' between separate modality specific pathways. Note that modest levels of channel summation are evident even when the visual target is presented in one hemifield, and the auditory target is presented 5° into the contralateral hemifield. This is especially apparent at the most extreme eccentricity for the visual target (25°). There was also a tendency for auditory stimuli presented at eccentricities less than the visual target to produce more summation than auditory stimuli presented at greater eccentricities than the visual targets.

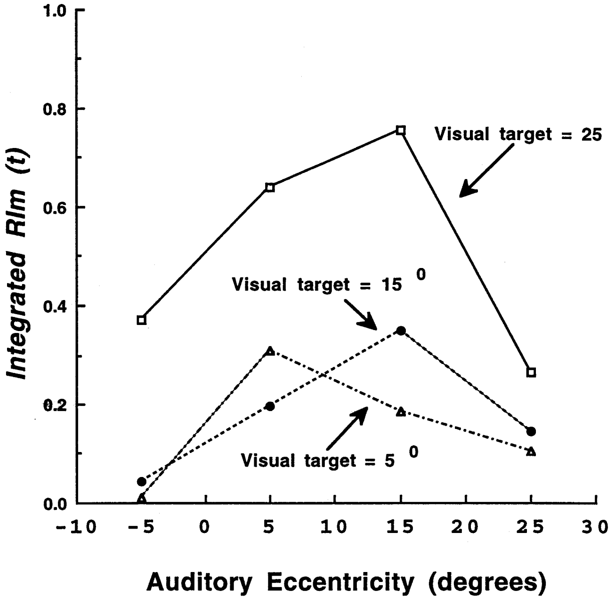

Fig. 2. Integrated positive areas of the race inequality measure plotted as a function of spatial alignment of the accessory auditory stimulus. The concave downward shape of the curves is indicative of the degree of spatial tuning for auditory-visual summation in saccades.

The broad spatial tuning suggested that Fig. 2 could result from a subject's inability to accurately identify the actual location of the sound sources. In this case, we might expect a great deal of variance in the accuracy's of the saccades to the acoustic targets. Fig. 3 presents amplitude histograms of the saccades directed to visual and auditory targets in observer RT. Whereas the accuracy of saccades to auditory targets was clearly not as precise as visually guided saccades, it is also apparent that acoustically guided saccades are substantially more accurate than the coarse spatial tuning of the summation effects illustrated in Fig. 2. We interpret this as indicating that summation effects on saccade latencies occur even though the component signals pre-

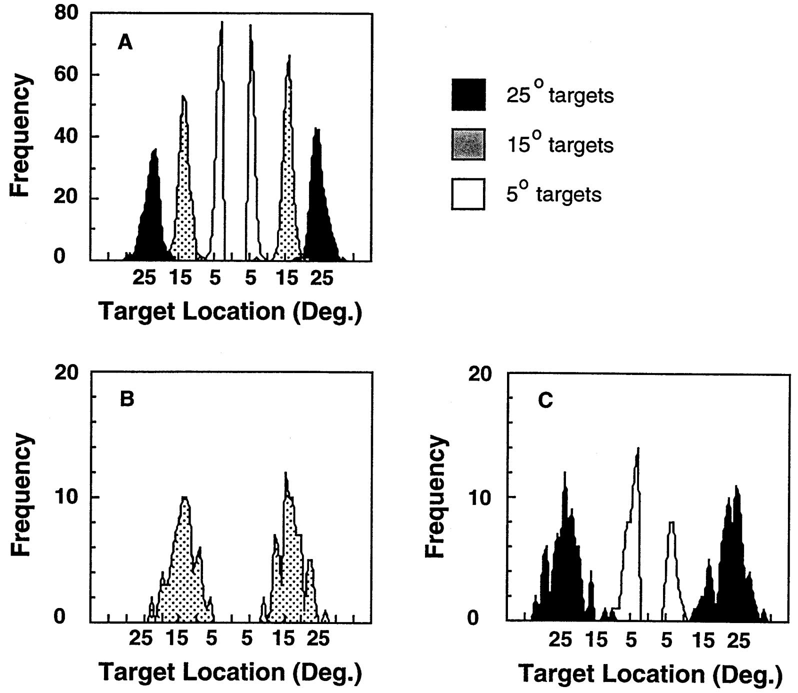

Fig. 3. Amplitude histograms illustrating of the accuracy of saccades to eccentric visual (A), and auditory (B, C) targets. Data from observer RT.

sented alone would generate topologically distinguishable saccades.

3.3. Accuracy of saccades to bimodal signals

Misaligned visual and auditory targets reduce the latencies of saccadic eye movements despite the fact that the movement vectors of saccades to each of the misaligned components can be substantially different (see Fig. 3). The magnitude of misalignment between the visual and acoustic signals did affect the resulting saccade amplitude, but only to a very limited extent. This is illustrated in Fig. 4. Recall that subjects were instructed to fixate the visual targets as quickly as possible. They can obviously comply with these instructions, so the faciliatory effects of a misaligned acoustic stimulus on saccade latencies can occur without substantially influencing the amplitudes.

3.4. Other characteristics of saccades to bimodal targets

Fig. 5 illustrates the average amplitude-velocity relationship for the saccades generated under the various stimulus conditions used in this experiment. These curves have been termed the main sequence for saccades [43,44], and reflect aspects of the mechanical properties of the saccadic control system. As previously reported, velocities increase with increasing amplitude [43,44]. There is evidence of velocity saturation in the present results, and the expression $V = b + a$ [log(M)] provided a reasonably good fit, where V represents the average velocity, M represents the amplitude of the saccade, and b and a are curve-fitting parameters.

4. Discussion

The present results indicate that auditory and visual signals are combined within the oculomotor pathways in a manner consistent with channel summation. The most plausible neural implementation of the channel summation processing architecture is the faciliatory convergence of visual and auditory afferent activity onto single neurons within the oculomotor pathways. As polymodal convergence is a conspicuous feature of sensory neurons located in the superior colliculus, we interpret the present findings as a behavioural manifestation of polymodal integration in the superior colliculus of humans. These findings replicate earlier work from this and other laboratories [36,45–47], but extend those findings by (1) examining gaze shifts when the head is free to move and (2) specifically evaluating the spatial tuning of the bimodal summation effect using proven diagnostics for identification of a channel summation architecture. Evidence of spatial tuning was observed, but the effects are coarse. This does not appear to reflect an inability to accurately localize the auditory targets, because saccades directed towards the auditory targets showed more precision than the spatial tuning of the summation effect.

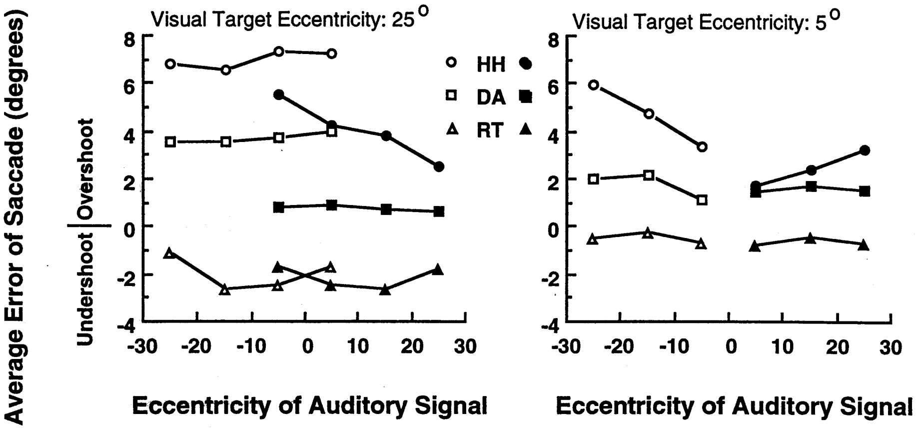

Fig. 4. Effects of misaligned auditory stimuli on the accuracy of saccades to visual targets. The abscissa represents the eccentricity of the auditory stimulus, the ordinate is saccade accuracy (expressed in terms of degrees of undershoot or overshoot), and the curves represent different locations for the visual targets. No center of gravity effect would produce horizontal lines. Strong center of gravity effects would produce inverted V-shaped curves in the upper panel, and V-shaped curves in the lower panel.

The results observed in this experiment are consistent with neurophysiological evidence concerning the function of neurons in the deep laminae of the mammalian superior colliculus. Approximately half of these cells respond to sensory information from multiple modalities [3,17,22,23,25–27], and such cells show over-additive summation effects [3,4,27,28,30]. In addition, these summation effects are dependent on the relative spatial and temporal alignment of the stimuli [23,27–29]. Although Stein and colleagues [29] found that spatial separations of 60° between the auditory and visual stimuli produced response depression in multimodal neurons, the spatial separation of our stimuli never exceeded 30°, which perhaps explains why no evidence of inhibition was evident in the present results. Given the large receptive field sizes of most neurons in the deep laminae of the superior colliculus [3,21,24–26] and the spatial correspondence between the auditory and visual receptive fields of these cells [17,21,24–27,29], it is probable that the stimuli used in our experiment were

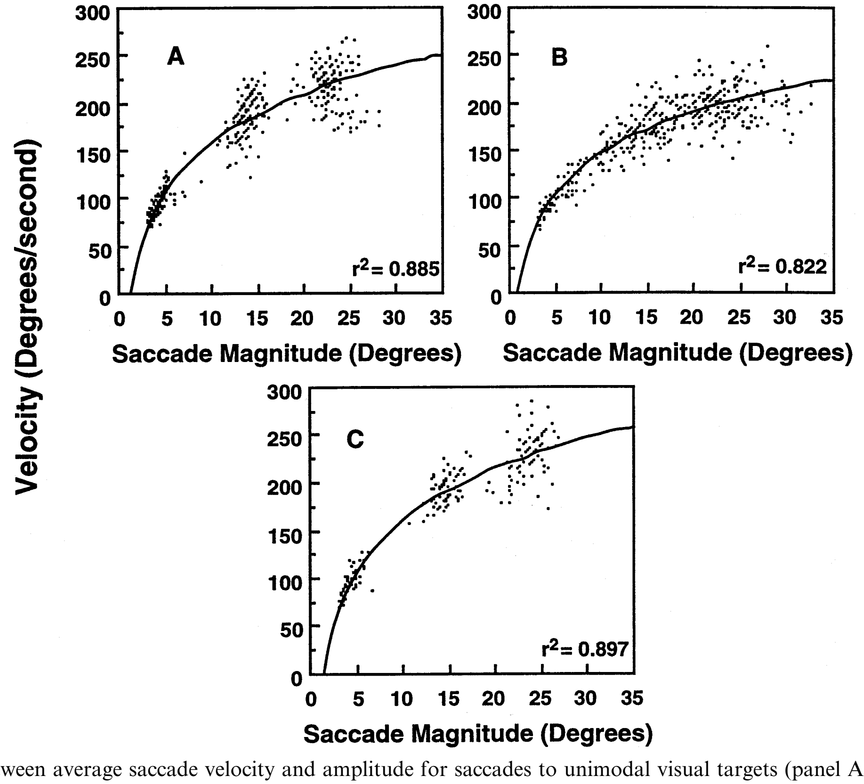

Fig. 5. Relationship between average saccade velocity and amplitude for saccades to unimodal visual targets (panel A), unimodal auditory targets (panel B) and bimodal targets (panel C) for observer RT. Mean R^2 across subjects for the three conditions were: 0.748 (unimodal visual), 0.675 (unimodal auditory), and 0.801 (bimodal).

processed simultaneously by multimodal neurons in the deep laminae of the superior colliculus. Finally, the SC sends afferent projections to oculomotor areas of the brain stem and to cervical levels of the spinal cord, which are associated with rapid shifts of eye and head position, respectively [3,17,18,48]. Thus, these summation effects seem most readily attributable to either polymodal integration in the superior colliculus or to the ways in which pre-motor elements access this polysensory information.

A misaligned auditory stimulus can facilitate the execution of a saccade to a visual target without dramatically affecting the amplitude of the resulting saccade. Substantially greater effects on saccade amplitudes have been observed using multiple visual stimuli [49–53]. There are two obvious differences between these earlier observations and the present results. One difference is of course the fact that the previous work involved intramodal stimulus pairs, whereas the present work involves intermodal stimulus pairs.

The effects of multiple visual inputs on saccadic movement vectors has typically been interpreted in terms of sensory interactions between elements that comprise the compound stimulus [52]. The present results indicate that intermodal sensory interactions can affect saccadic latency to a much greater extent than they affect saccadic amplitude. This finding is consistent with the model of Becker and Jürgens [54], who hypothesized that saccadic programming involves two processes, one which determines the latency and direction of the impending saccade, and one which determines its amplitude.

Acknowledgements

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