

# Non-lateralized auditory input enhances averaged vectors in the oculomotor system

N. Van der Stoep · T. C. W. Nijboer ·  
S. Van der Stigchel

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**Abstract** The decision about which location should be the goal of the next eye movement is known to be determined by the interaction between auditory and visual input. This interaction can be explained by the vector theory that states that each element (either visual or auditory) in a scene evokes a vector in the oculomotor system. These vectors determine the direction in which the eye movement is initiated. Because auditory input is lateralized and localizable in most studies, it is currently unclear how non-lateralized auditory input interacts with the vectors evoked by visual input. In the current study, we investigated the influence of a non-lateralized auditory non-target on saccade accuracy (saccade angle deviation from the target) and latency in a single-target condition in Experiment 1 and a double-target condition in Experiment 2. The visual targets in Experiment 2 were positioned in such a way that saccades on average landed in between the two targets (i.e., a global effect). There was no effect of the auditory input on saccade accuracy in the single-target condition, but auditory input did influence saccade accuracy in the double-target condition. In both experiments, saccade latency increased when auditory input accompanied the visual target(s). Together, these findings show that non-lateralized auditory input enhances all vectors evoked by visual input. The results will be discussed in terms of their possible neural substrates.

**Keywords** Saccade · Accuracy · Vector · Averaging · Oculomotor · Superior colliculus

## Introduction

Whereas people are accurate in making eye movements to a single visual target, eye movements are generally less accurate when executed to a single auditory target in the absence of visual information (Frens and Van Opstal 1995; Zambbarbieri et al. 1982). Furthermore, saccade latencies are known to be shorter to an auditory stimulus than to a visual stimulus (Hughes et al. 1994). When one visual and one auditory stimulus are presented at the same location and at the same time, these signals are integrated and saccade reaction times are even shorter than to an auditory stimulus (i.e., intersensory facilitation, Frens et al. 1995; Hughes et al. 1994). The aim of the present study was to investigate the effect of a non-lateralized auditory stimulus on initial saccade direction in the presence of one or two peripheral visual targets.

When two visual targets are presented in close proximity, the endpoint of an eye movement toward these elements is generally not positioned on one of the two elements but rather on a location in between the two elements (i.e., the “global effect”; Findlay 1982; Van der Stigchel and Nijboer 2011). Generally, this effect is stronger for shorter saccade latencies and smaller distances between the two elements (Ottes et al. 1985). The global effect has been explained by the center of gravity account (Pitts and McCulloch 1947). Pitts and McCulloch (1947) suggested that a saccade is initiated to the “center of gravity of the distribution of brightness” (p. 137). However, this explanation could not account for the finding that the global effect is only apparent when two stimuli are in

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N. Van der Stoep (✉) · T. C. W. Nijboer · S. Van der Stigchel  
Experimental Psychology, Helmholtz Institute, Utrecht  
University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands  
e-mail: N.VanderStoep@uu.nl

T. C. W. Nijboer  
Rudolf Magnus Institute of Neuroscience and Center of  
Excellence for Rehabilitation Medicine, University Medical  
Center Utrecht and Rehabilitation Center De Hoogstraat,  
Utrecht, The Netherlands

close proximity. A more recent theory by Tipper et al. (1997) could account for these results. Whereas this theory was initially used to explain reaching behavior, it also became an explanation for the way in which eye movements are initiated (for a review, see Van der Stigchel 2010). The theory proposes that elements in a visual scene are processed in parallel during initial perceptual analysis and evoke activity in neurons coding for a specific direction. Together, these neurons form a neuronal population and represent a vector that codes for the movement toward the location of an element in the visual scene. When two elements in a visual scene are in close proximity, the activity of neural populations that is evoked by these elements overlaps. Consequently, the vectors are averaged, which results in the initiation of saccades to the average direction (i.e., a global effect). Although a robust finding, saccade averaging does not occur in every trial, and a subset of eye movements is still directed to one of the two visual elements (Van der Stigchel and Nijboer 2011). When two visual elements are further apart, the activity of neural populations does not overlap and the resulting vectors are not averaged. This results in saccades being initiated to one of the two elements (i.e., no global effect). When two visual elements are in close proximity, but one of the elements evokes a stronger vector (because, for example, this element is brighter), the direction of the initiated saccade will deviate on average more toward the element associated with the stronger vector (i.e., less strong global effect).

One of the brain areas that is thought to be responsible for saccade programming and is assumed to be involved in representing these population vectors is the superior colliculus (SC), a retinotopically organized saccade map area in the midbrain (Lee et al. 1988). The SC responds not only to stimuli presented in the visual modality but also to stimuli presented in other modalities (Sparks and Nelson 1987). Because this important area in the oculomotor system appears to respond to stimuli of various modalities, previous studies have investigated the influence of multi-sensory input on eye movements. For example, Doyle and Walker (2002) showed that visual, auditory, and tactile distractors influenced the trajectory of saccades to a single visual target. Furthermore, in a study by Frens et al. (1995), a single visual stimulus and a single auditory stimulus were presented simultaneously. They observed a cross-modal global effect when a low-intensity visual stimulus and an auditory stimulus were presented simultaneously in close proximity. These results are in line with the findings by Lueck et al. (1990) who showed that the amplitude of a saccade to a horizontal auditory target on the left or right of fixation could be increased or decreased with a visual distractor in the same hemifield. These results suggest that stimuli from different modalities each evoke their own

vector in the oculomotor system and are combined before an eye movement is initiated.

Although the influence of lateralized stimuli of different modalities is known, it is unclear how vectors are integrated when both lateralized visual and non-lateralized auditory information is presented. To this end, we measured eye movements to unimodal (visual) and bimodal (visual and auditory) stimuli under single- and dual-target conditions. The auditory stimulus was presented through headphones to the left and the right ears simultaneously. This allowed us to investigate how eye movements to visual stimuli are influenced by a non-lateralized auditory stimulus. We hypothesized that the auditory input in our experiments would not evoke an individual vector in the oculomotor system due to its non-lateralized nature. In contrast, we expected that the auditory input would be coupled with the vectors evoked by the lateralized visual targets, enhancing the activity of all vectors present in the oculomotor system. In Experiment 1, we measured saccade angle deviation and saccade latency in response to a single visual target with and without an additional non-lateralized auditory non-target. In terms of the population coding theory, we hypothesized that when a visual target is presented together with a non-lateralized auditory non-target, the vector elicited by the visual stimulus will be strengthened by the auditory input. A stronger vector would imply a higher probability to initiate saccades in the direction of the vector. However, because saccades to single visual targets are already quite accurate, no effect on saccade endpoints was expected. In Experiment 2, we investigated the influence of the non-lateralized auditory input on saccade angle deviation and latency when two visual targets are presented at the same time. The two visual stimuli were presented in such a configuration that we expected them to elicit a global effect. Under dual-target conditions, we expected a stronger global effect (i.e., a higher proportion of saccades being initiated to the average vector) in the presence of auditory information than when no auditory information is present. Based on Tipper's vector theory, we assume that auditory information enhances both vectors and the average vector will therefore be stronger compared to when no sound is presented (even though the average vector has the same direction in both conditions). As mentioned, saccade averaging does not occur on every trial and only occurs when saccade vectors are averaged. Therefore, the stronger averaged vector due to the presence of the auditory information will increase the probability that saccades are initiated to the average vector and will result in more trials in which the global effect is observed. Another possibility is that the auditory stimulus will automatically be associated with one of the two visual targets. This would lead to only one of the vectors being strengthened and consequently results in more saccades

being initiated toward one of the two targets (i.e., a weaker global effect).

## Experiment 1

### Materials and methods

#### Participants

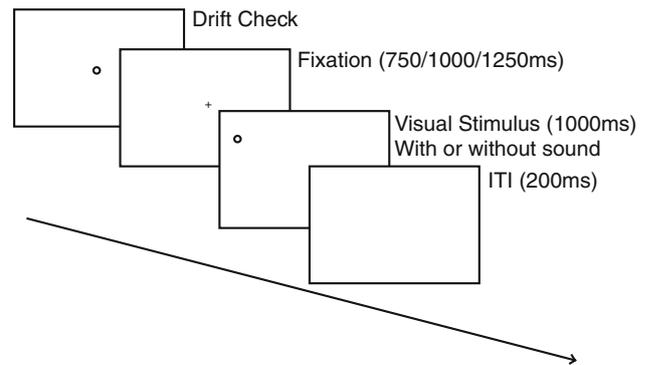
Six participants (mean age = 24.00, SD = 4.14 years; 3 male) were tested in this experiment for either money or course credits and had normal or corrected-to-normal visual acuity. All participants reported that they were able to hear the auditory stimulus. The experiment was performed in accordance with the Declaration of Helsinki. Written informed consent was obtained from all participants.

#### Apparatus

To record eye movements, a desktop-mounted Eyelink 1,000 system (SR Research Ltd., Canada) was used with a temporal resolution of 1,000 Hz and a spatial resolution of  $0.01^\circ$ . Each participant's head was stabilized with a chin rest. For all participants, the left eye was monitored. The monitor was positioned at a distance of 70 cm from the participants.

#### Stimuli, task, and procedure

Participants were tested in a dimly lit, sound-attenuated room. The experiment was presented on a 22-inch monitor (100 Hz, resolution:  $1,024 \times 768$  px). The experiment consisted of three blocks, each containing 128 trials adding up to a total of 384 trials. Before each trial, a drift check was performed. Next, a fixation cross was shown with a duration of either 750, 1,000, or 1,250 ms (for each participant a pre-generated random list was used). The fixation cross was a black plus sign ( $0.9^\circ \times 0.9^\circ$ ,  $0.14 \text{ cd/m}^2$ ) positioned at the center of the screen. After the offset of the fixation cross, a black target circle (diameter =  $0.9^\circ$ , line width =  $0.15^\circ$ ,  $0.14 \text{ cd/m}^2$ ) was presented for 1,000 ms. Targets were positioned at an imaginary circle around the fixation point at the center of the screen (radius =  $9.6^\circ$ ). Target locations were at  $35^\circ$  and  $55^\circ$  (upper right quadrant), at  $125^\circ$  and  $145^\circ$  (lower right quadrant), at  $215^\circ$  and  $235^\circ$  (lower left quadrant), and  $305^\circ$  and  $325^\circ$  (upper left quadrant) with  $0^\circ$  being the top position. In each trial, the target randomly appeared at one of the eight target locations. All stimuli were presented on a gray background ( $5.6 \text{ cd/m}^2$ ). On half of the trials, the visual target was accompanied by a 440-Hz square wave (100 ms, 70 dB SPL) presented through headphones (stereo) synchronous



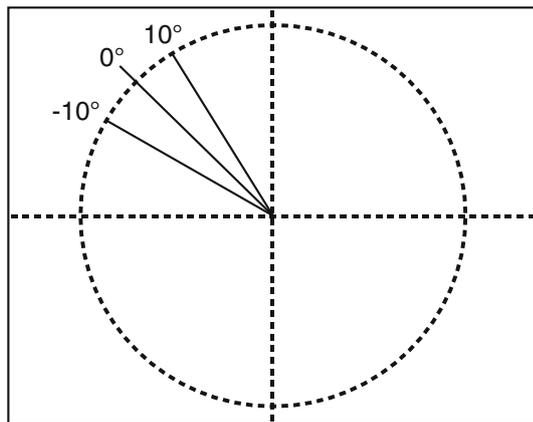
**Fig. 1** A schematic presentation of the procedure of Experiment 1

with the onset of the visual target. Unimodal and bimodal trials were randomized. After the target disappeared, only the gray background was presented for 200 ms before going to the next trial. Figure 1 shows the procedure for Experiment 1. Participants were instructed to fixate on the fixation cross and, as soon as it disappeared, to look as fast as possible to the element appearing on the screen. The duration of the experiment was approximately forty minutes.

#### Data analysis

**Pre-processing** Saccade latency was defined as the interval between target onset and the initiation of the first saccadic eye movement. For each trial, the first saccade executed after target onset was analyzed. Saccade landing positions for all four quadrants on the screen were recalculated to the upper left quadrant. Saccades were filtered on amplitude (min.  $4^\circ$ , max.  $30^\circ$ ) and onset latency (min. 60 ms, max. 500 ms). Only saccades that started within a radius of  $1.8^\circ$  (two times the diameter of the fixation cross) from the center of the fixation cross were included.

Saccade angle deviations were calculated as the absolute difference in saccade angle between the saccade landing position and the position in between the two possible target stimuli in a quadrant ( $10^\circ$  from both targets), from saccade starting position. This way, saccades landing on the target closest to the horizontal axis had a relative angle deviation of  $-10^\circ$  (absolute  $10^\circ$ ), whereas saccades landing on the target closest to the vertical axis had a relative angle deviation of  $10^\circ$ . A schematic representation of saccade angle deviations is shown in Fig. 2. Saccade angle deviations larger than two and a half standard deviations from the mean in a condition were removed from further analysis as they were considered outliers. Average saccade angle deviations for each condition were based on absolute saccade angle deviations. Absolute saccade angle deviations were averaged over all targets locations. After



**Fig. 2** A schematic representation of the saccade angle deviation measure that is used in Experiments 1 and 2

applying all filters, 6 % of the trials in the sound condition and 5 % of the trials in the no-sound condition were removed from further analysis.

**Statistical analysis** A two-tailed paired-samples *t* test on saccade latencies and saccade angle deviations between the sound and the no-sound conditions was done. To test whether the variance in absolute saccade angle deviations differed between the sound and the no-sound conditions for each participant, a paired-samples *t* test on the average variances in saccade angle deviation between the sound and the no-sound conditions was performed.

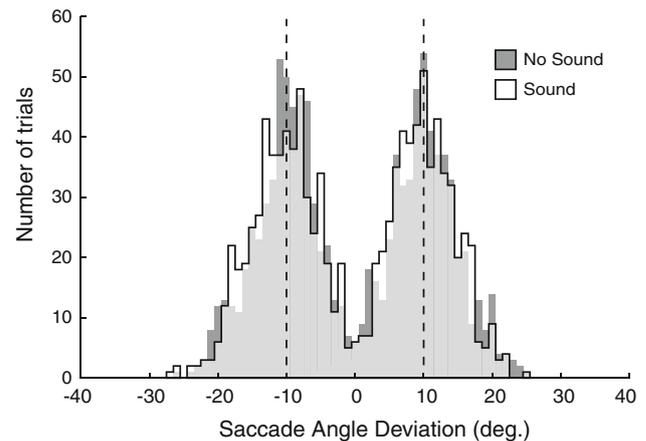
## Results

### *Saccade latencies*

There was a significant difference in saccade latency between the sound and the no-sound conditions [ $t(5) = 6.230, p < .005$ ]. The average saccade latency was shorter for the no-sound condition (mean = 229 ms, SD = 6.8 ms) than for the sound condition (mean = 240 ms, SD = 3.7 ms).

### *Saccade angle deviation*

There was no significant difference in average absolute saccade angle deviation from the target between the sound and the no-sound conditions [ $t(5) = .097, p > .90$ ]. The average saccade angle deviation was  $10.30^\circ$  (SD =  $.52^\circ$ ) for the sound condition and  $10.29^\circ$  (SD =  $.45^\circ$ ) for the no-sound condition. The distributions of relative saccade angle deviations for the two possible target locations in a quadrant in the sound and the no-sound conditions are shown in Fig. 3.



**Fig. 3** Distribution of relative saccade angle deviations for the no-sound (gray) and the sound condition (transparent white with black outline) of Experiment 1. The dashed lines indicate the two possible target locations

There was no significant difference in absolute saccade angle deviation variance between the sound (23.897) and the no-sound conditions (24.226) [ $t(5) = .142, p = .893$ ]. This means that the auditory input did not cause saccades to single targets to be more accurate.

## Discussion

The non-lateralized auditory non-target did not influence primary saccade accuracy to a single visual target as measured by absolute saccade angle deviation. This can be explained in terms of Tipper's vector theory. The visual target would elicit a vector in the oculomotor system in both the unimodal and the bimodal conditions. In the bimodal condition, the auditory input enhanced the vector, increasing the probability that a saccade is initiated in the direction of the average vector and possibly saccade accuracy. Although this effect was not observed, this can be explained by a ceiling effect of saccade accuracy to a single visual target. The auditory input did influence saccade latency to single visual targets. Saccade latencies to bimodal targets were significantly longer than to unimodal visual targets. As mentioned previously, intersensory facilitation has been frequently reported during bimodal stimulation (e.g., visual and auditory), resulting in shorter response times or shorter saccade latencies compared to unimodal stimulation (in this case, visual only) (Colonius and Diederich 2004; Frens et al. 1995; Gielen et al. 1983). Intersensory facilitation, however, is subject to several rules. Perhaps the most important of these rules are the spatial and the temporal rules (Colonius and Arndt, 2001). These rules suggest that intersensory facilitation is stronger when an auditory stimulus and a visual stimulus are closer to each other in space and time. In Experiment 1, the visual and auditory stimuli were aligned in time. However, it is likely that the auditory stimulus was not

associated with one specific location, as it was presented through headphones. This might have resulted in an absence of intersensory facilitation.

To further investigate the influence of non-lateralized auditory input on initial saccade direction, we presented two visual targets instead of one in Experiment 2. Because saccade accuracy is diminished when two visual targets are presented in close proximity (a global effect/saccade averaging), there is more room for change in saccade accuracy when the visual stimulus is accompanied by auditory input. An enhancement of the vectors to the two visual targets would result in a stronger average vector and a higher probability of saccades landing in the average direction of the visual targets and thus a stronger global effect. Because auditory input did not change the variance in saccade angle deviation in a single-target condition, a stronger global effect in the sound condition can be explained by a stronger average vector, but not by differences in saccade angle deviation variance between the sound and the no-sound condition.

## Experiment 2

### Materials and methods

#### Participants

Eleven participants (mean age = 27.8, SD = 4.9 years; 7 males) were tested in this experiment for either money or course credits. All participants had normal or corrected-to-normal visual acuity and reported that they were able to hear the auditory stimulus. The experiment was performed in accordance with the Declaration of Helsinki. Written informed consent was obtained from all participants.

#### Apparatus

The same apparatus as described under Experiment 1 was used.

#### Stimuli, task, and procedure

The same experimental setup as in Experiment 1 was used. The only difference between Experiments 1 and 2 is that instead of one visual target, two visual targets were presented in each trial. The 8 stimulus locations were the same as in Experiment 1, but the two visual targets were always presented in the same quadrant of the screen.

#### Data analysis

*Pre-processing* The same filters and conditions as in Experiment 1 were used to select saccades. In this

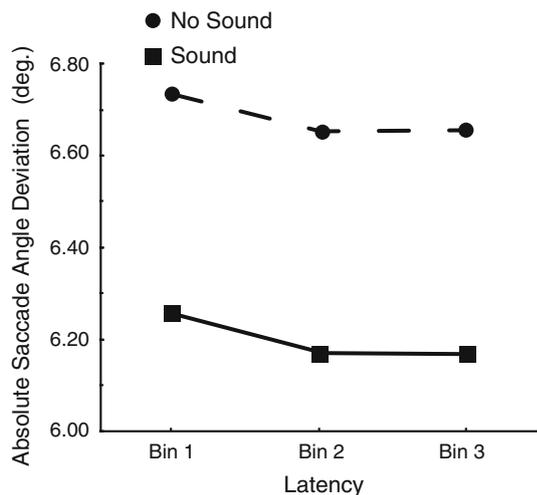
experiment, a global effect could occur, so we expected saccades to land on average in between the two target locations (between  $-10^\circ$  and  $10^\circ$ ). After applying all filters, 5 % of the trials in the sound condition and 6 % of the trials in the no-sound condition were removed from further analysis.

*Statistical analysis* Because the global effect tends to be stronger at shorter saccade latencies, we did a repeated-measures analysis of variance (ANOVA) with latency bin (three bins) and modality (unimodal vs. bimodal) as independent variables and saccade angle deviation as dependent variable. This allowed us to investigate not only a main effect of modality but also whether there was an interaction between saccade accuracy and saccade latency. In addition, a two-tailed paired-samples *t* test between the sound and the no-sound conditions was performed on saccade latencies.

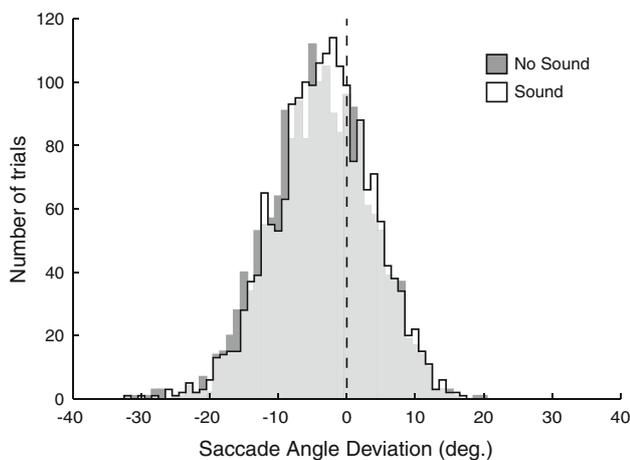
## Results

### Saccade angle deviation

Mauchly's test of sphericity indicated that the assumption of sphericity had been violated for bin and the interaction of condition and bin. Therefore, we used Greenhouse–Geisser-corrected values for the results of the repeated-measures ANOVA of these variables. The repeated-measures ANOVA showed a significant main effect of condition [ $F(1,10) = 6.272$ ,  $p < .05$ ], but not of bin [ $F(1.006,10.064) = .083$ ,  $p > .05$ ,  $\epsilon = .503$ ]. Furthermore, the interaction between bin and condition was not significant [ $F(1.024,10.243) = .000$ ,  $p > .9$ ,  $\epsilon = .512$ ]. Average saccade angle deviations from the center between the two visual stimuli were smaller in the sound condition (mean =  $6.27^\circ$ , SD =  $1.81^\circ$ ) than in the no-sound condition (mean =  $6.63^\circ$ , SD =  $2.14^\circ$ ), indicating that the global effect was stronger in the sound than in the no-sound condition. The main effect of bin did not reach significance, which shows that saccade angle deviations were on average not larger or smaller for different saccade latencies. The interaction between condition and latency did not reach significance, indicating that the auditory stimulus did not influence saccade angle deviation differently in the sound than in the no-sound condition. The average saccade angle deviation for each bin for the sound and the no-sound conditions is shown in Fig. 4. The distribution of relative saccade angle deviations is shown in Fig. 5 and shows a larger amount of saccades made to the average direction of the targets in the sound condition compared to the no-sound condition. A perfect averaging of vectors would result in an absolute average saccade deviation angle of  $0^\circ$ , while this would be  $10^\circ$  if saccades always landed on one of the two targets.



**Fig. 4** Mean saccade angle deviations for the three latency bins in the sound (straight line) and the no-sound conditions (dashed line)



**Fig. 5** Distribution of relative saccade angle deviations for targets one and two in the no-sound condition (gray) and the sound condition (transparent white with black outline) of Experiment 2. Dashed line indicates the perfect average of the two target locations. Distribution of the sound condition has more values around a saccade angle deviation of zero than that of the no-sound condition, which results in a stronger global effect

### Saccade latencies

A two-tailed paired-samples *t* test again revealed a significant difference in saccade latencies between the sound and the no-sound conditions [ $t(10) = 8.811$ ,  $p < .001$ ]. Saccade latencies were shorter in the no-sound condition (mean = 223 ms, SD = 16 ms) compared to those in the sound condition (mean = 240 ms, SD = 19 ms).

### Discussion

A global effect was found in both the sound and the no-sound condition. Moreover, as we expected, the global

effect was significantly stronger in the sound condition (i.e., closer to the center between the two targets). This supports the idea that non-lateralized auditory input enhances vectors that arise from visual input. An enhancement of the vectors does not result in a different average vector, but it does enhance the probability that a saccade is initiated to the average vector. This is also visible in the distribution of saccade angle deviations shown in Fig. 5. More saccades landed close to the center between the two targets in the sound compared to the no-sound condition.

It could be argued that the global effect in the sound condition is stronger because of a broader distribution of saccade endpoints in the sound condition, irrespective of the presentation of the two elements. This would then result in a larger number of saccade endpoints landing in between the two targets in the sound condition. The average of saccade angle deviations in the sound condition would then be closer to 0° (a stronger global effect) than in the no-sound condition. However, the distribution of relative saccade angle deviations in Fig. 5 does not support this explanation, because it shows a clear unimodal distribution of relative saccade angle deviations. In addition, there was no difference in variance of absolute saccade angle deviations between the sound and the no-sound conditions in Experiment 1; therefore, this cannot account for the stronger global effect in the sound condition.

It has been shown that the global effect is generally stronger at shorter saccade latencies (Findlay 1982; Van der Stigchel and Nijboer 2011). However, latency cannot account for the current findings as we found significantly longer saccade latencies and a significantly stronger global effect in the sound condition compared to the no-sound condition.

### General discussion

In the current study, we showed that a non-lateralized auditory input enhances vectors in the oculomotor system that arise from visual input in a double-target condition. Additionally, we did not find an enhancement of the visual vectors by the auditory input in a single-target condition, which can be explained by a ceiling effect of saccade accuracy to single visual targets. In Experiment 2, we did find an enhancement of the visual vectors by the auditory input in the double-target condition, as indicated by a stronger global effect during bimodal stimulation compared to unimodal stimulation. Both results can be explained in terms of the vector theory (Tipper et al. 1997). The theory states that a visual stimulus evokes a neural population that produces a vector. Subsequently, an eye movement is initiated in the direction of the vector. When two visual elements are close enough in space, the neural

populations overlap and the vectors are averaged, which results in the initiation of a saccade into the average direction. We argue that the vectors that are evoked by the visual input in Experiments 1 and 2 were strengthened by the auditory input. An enhancement of the vectors resulted in a stronger global effect during bimodal stimulation in Experiment 2, because the average vector was also stronger compared to the no-sound condition. This stronger vector implies a higher probability that a saccade is initiated in the direction of the vector.

The shorter saccade latency in the no-sound condition compared to the sound condition in Experiments 1 and 2 can be explained in several ways. First, as has been mentioned previously, the spatial and temporal rules are specifically important for intersensory facilitation to occur (Frens et al. 1995). Our experimental setup did adhere to the temporal rule in the sound condition, but not the spatial rule. This spatial incongruity could have caused longer saccade latencies. Although it might explain why the saccade latencies in the sound condition are not shorter compared to the no-sound condition, it does not explain why the saccade latencies in the sound condition are *longer* than those in the no-sound condition. The difference in saccade latencies between the sound and the no-sound conditions in both experiments may be explained by the fact that the auditory stimulus was presented through headphones to both ears simultaneously with the same loudness, and therefore, the auditory stimulus might be associated with the entire visual scene. This way, the auditory stimulus might have acted as an auditory fixation stimulus, prolonging the visual fixation stimulus in the auditory modality after the offset of the visual fixation stimulus. A study by Taylor et al. (1999) showed that an auditory fixation stimulus is, just as a visual stimulus, able to produce longer latencies in an overlap condition compared to a gap condition. This might explain why the saccade latencies in the sound condition are slower compared to those in the no-sound condition.

The lack of an interaction between latency and saccade angle deviation appears to contradict previous findings (e.g., Ottes et al. 1985), which showed a decline in the global effect for longer latencies. In these paradigms, however, there was a strong top-down component, because it was clear which of the two visual elements was the target and which was the distractor. As it is known that top-down selection is stronger for longer latencies (Van Zoest et al. 2004), this explains why the global effect generally decreases later in the selection process. However, in our study, we limited top-down selection by giving a general task instruction (“Look to the elements that appear on screen as fast as possible”). Therefore, the two stimuli had the same status in the oculomotor selection process. For that reason, we assume that selection in our study is mostly

based on bottom-up information. The fact that we did not find an interaction between saccade angle deviation and saccade latency can then be explained by a lack of top-down selection, resulting in a global effect for all latencies. These results are in line with a previous study on saccade averaging without a strong top-down selection (Van der Stigchel et al. 2012).

With respect to the neural correlates of these results, it is likely that the SC is responsible for the observed findings. King and Palmer (1985) showed that the response of a specific type of neurons in the superficial layers of the SC that responded exclusively to visual stimuli was enhanced by an auditory stimulus. In the deeper layers, however, they found neurons responding to both visual and auditory stimuli, which showed an enhanced or depressed response when visual and auditory stimuli were presented together. These multimodal neural interactions are bound to the spatial and temporal rules and might underlie the intersensory facilitation effect found in many studies (e.g., Gielen et al. 1983; Hughes et al. 1994; Frens et al. 1995; Colonius and Arndt 2001; Colonius and Diederich 2004). As visual and auditory receptive fields of unisensory and multisensory cells in the SC are topographically arranged, we hypothesize that the visual input in our study evoked activity in those cells in the SC whose receptive fields corresponded to the specific locations of the targets in the visual field. However, as the auditory input was non-lateralized and presented through headphones, the auditory input might have evoked activity in a wider range of cells, together covering a large part of the auditory field with their auditory receptive fields. Consequently, two types of cells might have had an enhanced response: auditory-enhanced visual cells (not responding to auditory input in isolation) and multisensory cells (responding to both visual and auditory input in isolation). Yet, the activity in these types of cells is not directly related to the production of eye movements. Eye movements are generated in saccade-related neurons in the deeper layers of the SC, and only a small amount of neurons in the superficial layers of the SC that respond to visual input directly cause activity in saccade-related neurons in the deeper layers of the SC (Mays and Sparks, 1980). Thus, activity in neurons sensitive to visual and auditory input does not necessarily lead to saccades being initiated to the corresponding locations in space. Lee et al. (1988) investigated population coding of saccadic eye movements by neurons in the deeper layers of the SC and provided support for the idea that saccades are initiated in the direction of the average activity of a population of saccade-related neurons. The generation of saccades is influenced by both bottom-up and top-down input (Van Zoest et al. 2004), but we minimized top-down influences in the current study with our specific task instruction. Therefore, we hypothesize that the bottom-up

activity in the described auditory-enhanced and multisensory neurons greatly influenced the direction in which eye movements were initiated. An increased activity in these neurons during bimodal input compared to unimodal visual input could be the basis of the larger theoretical vectors and of the larger average vector in the sound condition in Experiment 2.

To summarize, the results of Experiments 2 indicated that when primary saccades are less accurate, a non-lateralized sound enhances the vectors evoked by the visual stimuli and thus the average vector, resulting in a higher proportion of saccades landing in between the two targets. While we were not able to show that vectors evoked by single visual targets were enhanced by auditory input, this might be explained by the fact that saccades to single visual targets are quite accurate. The global effect might be a useful phenomenon in investigating complex interactions between multiple stimuli from different modalities because the global effect itself is the result of the competition between multiple stimuli.

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