Exp Brain Res (2005) 166: 427–439
DOI 10.1007/s00221-005-2382-y

RESEARCH ARTICLE

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Crossmodal coupling of oculomotor control and spatial attention in vision and audition

Received: 29 July 2004 / Accepted: 26 September 2004 / Published online: 20 July 2005

Abstract Fixational eye movements occur involuntarily during visual fixation of stationary scenes. The fastest components of these miniature eye movements are microsaccades, which can be observed about once per second. Recent studies demonstrated that microsaccades are linked to covert shifts of visual attention. Here, we generalized this finding in two ways. First, we used peripheral cues, rather than the centrally presented cues of earlier studies. Second, we spatially cued attention in vision and audition to visual and auditory targets. An analysis of microsaccade responses revealed an equivalent impact of visual and auditory cues on microsaccade-rate signature (i.e. an initial inhibition followed by an overshoot and a final return to the pre-cue baseline rate). With visual cues or visual targets, microsaccades were briefly aligned with cue direction and then opposite to cue direction during the overshoot epoch, probably as a result of an inhibition of an automatic saccade to the peripheral cue. With left auditory cues and auditory targets microsaccades oriented in cue direction. We argue that microsaccades can be used to study crossmodal integration of sensory information and to map the time course of saccade preparation during covert shifts of visual and auditory attention.

Keywords Microsaccades · Covert orienting · Fixational eye movements · Multisensory

Introduction

Saccades (rapid, directed eye movements) align gaze with visual and auditory signals to optimize the perception of events by bringing areas of interest onto the fovea. Typically, saccades are preceded by covert shifts of visual attention to the target location (Hoffman and Subramaniam 1995; Kowler et al. 1995; Deubel and Schneider 1996) and can enhance hearing performance at that location prior to the movement (Rorden and Driver 1999). In turn, shifts of covert attention were linked to saccade preparation (Rizzolatti et al. 1987, 1994; Kustov and Robinson 1996) but do not necessarily initiate saccades, i.e. we can attend to locations in the visual periphery without large eye movements. However, microsaccades (smaller than 1° of visual angle), the fastest component of miniature eye movements involuntarily altering eye position during fixation, were recently shown to be influenced by covert shifts of attention. In an attentional cuing task, Engbert and Kliegl (2003) reported (1) effects of central visual cue onsets on microsaccade rate and (2) effects of cue direction, i.e. the direction of the attentional shift, on microsaccade direction (see also Hafed and Clark 2002; Rolfs et al. 2004). Thus, microsaccades can indicate the orientation of covert attention shifts and may be used to study the dynamics of oculomotor preparation during fixations.

Finding a specific function for microsaccades has been a long-standing problem of eye movement research (e.g. Bridgeman and Palca 1980; Kowler and Steinman 1980). Recent evidence suggests that microsaccades serve important behavioral (Engbert and Kliegl 2004) and neurophysiological functions (see Martinez-Conde et al. 2004 for a recent review) and represent a sophisticated motor process rather than oculomotor noise. In the present study, we examined a related issue on the attentional basis of microsaccades. Engbert and Kliegl (2003; also Hafed and Clark 2002; Laubrock et al. 2005) employed visual cues to elicit covert attention shifts. Here, we compare the impact of visual attention shifts to the crossmodal impact of auditory attention shifts on oculomotor control using microsaccade statistics as a dependent measure. It is well known that covert attention can also be shifted within audition and across modalities (see Driver and Spence 1998, for a review).

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Given the established link between microsaccades and covert attention, we tested their sensitivity to all combinations of auditory and visual cues and targets. Obviously, if microsaccade rate and direction were affected by auditory shifts of attention, the attentional link of this oculomotor phenomenon would be substantiated. In that way, microsaccades could be used as a tool to study neurophysiological mechanisms underlying multisensory integration in oculomotor control.

Experiment 1: visual cuing of attention

In experiment 1 we examined microsaccade statistics in a visual cuing task using peripheral cues, namely short white flashes presented to the visual periphery.[1]

Materials and methods

Participants

Twenty-eight undergraduate students were paid or received study credit for their participation. They were 19–29 years old (mean = 22.54 years), had normal or corrected-to-normal vision, and were in good health. This and the following three experiments were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and participants gave their informed consent prior to their inclusion in the study.

Apparatus and stimuli

Participants were seated in a silent and darkened room in front of a computer screen with the head positioned on a chin rest, 50 cm in front of the monitor. Eye-movement data were recorded using an EyeLink-II system (SR Research, Osgoode, Ontario, Canada) with a sampling rate of 500 Hz and an instrument spatial resolution of less than 0.005°. Stimuli were presented on a 19-in. EYE-Q 650 Monitor (1024×768 resolution; frame rate 100 Hz). The experiment was controlled by an Apple Power Macintosh G4 computer. Responses to target stimuli and reaction times were recorded via the standard keyboard connected to the computer. The experimental software controlling stimulus display and response collection was implemented in Matlab, using the Psychophysics (Brainard 1997; Pelli 1997) and EyeLink (Cornelissen et al. 2002) toolboxes.

Stimuli were presented on a gray background (30.1 cd/m^2). The fixation spot was a ring with a diameter of 0.8° of visual angle in dark gray color (3.4 cd/m^2) and an inset with a diameter of 0.1°. Cues were white circles (0.8° diameter; 116.0 cd/m^2) flashing 12.7° to the left or to the right of the fixation spot along the horizontal axis. Targets were presented for a maximum time of 500 ms or until the participant's response. Targets were either green (81.4 cd/m^2) or red (22.6 cd/m^2) squares (width: 0.8°; eccentricity: 12.7° to the left or to the right of the fixation point along the horizontal axis). Errors triggered visual and auditory feedback (central white circle with a diameter of 2.4° and a binaural 660 Hz tone at 70 dbA for 100 ms).

Procedure

After key training, linking "red" to the up and "green" to the down arrow key, participants performed five randomly ordered practice trials introducing the task and 120 test trials. Practice trials were comparable to test trials in all respects except that there was no fixation check at the beginning of a trial (see below).

Before the first and after every 15th test trial, a standard 9-point (grid) calibration was performed and validated by the eye tracker. On every fifth trial, a drift correction was carried out. Before each trial, the fixation spot was displayed at the center of the computer screen. Participants began fixating and correct fixation was checked. If gaze position was not detected in a region 4 times as large as the fixation spot, the experimenter carried out a drift correction and started again. If eyes were still not detected within the critical area, the calibration was repeated.

The first row of Fig. 1 shows a trial of experiment 1. Participants were required to look at the fixation spot during the whole trial. After a random pre-cue interval a cue was presented for 100 ms. After a random cue-target interval the target appeared. Pre-cue and cue-target intervals were selected from a uniform distribution between 1000 and 1500 ms. Participants made speeded manual responses discriminating which of two alternative targets, a green or a red square, occurred. Incorrect responses released an error message; correct responses directly initiated the next fixation check.

Cue position (left or right) as well as target alternative (red or green) had equal probability over the 120 trials. Thirty trials of every combination of cue position

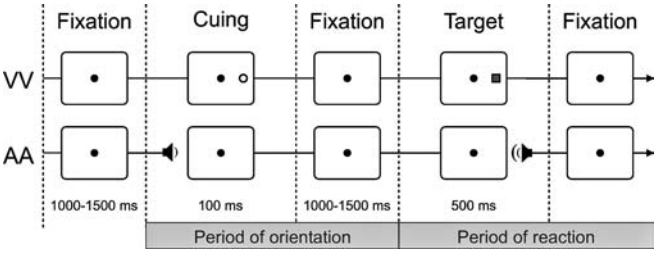

Fig. 1 Trial procedure in experiments 1 (*VV* visual cue and target) and 2 (*AA* auditory cue and target). Note that in AA there is an example of an invalid cue. Procedures for experiments 3 (*AV*) and 4 (*VA*) combined corresponding stimuli from VV and AA

[1]Pilot data of experiment 1 based on a subset of participants were reported in a commentary on Tse et al. (2003). We showed that microsaccade orientations were in good agreement with contralateral shifts of covert attention observed in response to peripherally flashed stimuli.

Table 1 Numbers and percentages of trials rejected in the four experiments

	IMR	SRT	LRT	BLI	SAC	TEC	Total
Experiment 1	60 (2.0%)	0 (0.0%)	118 (3.9%)	601 (20.0%)	903 (30.1%)	96 (3.2%)	1092 (36.4%)
Experiment 2	38 (1.6%)	1 (0.0%)	101 (4.2%)	422 (17.6%)	730 (30.4%)	66 (2.8%)	868 (36.2%)
Experiment 3	33 (1.3%)	0 (0.0 %)	84 (3.2%)	601 (22.8%)	887 (33.6%)	115 (4.4%)	1068 (40.5%)
Experiment 4	34 (1.2%)	0 (0.0%)	101 (3.7%)	593 (21.5%)	949 (34.4%)	75 (2.7%)	1086 (39.3%)

Rejection criteria were incorrect manual responses (*IMR*), very short (*SRT*) and long reaction times (*LRT*), respectively, blinks (*BLI*), saccades larger than 1° (*SAC*), and technical problems (*TEC*). Note that a trial could violate more than one of the criteria

and target alternative included 24 trials with a valid cue and six trials with an invalid cue (80% cue validity). Trials were presented in a random order, with a maximum of three subsequent trials with the same cue position, cue validity, and target alternative.

Data analyses

Data pre-processing Trials with incorrect responses or with response latencies less than 200 ms or more than 2 SD slower than a participant's median reaction time (computed separately for trials with the same cue modality, target modality, and cue validity) were discarded as were trials including blinks or saccades larger than 1° of visual angle. Moreover, a few trials had to be excluded due to technical problems. Table 1 displays the numbers of trials that violated our rejection criteria. At least 40 out of 120 of a participant's trials had to meet the criteria (20 for each cue location). Data of three participants did not meet this criterion before final data analyses, which led to a final sample of $N = 25$ participants contributing a total of 1908 trials (from 3000 or 63.6%).

Microsaccade detection Microsaccades were detected using an algorithm based on a transformation of fixation positions to two-dimensional velocity space (see Engbert and Kliegl 2003, for details). The detection algorithm is motivated by the fact that microsaccades can be distinguished from other forms of fixational eye movements by their dynamical overshoot component. Thresholds for peak velocity and minimum duration were used. For at least 8 ms (or four data samples), the velocity during a microsaccade had to exceed a threshold of six standard deviations of the eye's velocity during a trial; thresholds of velocities were computed separately for horizontal and vertical velocity components. To further reduce noise, we applied binocular recording of eye positions and required microsaccades to occur in both eyes simultaneously, i.e. with a temporal overlap of at least one data sample.[2] For microsaccade detection, we considered the time interval between trial onset and target presentation. Using this procedure, we identified a total of 4828 microsaccades.

[2]A Matlab implementation of the algorithm with a short sequence of experimental data can be downloaded at http://www.agnld.uni-potsdam.de/~ralf/micro/.

Results

Response latencies

Response latencies were analyzed to validate attentional cuing. A 2×2 repeated measures ANOVA including the factors cue validity and cue position yielded a significant cuing effect [$F(1,24) = 21.80$; $P < 0.001$], i.e. participants responded faster in trials with valid cues (mean = 569 ms) than with invalid cues (mean = 623 ms). Cue position had no influence on reaction times [$F(1,24) < 1$]; there was no reliable interaction between the factors [$F(1,24) < 1$].

Microsaccade statistics

First, we analyzed microsaccade-rate evolutions. Figure 2a shows the frequency of microsaccades in experiment 1 across time, logged to cue onset. These rate evolutions represent an average of individual rates computed with a moving time window of 100 ms centered at the current point in time. From a relatively stable baseline (0.8 s^{-1}) during visual fixation, the average microsaccade rate declined about 50 ms after cue onset (inhibition). A minimum (0.4 s^{-1}) is reached 100–230 ms after cue onset before rising toward a maximum (1.4 s^{-1}) reached about 200 ms later (enhancement). Finally, microsaccade rate resettled near the baseline.

Second, we evaluated the correspondence of microsaccade and cue directions. For this purpose, we compared the frequency of leftward and rightward microsaccades across time. Only horizontal microsaccades (72.3% of all detected microsaccades) were considered for these analyses. In other words, within the subpopulation of horizontal microsaccades we tested for a bias of microsaccade direction (leftward direction angle: $\phi > 3\pi/4$ or $\phi < -3\pi/4$; rightward: $-\pi/4 < \phi < \pi/4$) depending on cue direction. We compared the empirical data to surrogate data representing the null hypothesis that microsaccade directions were not affected by the attentional cue. Surrogate data were created by randomly rearranging a participant's original data: microsaccade onsets were kept constant. Original microsaccade-direction angles, however, were randomly scrambled across all microsaccades, i.e. each microsaccade could have any of the directions available in the data set. Hence, while every microsaccade event took

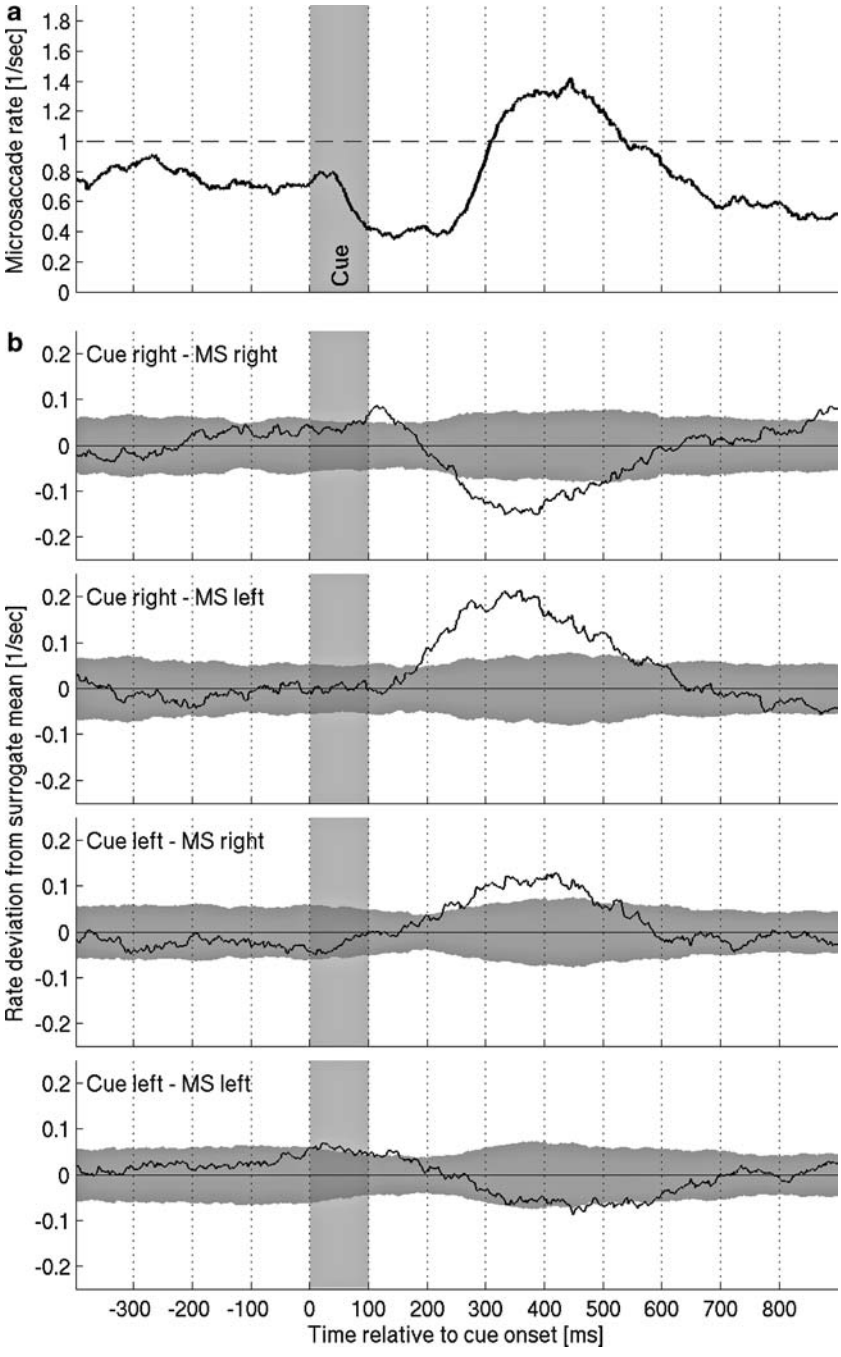

Fig. 2 Microsaccade-rate statistics in experiment 1 (*VV*) time-logged to cue onset. Data points reflect averages in a time span (**a** 100 ms, **b** 200 ms) centered at the current point in time. **a** Overall microsaccade-rate evolution. **b** Microsaccade-direction effects are indicated by deviations of empirical microsaccade rates (computed separately for each combination of microsaccade (MS) and cue directions) from the mean of surrogate data representing the null hypothesis that there are no direction changes due to the presentation of an attentional cue. *Shaded areas* represent ±2 SD around surrogate means. Accordingly, whenever empirical rate leaves these areas, the deviation is statistically significant

place at the same point in time in both the empirical and the surrogate data set, the direction of each empirical (leftward or rightward) microsaccade was now randomly reassigned to one of the surrogate events. Using these surrogate data, separate surrogate rate evolutions of leftward and rightward microsaccades, respectively, were computed for each individual as it was done in Fig. 2a but with 200 ms time windows to counteract additional noise caused by a subdivision of data into two direction groups. Finally, individual rates were averaged. One hundred surrogate data sets were produced to obtain estimates of means and standard deviations representing the null hypothesis. Note that surrogate tests cannot be affected by baseline biases of empirical microsaccade directions, as these biases are still present in surrogate data.

Figure 2b depicts the deviation of empirical microsaccade rates (computed separately for each combination of microsaccade and cue directions) from the mean of the surrogate data. Shaded areas indicate two standard deviations around surrogate means. Accordingly, these areas represent the null hypothesis that rates—if split up into different directions—are not influenced by cue presentation. Hence, whenever empirical rates leave these areas, their deviation is statistically significant. To reduce the risk of random significances, we consider only

effects with a minimum duration of 20 ms as being relevant. In an early post-cue phase, there is a surplus of cue-oriented microsaccades in the right (96–142 ms after cue onset) and the left (16–58 and 130–150 ms after cue onset) cue condition. Following the epoch of microsaccade inhibition, we found overshoots of cue-opposing microsaccades for both cue locations (184–542 ms after right cues; 226–254 and 266–480 ms after left cues). Additionally, cue presentation to the right resulted in an undershoot of cue-directed microsaccades (250–496 ms after right cues; 444–478, 492-532, and 550-568 ms after left cues). Finally, there was a late cue-directed effect for cues presented to the right (860–900 ms).

Discussion

Using a spatial cuing paradigm, we successfully induced shifts of visual attention. Effects on microsaccade rate reported in a previous study by Engbert and Kliegl (2003) were reproduced successfully, i.e. following a stable baseline we found a decrease of microsaccade rate followed by an enhancement epoch, where rate overshoots prior to returning to the baseline level. Engbert and Kliegl (2003) used central cues (colors or arrows pointing in a certain direction). Here we employed peripheral visual cues. Thus, in the present experiment we generalized the findings on microsaccade-rate modulations along this dimension.

During the enhancement epoch, the majority of microsaccades had directions directly opposing cue location. We argue that peripheral cues resulted in an inhibition of (automatic) saccadic reactions in the cued direction given a situation where fixation is strongly required. Lateral inhibitory interactions in oculomotor areas (e.g. Munoz and Istvan 1998) suggest that as a consequence a bias of activation of oculomotor neurons for movements to the opposite hemifield might have built up. In addition to this cue-opposing bias of microsaccade directions, we found cue-directed effects shortly after cue presentation and shortly before target presentation. While the first can be attributed to an instantaneous attentional capture by the peripheral cue, the latter can be attributed to the expectancy of the target.

Experiment 2: auditory cuing of attention

The key question of the present study was to extend our knowledge about relations between the allocation of attention and microsaccades to audition. Although saccade programming is primarily a visual phenomenon, it can be strongly influenced by information from other modalities like audition or touch. Various behavioral measures have been used to study influences of auditory attention on oculomotor control including saccade latencies (for a review see Zambarbieri 2002) and amplitudes (Lueck et al. 1990; Yao and Peck 1997), as well as the curvature of saccade trajectories (Sheliga et al. 1994, 1995; Doyle and Walker 2002) and incorrect gaze shifts (e.g. Corneil and Munoz 1996). All of these studies examined properties of saccades as a function of preceding or intervening covert shifts of auditory attention.

The study of micromovements of the eyes may be ideally suited to probe covert shifts of auditory attention because we can ask participants to maintain fixation on a completely stable visual display and still recover a behavioral trace of spatial attention shifts. Conversely, a purely auditory attention-shift experiment may provide a particularly clean view of the dynamics of saccade preparation because of the absence of any potentially confounding visual events.

Materials and methods

Participants

Twenty-eight undergraduate students were paid or received study credit for their participation. They were 18–37 years old (mean = 23.15 years), had normal or corrected-to-normal vision, reported normal hearing, and were in good health.

Apparatus and stimuli

The setup was as for experiment 1 except that we used auditory cues and targets. Sennheiser HD 520 II headphones were used to present the auditory stimuli. Task setting and feedback were similar to those in experiment 1. A 70 dbA approximated white noise sound (duration: 82 ms) served as a spatial cue. It was monaurally played to the left or right ear. Target alternatives were two 70 dbA sinusoidal tones differing in tone pitch (440 or 880 Hz). Depending on cue location and cue validity, tones were monaurally presented either to the left or to the right ear.

Procedure

The procedure was similar to experiment 1. However, the task here was to discriminate auditorily cued tones of different pitch played to one ear. Consequently, the key training was modified. Participants were required to press the keys corresponding to tone pitch, i.e. the up arrow key whenever a high pitch tone was presented and the down arrow key if the target had a low pitch. The time course of a trial is shown in the second row of Fig. 1.

Data analyses

Data pre-processing Raw data were filtered using the same criteria as in experiment 1 (see Table 1). Conse-

quently, data from eight participants were excluded from further analyses, resulting in a final sample of $n = 20$ participants, contributing 1532 trials from 2400 trials (63.8%).

Microsaccade detection The algorithm (see experiment 1) identified 5301 microsaccades.

Results

Response latencies

Attentional cuing was validated using a repeated-measures ANOVA including the factors cue validity and cue position. The test yielded a significant cuing effect [$F(1,19) = 10.83$; $P = 0.004$], i.e. participants responded faster with valid cues (mean = 608 ms) than with invalid cues (mean = 658 ms). There was also an effect of cue position [$F(1,19) = 5.76$; $P = 0.027$]. Right cues (mean = 599 ms) triggered faster responses than left cues (mean = 620 ms). Finally, there was a significant interaction between these factors [$F(1,19) = 9.85$; $P = 0.005$], i.e. the validity effect was larger for right cues (valid: mean = 606 ms, invalid: mean = 686 ms) than for left cues (valid: mean = 609 ms, invalid: mean = 630 ms).

Microsaccade statistics

Microsaccade analyses were analogous to those reported in experiment 1 (VV). Rate signatures (Fig. 3a) were comparable to those found in visual spatial cuing tasks: A stable baseline rate during visual fixation (1.2 s^{-1}) declined briefly after cue onset. Microsaccade rate was minimal at 120 ms (0.4 s^{-1}), reached a maximum (1.8 s^{-1}) approximately at 300–350 ms before gradually returning to baseline. Note that microsaccade rate was generally higher in experiment 2 (AA) than in the purely visual condition.

Microsaccade direction was differently influenced by spatial cuing than in VV. Figure 3b depicts the deviation of empirical rates of horizontal microsaccades (67.3% of all detected microsaccades) from the mean of the surrogate data (see description in experiment 1). No significant deviations were found after right cues. After left cues, the empirical deviation lines indicate an overshoot of cue-congruent microsaccades in a time window between 130 and 268 ms. In temporal proximity (124–248 ms), there was an undershoot of cue-opposing microsaccades. Additionally, there was a small overshoot of cue-opposing microsaccades from 606 to 666 ms.

Discussion

Auditory cuing for auditory targets resulted in microsaccade-rate evolutions very similar to the typical signature after visual cuing of attention to visual targets. An inhibition epoch after cue presentation was followed by a clear enhancement and a final resettlement of microsaccade rate close to baseline level. This new finding is quite remarkable because fixational eye movements were strongly modulated despite the absence of any visual event such as a display change.

In strong contrast to the visual condition, however, we find no cue-opposing microsaccade directions following the lateralized cues. Rather, there is a cue-directed bias of microsaccades for left cues whereas directions were not reliably affected by right cues. Why did the allocation of auditory attention affect microsaccade direction only with left cues, and why was the effect in this direction? Brown and Nicholls (1997 and Nicholls et al. 1999) reported a left-hemisphere advantage for processing brief auditory stimuli (like our cue), that is, according to Kinsbourne's (1970) activation-orienting hypothesis, for stimuli presented to the right ear. Moreover, attention is hemispherically biased to the right (Reuter-Lorenz et al. 1990). In our task, participants were required to continue fixating the central spot after cue presentation. Therefore, a reduced control of spatial attention processes for left cues could have resulted in a less effective inhibition of microsaccades in cue direction. The interpretation of our results in terms of a hemispheric asymmetry is corroborated by faster reaction times for right cues.

In summary, we report a new effect of auditory attention on oculomotor behavior in the absence of any visual display changes. Microsaccade rate is influenced by visual and auditory stimuli alike, whereas effects are different for microsaccade direction. However, direction effects in experiments 1 (VV) and 2 (AA) can be generally attributed to the same processes. Apparently, overall microsaccade rate and microsaccade direction reflect different processes or different stages of the same process, respectively. While microsaccade rate, an indicator of *when* saccades occur, seems to be controlled supramodally, microsaccade direction as a measure of *where* saccades go clearly depends on the modality within which attention is shifted. Intuitively, where a saccade is oriented is determined later than the decision whether to make a saccade at all, a point of view that is also held by models of oculomotor control (e.g. Findlay and Walker 1999). Seemingly, the knowledge that shifts of visual attention or gaze are not required (as in AA) interferes with saccade programming at that later stage resulting in a weaker control of fixation stability in the purely auditory task. The higher baseline rate in AA as compared to VV corroborates this conclusion.

Experiments 3 and 4: intermodal cuing of attention

In experiments 1 (VV) and 2 (AA) we found contrary results of cues on microsaccade direction. In two additional experiments 3 and 4, combining auditory cues with visual targets (AV) and visual cues with

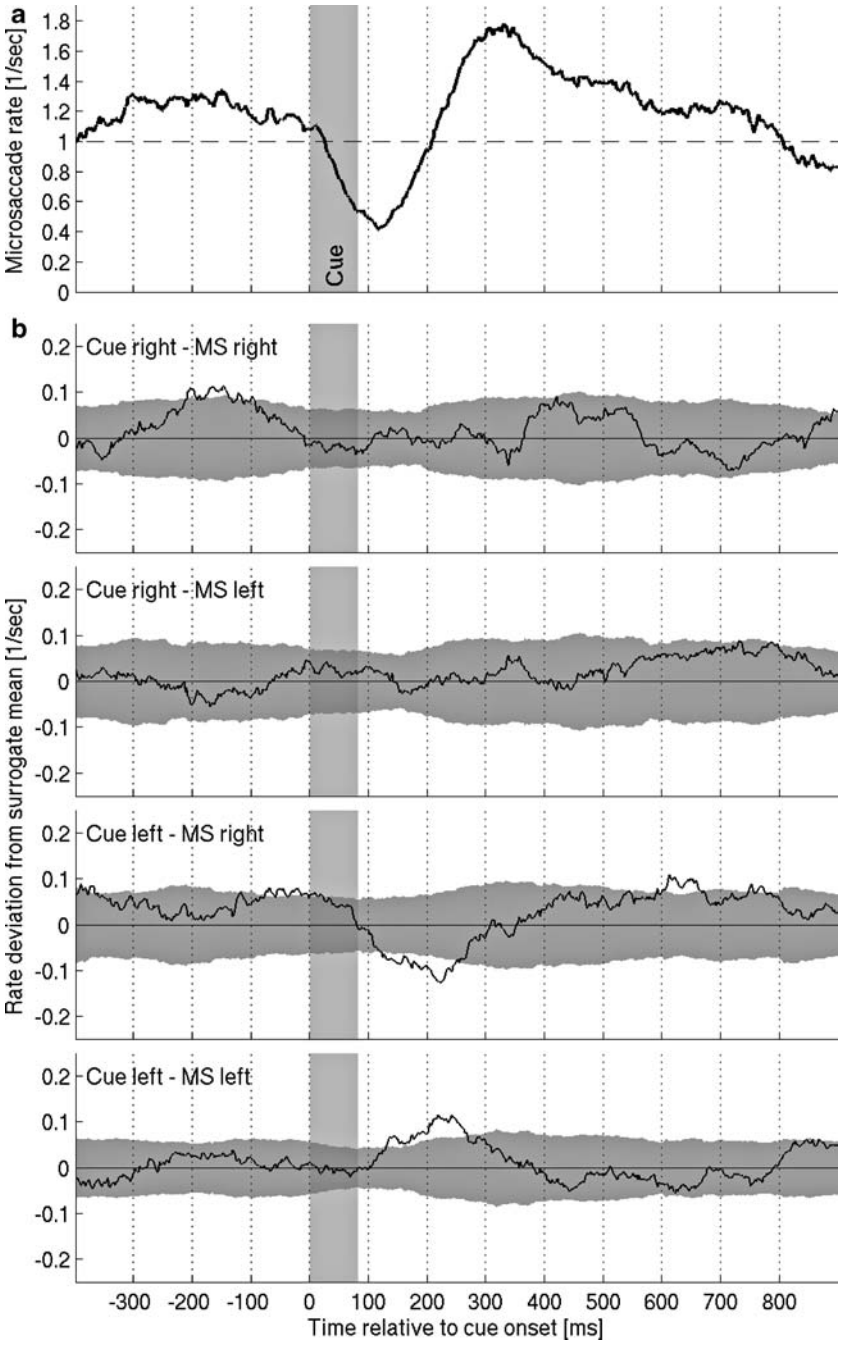

Fig. 3 Microsaccade-rate statistics in experiment 2 (*AA*) time-logged to cue onset. **a** Overall microsaccade-rate evolution. **b** Microsaccade-direction effects are indicated by deviations of empirical microsaccade rates from the mean of surrogate data. See caption of Fig. 2 for details

auditory targets (VA), respectively, we tested whether the modulation was linked to cue modality or target modality.

Materials and methods

Participants

Twenty-five undergraduate students in experiment 3 (age range: 20–28 years; mean = 22.64 years) and 31 in experiment 4 (age range: 19–30 years; mean = 22.42 years) were paid or received study credit for their participation. All participants reported normal or corrected-to-normal vision, normal hearing, and good health.

Apparatus, stimuli, and procedure

Depending on cue and target modality, the same task settings, stimuli, and procedure were used as in experiments 1 and 2 (see also Fig. 1).

Data analyses

Data pre-processing Raw data were filtered using the same criteria as for experiment 1 (see Table 1). Conse-

quently, data from three participants in experiment 3 and eight participants in experiment 4 were dropped before final analyses. Finally, $n = 22$ and 23 participants contributed a total of 1572 trials (from 2640 or 59.5%) and 1674 trials (from 2760 or 60.7%), respectively.

Microsaccade detection Using the algorithm described in experiment 1 we identified a total of 4765 (experiment 3) and 5280 (experiment 4) microsaccades, respectively.

Results

Response latencies

Spatial cuing of attention was tested with an ANOVA including the within-subject factors cue validity and cue position and the between-subject factor condition. The cuing effect was significant [$F(1,44) = 10.33$; $P = 0.002$]. Faster responses were detected in trials with valid cues (overall mean = 641 ms; AV: mean = 577 ms; VA: mean = 701 ms) than with invalid cues (overall mean = 677 ms; AV: mean = 621 ms; VA: mean = 730 ms). No other main effects or interactions were significant.

Microsaccade statistics

Using the same analytic tools, results in experiments 3 (AV) and 4 (VA) were similar to those of experiment 1 (VV). First, as depicted in Fig. 4a (AV) and 5a (VA), a stable baseline microsaccade rate (AV: 1.2 s^{-1}; VA: 1.0 s^{-1}) during visual fixation declined immediately after cue onset. In AV, microsaccade rate was minimal (0.3 s^{-1}) about 130 ms after cue onset, in VA approximately 180 ms after cue onset (0.2 s^{-1}). In these intermodal conditions, however, there was little (AV) or no (VA) overshoot of microsaccade rates following the inhibition epoch. Instead, rates directly resettled at the baseline.

The most notable similarity to VV, however, was the direction pattern of microsaccades across time (see Figs. 4b for AV and 5b for VA). During the enhancement epoch following the inhibition of microsaccades after cue onset, directions were biased to the side opposite to cue location. We conducted the same surrogate data analysis as in experiment 1 to test this effect statistically.

For left cues, directions of horizontal microsaccades (71.2% of all detected microsaccades in AV, 66.7% in VA) in both AV and VA exhibited overshoots in the cue-opposing direction in the period from inhibition to resettlement of microsaccade rate (292–414 ms after cue onset in AV; 244–460 ms in VA) and temporally corresponding undershoots of cue-directed microsaccades (352–428 ms in AV; 234–590 ms in VA). Moreover, there was an early undershoot of cue-opposing microsaccades in AV (96–116 ms).

For right cues, these effects were only reliable in VA. Here, cue-opposing microsaccades overshot surrogate data from 266 to 484 ms, while cue-directed microsaccades were underrepresented from 220 to 386 and 404 to 430 ms after cue onset. There were also early cue-congruent biases of microsaccade direction (overshoot of rightward microsaccades: 20–50 and 86–160 ms; undershoot of leftward microsaccades: 16–178 ms).

Finally, there were some late microsaccade-direction effects corresponding to cue direction with cues to the right (AV: overshoot of rightward microsaccades from 782 to 900 ms; VA: undershoot of leftward microsaccades from 692 to 718 ms) and with cues to the left but only in VA (undershoot of rightward microsaccades from 790 to 822 ms).

Discussion

Combining auditory cues with visual targets in experiment 3 (AV) and visual cues with auditory targets in experiment 4 (VA), we tested, whether the contrary modulation of microsaccade direction as found in experiments 1 (VV) and 2 (AA) was linked to cue modality or target modality.[3] Basically, microsaccade rate evolved in the pattern reported for VV and AA. Beyond that, there were striking similarities between these new experiments and VV concerning microsaccade statistics, mainly showing a cue-opposing bias in microsaccade directions following the inhibition period after cue onset. In the case of VA, this finding was expected since we argue that it is mainly produced by the peripheral onset of the visual cue. However, a very similar effect was found using auditory cues for visual targets (at least for cues to the left). From AA we know that the auditory cue itself cannot solely be the cause of this effect. Although fixation was required, the spatial auditory cue did not cause microsaccades to tend in the direction opposite to cue location. We interpret this result as an involvement of visual attention that results in an inhibition of saccades, which would have been triggered automatically to the spatial auditory cue. In other words, in tasks where visual attention is involved, the oculomotor system seems to be activated to a greater extent. Hence, in these situations it is more likely that it is not only specified when saccades will appear, but also where they are oriented. Accordingly, and as in VV, we also found cue-directed biases in microsaccade directions shortly after cue onset just before the target was expected. Again, we argue that these microsaccades accompany attentional shifts during these time periods, triggered by peripheral cue onset in the first and target expectancy in the latter case.

[3]Note that AV and VA must be primarily looked upon as control studies in the context of VV and AA rather than as experiments for the investigation of crossmodal effects. In our paradigm, the attentional shifts in the target modality induced by the spatial cues in their modality were not implicitly evoked, i.e. target modality was known in advance of target presentation. Therefore, attention shifts in AV and VA are not *hard-wired* crossmodally cued as for example Spence and Driver (1996, p1007) would say.

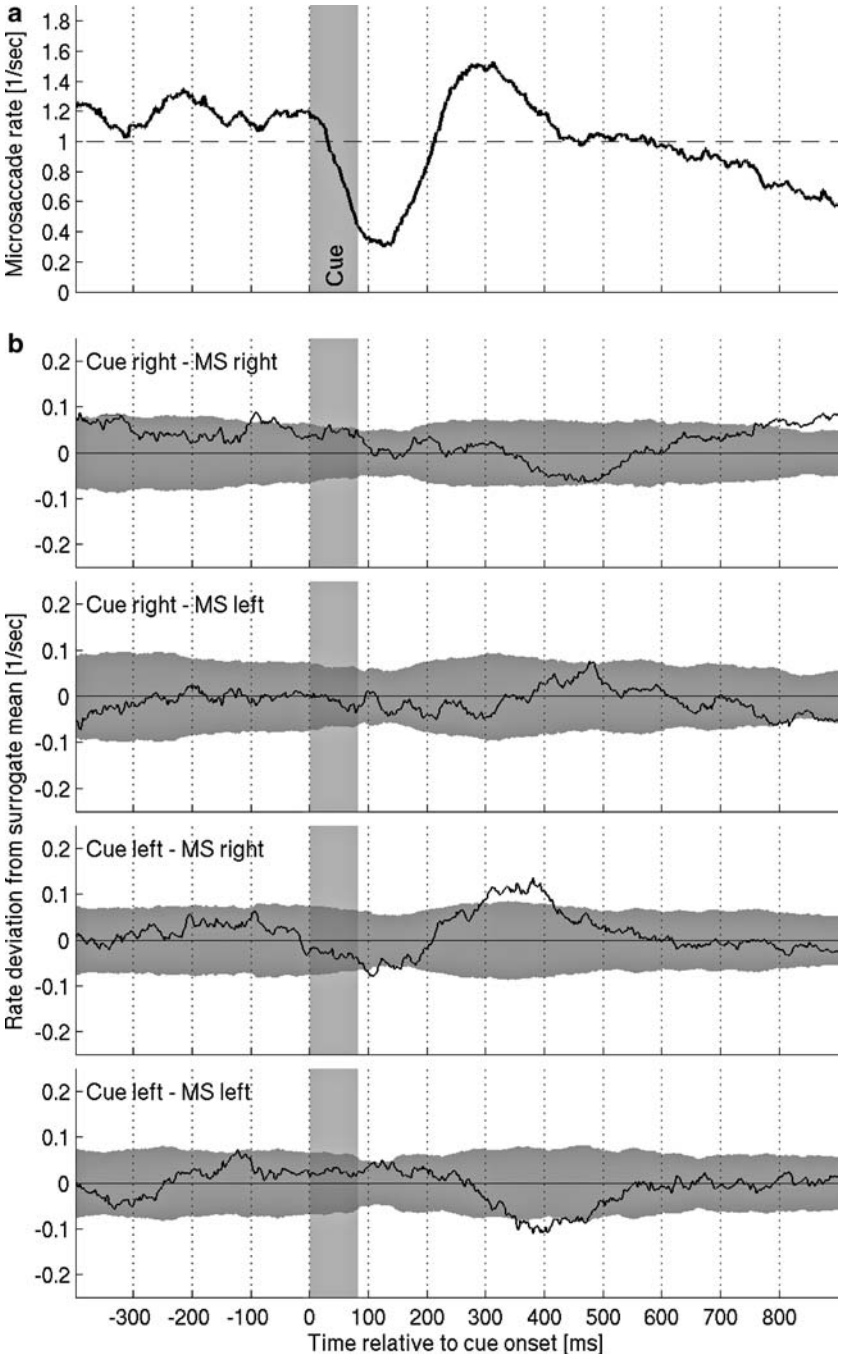

Fig. 4 Microsaccade-rate statistics in experiment 3 (*AV*) time-logged to cue onset. **a** Overall microsaccade-rate evolution. **b** Microsaccade-direction effects are indicated by deviations of empirical microsaccade rates from the mean of surrogate data. See caption of Fig. 2 for details

General discussion

During a required fixation, studies normally control for receptor shifts to protect from examining overt instead of covert shifts of attention. Head movements are precluded through chin rests and cheek pads and trials including substantial eye movements (larger than 2.5° of visual angle in conservative cases) are excluded from analyses in most of the experiments. This procedure is appropriate and useful but it leaves open what happens to eye movements within the allowed range of amplitudes, i.e. microsaccades with maximum amplitudes of 1°, and what these movements may tell us about processes of oculomotor control. In the present experiments, we addressed this issue and demonstrated noticeable effects of shifts of covert visual and auditory attention on microsaccade statistics. Evidently, attentional processes are rigorously mirrored in oculomotor behavior, emphasizing the distinct linkage of covert attention and saccade programming and the suitability of microsaccades to examine these issues.

In a classical cuing paradigm using spatial cues and targets differing in modality of presentation (visual or auditory), we induced spatial shifts of visual and audi-

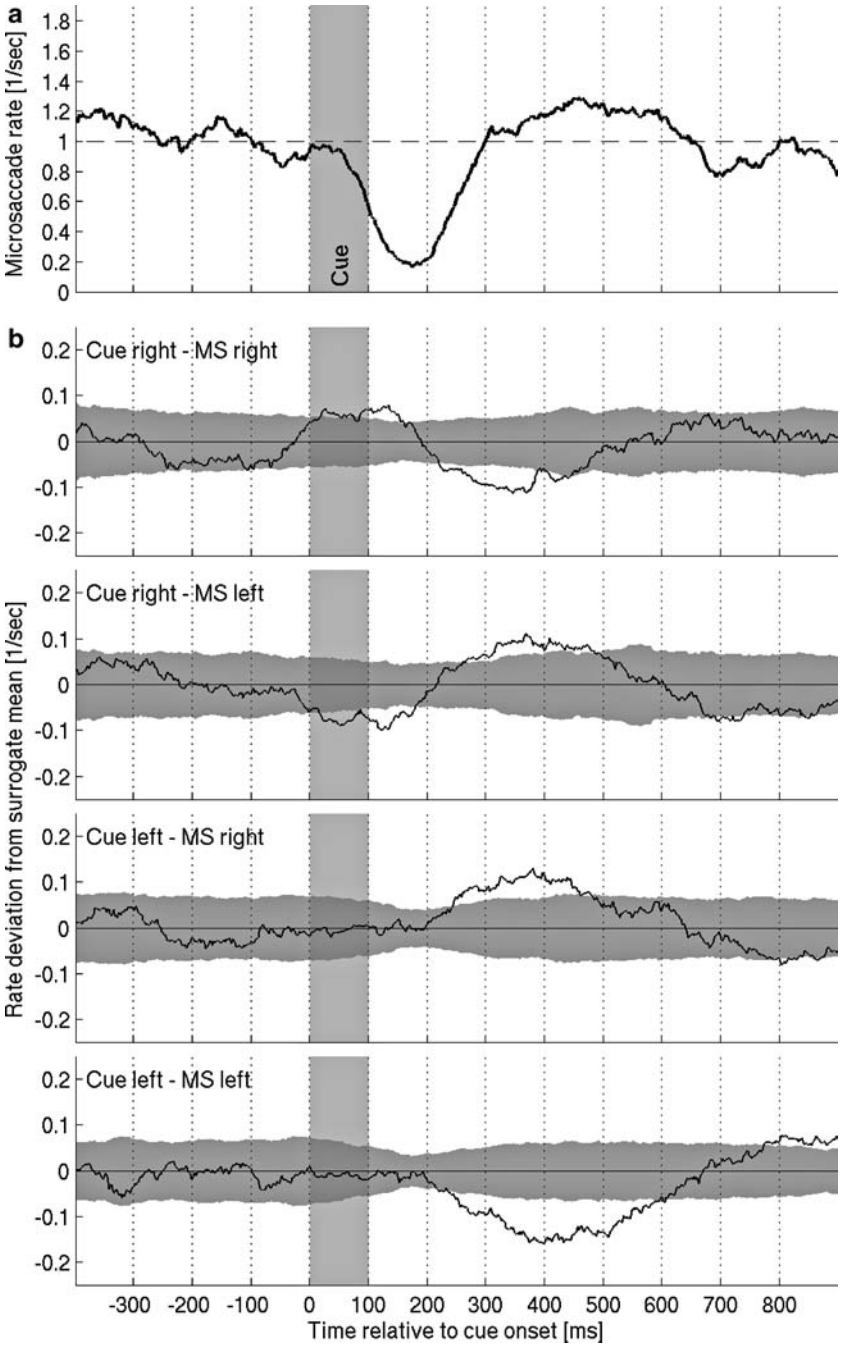

Fig. 5 Microsaccade-rate statistics in experiment 4 (*VA*) time-logged to cue onset. **a** Overall microsaccade-rate evolution. **b** Microsaccade-direction effects are indicated by deviations of empirical microsaccade rates from the mean of surrogate data. See caption of Fig. 2 for details

tory attention. Response latencies showed the expected effects, i.e. benefits from valid cues, which correctly indicated later target locations. In all conditions, microsaccade rate showed a temporal pattern similar to the one found by Engbert and Kliegl (2003) in a previous (purely visual) study. Before cue onset, rate was relatively stable at a baseline level. After the cue, microsaccade rate decreased dramatically until a minimum was reached, approximately 180 ms after visual cues and about 120–130 ms after auditory cues, then overshot baseline in an enhancement epoch and finally resettled at baseline. The shape and the time course of this rate modulation effect is comparable to saccadic inhibition, a knee-jerk effect of decreased frequency of large saccades observed 47–70 ms after abrupt onsets of irrelevant stimuli (e.g. Reingold and Stampe 2002, 2004). Reingold and Stampe associated saccadic inhibition with inhibitory processes in the superior colliculus (SC), one of the most important brain structures controlling saccade generation (for reviews, see Munoz et al. 2000; Scudder et al. 2002; Sparks 2002). We also propose that the inhibition of microsaccades can be attributed to an enhanced fixation of gaze and a corresponding inhibition of saccade-related neurons in this oculomotor area.

Temporal modulations of microsaccade directions matched to a large extent across experiments 1,3, and 4 (VV, VA, and AV). After early cue-directed effects (within the first 160 ms after cue onset), there was a cue-opposing bias in directions mainly following the inhibition epoch and lasting throughout the enhancement epoch. Microsaccades tending to the side opposite from cue location were overrepresented in this period, while directions in cue direction were below chance level. Obviously, the occurrence of the effect of cue-opposing microsaccade directions follows a simple rule: it is present as soon as visual attention is involved (due to a visual cue or a visual target). This pattern could be explained by an inhibition of saccade directions in cue direction, which was induced by required fixation in our tasks. Physiologically, this assumption seems plausible, since saccade directions are population coded in the SC (Lee et al. 1988). Hence, for visual cue conditions, we propose that similar angular directions of saccades were commonly inhibited in response to cue presentation to counteract automatic saccadic movements in direction of the cue. In AV there was no peripheral visual cue but a spatial auditory cue, which alone cannot have caused the cue-opposing bias as experiment 2 (AA) revealed. Again, we argue that the involvement of visual attention might have resulted in an inhibition of saccade directions in direction of the spatial auditory cue. Seemingly and intuitively, visual attention is more likely to activate our oculomotor system than auditory attention. Hence, it is conceivable that as soon as visuospatial attention is addressed and a visual reference frame can be established, the direction of saccades becomes specified suitably. An additional indicator for the coupling of attention and microsaccadic directions is given by the late excess of cue-directed microsaccades. These effects were found throughout experiments 1, 3, and 4 in time periods of 700 ms after cue onset and later. That means that shortly before target appearance, microsaccades where aligned with the expected target direction.

In the purely auditory condition (experiment 2), microsaccades were solely aligned with cue location. Thus, microsaccade rate was influenced as in the visual condition, but microsaccade direction effects were in the opposite direction. We already concluded that overall microsaccade-rate and microsaccade direction mirror different levels of interaction between attentional and oculomotor processes. Physiological studies (e.g. Wurtz 1996; Carpenter 2000) and theoretical models (e.g. Findlay and Walker 1999; Engbert et al. 2002) suggest that the decision *when* a saccade program is initiated is made earlier than *where* it will be oriented. We argued that the later stage might not be reached in situations, which do not require visual attention. Accordingly, microsaccade direction might be less tightly controlled under these conditions and, consequently, allow for a bias in cue direction, as observed in our data. Note, however, that direction effects in AA can be generally attributed to the same processes as those in VV.

A related explanation for the differences in microsaccade directions across conditions can be derived from a recent study by Bell et al. (2004). These authors studied inhibition of return (IOR) in response to visual and auditory stimuli and related the behavioral results to neuronal activity in the SC. IOR refers to the effect that it takes longer to initiate a saccade to a location that has already been attended as compared to other saccade targets. In contrast to previous studies (e.g. Reuter-Lorenz et al. 1996; Spence and Driver 1998), Bell et al. (2004) found no effect of auditory cues on saccadic reaction times and attributed their results to a lack of inhibition of neuronal activity at that site in the SC associated with the saccade target. Since microsaccade directions could be associated with IOR (Galfano et al. 2004), our results can also indicate a failure of our stimuli to release an inhibition of the cued location. However, to investigate auditory and audiovisual IOR in the framework of microsaccade statistics directly, one must use uninformative exogenous cues (Galfano et al. 2004).

We consider it remarkable that oculomotor control was impacted strongly in the absence of any visual changes or relevant visual information, respectively. This indicates, how closely attention across modalities and oculomotor control are bound together. Of course, models of oculomotor control (e.g. Rizzolatti et al. 1987, 1994; Findlay and Walker 1999) have proposed such a coupling of spatial shifts of attention (independent of modality) and the preparation of saccadic movements for some time. The SC is the usual suspect in being a neurological counterpart to these models since it is involved in the coordination of covert shifts of attention (Albano et al. 1982; Desimone et al. 1989; Kustov and Robinson 1996) and the initiation of saccades (reviews in Munoz et al. 2000; Scudder et al. 2002; Sparks 2002). Moreover, cell organization in the SC is well adapted to the task of shifting gaze to peripheral targets. Sensory input cells activated by visual information as well as discharges of responsive cells connected to eye movements are topographically organized in a way that information from visual receptive fields may lead to coding saccadic movement vectors (for reviews, see Munoz et al. 2000; Scudder et al. 2002; Sparks 2002). In the deep layers of the SC, visual and auditory inputs converge (reviewed in Stein and Meredith 1993). Cells that are sensitive to auditory input show topographic cell arrangements for the representation of auditory space. This representation is similar to that of visual space (Stein and Meredith 1993) such that eye movement commands in response to visual and auditory stimuli have a common code (Jay and Sparks 1987a, b). Therefore, the far-reaching interplay of motor control and attention in vision and audition as found in this study is physiologically highly plausible.

The experiments demonstrated consistently the influence of auditory cues and targets on microsaccade statistics. In our design, we opted for a clear spatial

separation of auditory and visual stimuli, that is auditory cues and targets were presented to the left or right ear rather than virtually mapped to the location of visual cues and targets as is customary in crossmodal research. The main reason for this implementation was to reduce the visual character of the task as much as possible, assuming that an auditory stimulus at a virtual location in the visual field might be a more attractive visual target than one clearly outside it. Thus, the observed modulation of microsaccade rate associated with the purely auditory condition (experiment 2) expressed itself despite the low visual relevance of the stimulus location. In future crossmodal research, microsaccade statistics could be used to examine the spatial integration of visual and auditory information with systematic manipulations of distances between visual and auditory stimuli within the visual field. Similarly, as one reviewer noted, differences between auditory and visual results might be due to differences in stimulus quality. For example, the auditory-cue noise might be perceived as more diffuse than the high-contrast visual cue. Psychophysical matching of visual and auditory stimuli with respect to perceptual "crispness" was beyond the scope of the present experiment. The proposal is pertinent, however, because physical stimulus properties influence multisensory processing in the SC (Bell et al. 2001), which in turn should express itself in microsaccade statistics.

We set out to test whether auditory covert attention like its visual counterpart can be traced to rate and directions of microsaccades. The results provided very clear support for this proposition and are in agreement with other research. How does our study fit into the current research landscape? Over the last years we have witnessed much progress in relating visual attention and oculomotor processes and especially how both are linked to the dynamics of activation and inhibition in the SC (reviews in Munoz et al. 2000; Scudder et al. 2002; Sparks 2002). Moreover, there is solid evidence that auditory and possibly other sensory information is integrated at this site as well (reviewed in Stein and Meredith 1993). This research is carried out in neurophysiological and psychological experiments. Obviously, single and multiple cell recordings from the SC offer a unique window on the underlying process dynamics. We submit that the evolution of rate and direction of microsaccades under covert visual and auditory attention revealed in our experiments may provide a behavioral analog of these dynamics and, in particular with respect to multisensory integration, the paradigm allows us to move beyond the, e.g. 2×3 pattern of means typical for traditional experimental designs and provides strong constraints for neurocomputational models.

Acknowledgements We thank Jochen Laubrock, Hans Arne Trukenbrod, and three anonymous reviewers for their helpful comments on the manuscript. This research was supported by Deutsche Forschungsgemeinschaft (grants KL-955/3 and KL-955/6).

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