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ORIGINAL ARTICLE

Microsaccadic responses in a bimodal oddball task

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Abstract In a visual oddball task the presentation of rare targets induces a prolonged microsaccadic inhibition as compared to standards. Here, we replicated this effect also in the auditory modality. In addition, although auditory standards induced a more limited modulation of microsaccadic frequency as compared to visual standards, auditory oddballs induced a prolonged microsaccadic inhibition. With bimodal standard stimuli the microsaccadic response was determined by the attended modality, resembling that produced by attended unimodal stimuli. The present findings support the idea that the microsaccadic response to oddball and standard stimuli is partly driven by cognitive mechanisms common to both the visual and the auditory modality, and that microsaccades can be used as an implicit behavioral measure of ongoing cognitive processes.

Introduction

Microsaccades, i.e. the tiny rapid eye movements that humans execute at a rate of 1–2/s during fixation, have been a topic of research for at least 50 years (Martinez-Conde, Macknik & Hubel, 2004; Engbert, 2006). Originally, the research mainly focused on the functional role of microsaccades in the perceptual and oculomotor systems (Cornsweet, 1956; Ditchburn, Fender & Mayne, 1959; Steinman, Haddad, Skavenski & Wyman, 1973; Kowler & Steinman, 1980; Ditchburn, 1980). Only recently, research has provided extensive evidence for a role of microsaccades in counteracting the fading of peripheral visual stimuli during fixation (Martinez-Conde, Macknik & Hubel, 2000, 2002; Martinez-Conde, Macknik, Troncoso & Dyar, 2006; Engbert & Mergenthaler, 2006), also showing that microsaccades contribute to the maintenance of visual fixation (Engbert & Kliegl, 2004; Mergenthaler & Engbert, 2007).

Additionally, in the last five years new evidence has accumulated indicating that microsaccades can be used as a powerful implicit index of the state of the perceptual-cognitive system. In particular, a series of studies have been published demonstrating that the preferential direction of microsaccades is influenced by the orienting of spatial attention in response to central visual cues (Engbert & Kliegl, 2003; Laubrock, Engbert & Kliegl, 2005; Laubrock, Engbert, Rolfs & Kliegl, 2007; but see Horowitz, Fine, Fencsik, Yurgenson & Wolfe, 2007), peripheral visual and auditory cues (Hafed & Clark, 2002; Rolfs, Engbert & Kliegl, 2004; Galfano, Betta & Turatto, 2004; Betta, Galfano & Turatto, 2007; Rolfs, Engbert & Kliegl, 2005), and during visual search (Turatto, Valsecchi, Tamè & Betta, 2007). Furthermore, the frequency of microsaccades has also been shown to vary as a function of the preparatory state of the manual (Betta & Turatto, 2006) and ocular (Rolfs, Laubrock & Kliegl, 2006) motor systems.

Interestingly, Valsecchi, Betta and Turatto (2007) recently showed that the frequency of microsaccades exhibits a distinctive response also to the presentation of rare targets (oddballs) in a visual oddball task. The presentation of frequent non-target visual stimuli (standards) elicits a biphasic modulation of the absolute frequency of microsaccades, with an early inhibition peaking at around

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100–150 ms post stimulus onset, followed by a rebound phase peaking at around 300–350 ms post stimulus onset. Such modulation was already observed quite ubiquitously in the studies addressing the direction of microsaccades and the orienting of attention in response to spatial cues (e.g. Engbert & Kliegl, 2003; Galfano et al., 2004; Rolfs et al., 2005). However, in the task used by Valsecchi et al. (2007), the inhibitory phase lasted longer, and the rebound phase was almost absent, when an oddball stimulus was presented. The authors convincingly showed that this effect was not due to a differential orienting of attention towards the stimuli, as it was observed both with peripheral and central stimuli, and was contingent on the task-relevance of the stimuli, being much weaker under passive viewing conditions.

In a subsequent study, Valsecchi and Turatto (2007), presented stimuli invisible to the Superior Colliculus (SC) in a visual oddball task, demonstrating that, far from being a mere subcortical oculomotor reflex, the modulation of microsaccades in response to both standard and oddball stimuli could be controlled by a cortical visual pathway. Nonetheless, the observation of a linear relationship between amplitude and peak velocity of microsaccades (Zuber, Stark & Cook, 1965), a feature common to regular saccades, and that can be evoked by the stimulation of the SC (Robinson, 1972), strongly suggests that the SC is probably involved in the generation of microsaccades. Moreover, given that the SC has multi-modal afferences (see Sparks, 1986; Wallace, Meredith & Stein, 1993), the fact that the biphasic modulation of microsaccades is observed in response to auditory (Rolfs et al., 2005) and visual stimuli (e.g. Engbert & Kliegl, 2003; Galfano et al., 2004) could be explained by the convergence of visual and auditory inputs in the SC. Hence, since a microsaccadic modulation elicited by auditory stimuli (Rolfs et al., 2005) has been documented, one may hypothesize that rare targets could elicit a prolonged microsaccadic inhibition in an auditory oddball task.

Audition was the first modality in which the oddball task was studied using electrophysiological techniques (Hillyard, Hink, Schwent & Picton, 1973; Näätänen, Gaillard & Mäntysalo, 1978). A comparison between the findings of electrophysiological studies in the auditory and visual modality indicates that the components elicited by rare targets, which are sensitive to the higher-level processing of the stimuli, e.g. stimulus categorization (Kok, 2001), are similar across modalities (Bennington & Polich, 1999; Katayama & Polich, 1999).

If the modulation of microsaccadic frequency induced by the presentation of visual oddballs is controlled by a modality-independent mechanism, we hypothesized that a similar microsaccadic response should be observed in an auditory oddball paradigm. To test this hypothesis, we conducted three experiments using unimodal and bimodal (audiovisual) stimulation.

Experiment 1

The aim of Experiment 1 was the one of investigating whether auditory oddballs induce a prolonged microsaccadic inhibition as observed by Valsecchi et al. (2007) in the visual modality. In the present experiment we used sinusoidal tones as stimuli, while participants observed a static visual display. As in Valsecchi et al. (2007), participants were required to silently count the oddball stimuli.

Methods

Participants

Twenty-two participants volunteered for Experiment 1 (10 female, mean age = 28.0). All of the participants reported normal or corrected-to-normal vision and hearing and were naïve as to the purpose of the study. Informed consent to participation was obtained from all participants, in accordance with the Declaration of Helsinki.

Stimuli

Stimuli were generated using Matlab (MathWorks, Natick, MA) and the PsychToolbox (Brainard, 1997).

Auditory stimuli were 1,000 or 1,500 Hz sinusoidal tones (67.9 and 81.6 dB, respectively), presented through Philips HP250 earphones (Royal Philips Electronics N.V., Amsterdam, the Netherlands). The duration of the tones was 100 ms, with a 3-ms ascending ramp at the beginning and a 3-ms descending ramp at the end.

The visual display consisted of a central white fixation point (diameter 0.5° of visual angle) on a black background. The stimulus was presented on a CRT 19′ monitor (Iiyama, Nagano-Shi, Japan), whose refresh rate was 100 Hz.

Procedure

Participants sat in front of the monitor (viewing distance = 72 cm) in a dimly illuminated room. Head movements were limited by a chin-rest. As in the Valsecchi & Turatto (2007) study, stimuli were presented in series of 10, at a rate of 1 every two seconds. Both the inter-stimulus interval and the inter-series interval were set at 1,900 ms in order to generate a continuous flow of stimuli across series. In 80% of the series, a target stimulus was presented in a random position between the second and the ninth stimulus, yielding an overall oddball frequency lower than 10%. The pitch of the oddball and standard stimuli was alternated between

participants. After each block of 10 series, participants were required to report the number of occurrences of oddball tones they had silently counted and were allowed to rest. Participants were required to fixate the point at the center of the screen and to minimize eye blinks during stimulus presentation. Each participant underwent eight blocks, 64 oddball stimuli were presented altogether. The whole experimental session lasted about 60 min.

Eye movement recording and microsaccade detection

Eye movements were recorded binocularly using an Eyelink II infrared system (SR Research, Ontario, Canada), with a sampling rate of 500 Hz and a spatial resolution of less than 0.01°. A standard nine-point calibration was performed at the beginning of each block and an automatic drift-correction was performed during the inter-series interval. If drifts exceeded 1.5°, the stimulus presentation was interrupted and a calibration was performed. Microsaccades were detected using the algorithm introduced by Engbert and Kliegl (2003), adapted for the 500 Hz sampling rate (Valsecchi et al., 2007). The algorithm was applied to 2,100 ms epochs of eye-position recordings, ranging from 50 ms prior to the onset of a stimulus to 50 ms after the onset of the following stimulus (Valsecchi & Turatto, 2007). Epochs with blinks or saccades exceeding 1.5° were discarded from the analysis.

Results

Seven participants were discarded from the analysis because we could not collect at least 30 artifact-free oddball epochs per participant. For the remaining 15 participants, we collected on average 44.7 oddball epochs and 342.8 standard epochs, the minimum number of epochs was 30 and 260, respectively.

The absolute frequency of microsaccades in response to oddball and standard stimuli is depicted in Fig. 1. Visual inspection of Fig. 1 clearly indicates that the inhibition of microsaccades following the presentation of the tone lasted longer in response to oddball stimuli. This impression was substantiated by statistical analyses, where we performed a series of *t* tests confronting the frequency of microsaccades in oddball and standard epochs in 20 successive 100-ms wide time windows. We decided not to perform tests on overlapping time windows in order to limit the dependency of the different tests. The 20 *p* values obtained were entered into the Benjamini and Yekutieli (2001) procedure to control the False Discovery Rate (FDR) under 0.05. The only test to survive the FDR control procedure was the one performed in the time-window from 200 to 300 ms post stimulus onset. This result is indicative of the fact that the inhibition of mirosaccades lasted longer in response to

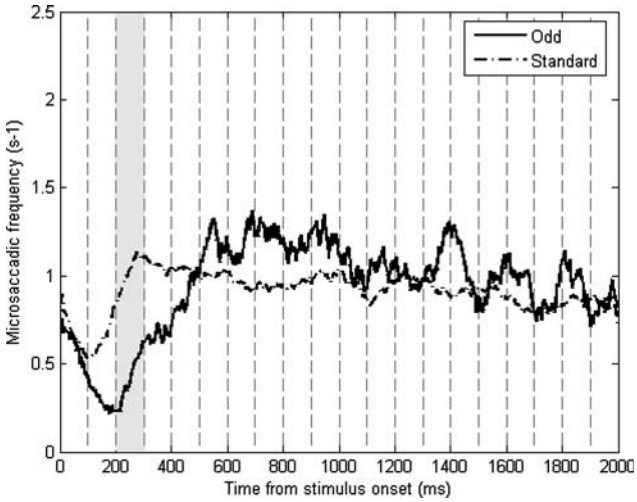

Fig. 1 Evolution of microsaccadic frequency in response to oddball and standard stimuli in Experiment 1. The plots were constructed calculating the frequency of microsaccades in a 100 ms wide time window moving in 2 ms steps. The *vertical dashed lines* delimit the time windows on which paired *t* tests have been conducted confronting the frequency of microsaccades in response to oddball and standard stimuli. The *gray* area corresponds to the time window where the *t* test detected a significant difference after FDR correction (see "Results")

oddball stimuli. Moreover, the inspection of Fig. 1 suggests that the minimum peak in the frequency of microsaccades might be lower in the case of oddball stimuli. To test for this, we performed a paired *t* test confronting the frequency of microsaccades in the time window centered on the point where the average curve reached the minimum value in response to oddball and standard stimuli (176 and 98 ms post stimulus onset, respectively). The minimum microsaccadic frequency was lower $t(14) = 2.966$, $p < 0.01$ in response to oddball epochs as compared to standard epochs.

Discussion

Similarly to what was observed by Valsecchi et al. (2007) and Valsecchi and Turatto (2007) in the visual modality, the results of Experiment 1 indicated that the frequency of microsaccades was inhibited longer in response to rare targets also in an auditory oddball task. This supports the idea that microsaccades can be controlled by a modality-independent cortical mechanism. This also suggests that microsaccades can be used as a tool to investigate the brain's responses to relevant stimuli from different modalities.

However, if one compares the results obtained in the current experiment with those from Valsecchi et al. (2007) and Valsecchi and Turatto (2007), the modulation of microsaccades in response to auditory standard stimuli seems to be weaker than the one observed in response to standard visual stimuli. In particular, the inhibitory phase was more limited and the following rebound phase was not clearly delineated. Moreover, whilst in the current experiment the

maximum inhibition level in response to oddball stimuli was reached at a lower microsaccadic frequency as compared to standard stimuli, the experiments in the visual modality produced approximately the same level of inhibition for standard and oddball epochs, even if the inhibition phase lasted longer in response to oddball stimuli.

Experiment 2

The results of Experiment 1 indicated that the frequency of microsaccades in response to auditory oddball stimuli has a profile similar to the one observed for visual oddball stimuli, whereas the biphasic response produced by standard stimuli seems to be characterized by a smaller rebound.

In Experiment 2, we decided to directly compare the microsaccadic response to auditory and visual stimuli in order to directly test within the same group of participants, to what extent the microsaccadic response differs between the two modalities.

We also added two conditions in which participants were presented with bimodal stimuli making either the auditory or the visual signals task-relevant. This manipulation had the purpose to ascertain whether a possible differential modulation of microsaccades was related to the stimulus modality or to the attended modality.

Methods

Participants

Twenty-two participants volunteered for Experiment 2 (eight female, mean age = 21.0). All of the participants reported normal or corrected-to-normal vision and hearing and were naïve as to the purpose of the study. Informed consent to participation was obtained from all participants, in accordance with the Declaration of Helsinki.

Stimuli

Auditory stimuli were the same as in Experiment 1. Visual stimuli were red or green circles (diameter = 2°) centrally presented at fixation. The green color was made equiluminant to the red color (41.3 cd/m^2) using 25 Hz flicker fusion (Wyszecki & Stiles, 1982). The duration of the visual stimuli was estimated to be 94 ms using the formula introduced by Bridgeman (1998). Stimuli were delivered using the same apparatus as in Experiment 1.

Procedure

Each participant underwent two sessions, in separate days, each containing 288 series of stimuli. In each session, participants were asked to silently count either the rare tones or the rare circles, and to report the number of oddball stimuli after each block of 12 series. The stimuli could be unimodal or bimodal (the auditory and the visual stimulus were presented simultaneously), with the modality of presentation alternated between blocks.

A bimodal oddball, i.e. the simultaneous presentation of a rare stimulus in both the auditory and the visual modality was delivered in 62.5% of the series with bimodal stimulation. In 12.5% of the series the stimulus was a rare one only in the attended modality and was frequent in the unattended modality. In 12.5% of the series a rare stimulus was presented only in the unattended modality and in the remaining 12.5% of the series only frequent stimuli were presented. In the unimodal series an oddball stimulus was presented on 75% of the trials. In order to limit the total duration of the experiment, we reduced the number of stimuli per series to eight, and the oddball stimuli could be presented in a random position between the second and the seventh in the series. This yielded an overall target frequency of less than 10%. In order to further limit the duration of the experiment, we raised the rate of presentation of the stimuli to 1 Hz.

Eye movement recording and microsaccade detection

Eye movements were recorded with the same equipment as in Experiment 1. Microsaccades were detected using the same procedure as in Experiment 1, applied to 1,100 ms epochs of recording, ranging from 50 ms prior to the stimulus presentation to 50 ms after the next stimulus presentation. Epochs containing blinks and/or saccades with an amplitude exceeding 1.5° were discarded from the analysis.

Results

The number of artifact-free epochs we collected for each participant is reported in Table 1. None of the participants was discarded from the analysis.

The frequency of microsaccades in Experiment 2 is depicted in Fig. 2. If only the standard curves (dashed lines) are considered, it emerges that a clear inhibition-rebound response was present in every condition with the exception of the auditory-unimodal one. In that case the average microsaccadic frequency did not show a clear inhibitory phase. The peak frequency in the rebound phase was reached between 200 and 220 ms post stimulus onset, with a peak value of around 1.7/s. In the other cases, i.e. in all cases in which standard visual stimuli were presented alone or in association with an auditory stimulus, the peak frequency on the average plot was reached between 250 and 300 ms post stimulus onset, and the frequency peaked above 2.5/s.

Table 1 Average and minimum number of artifact-free epochs per subject, in each cell of the experimental design of Experiment 2

	Bimodal				Unimodal			
	Attended sound		Attended vision		Attended sound		Attended vision	
	Mean	Minimum	Mean	Minimum	Mean	Minimum	Mean	Minimum
Oddball	67.3	37	69.8	39	64.6	36	72.1	39
Standard	574.2	439	596	417	538.5	353	611	413

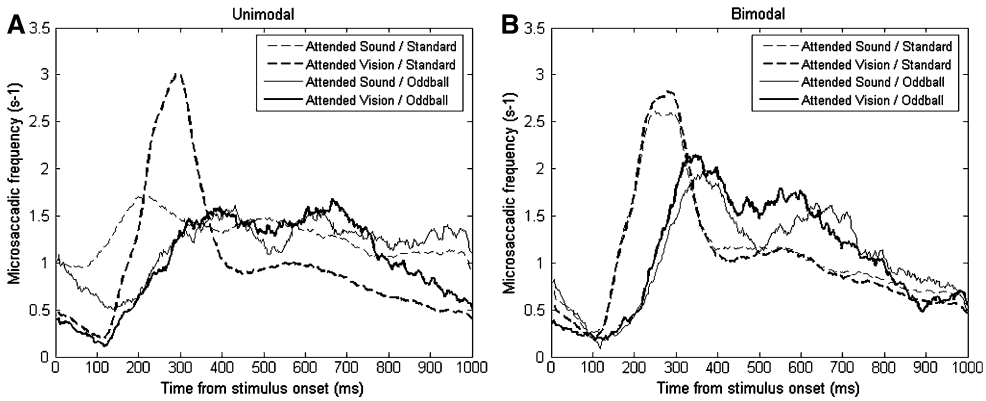

Fig. 2 Evolution of microsaccadic frequency in Experiment 2, in response to oddball and standard stimuli for unimodal (**a**) and bimodal (**b**) presentation. *Thick lines* correspond to the session where the visual channel was attended and *thin lines* correspond to the session where the auditory channel was attended. The plots were constructed calculating the frequency of microsaccades in a 100 ms wide time window moving in 2 ms steps

Although the difference in the latency of the rebound phase between the auditory-unimodal condition and the visual-unimodal condition might look striking in the average plots, it was not statistically significant. A standard analysis of latency such as the one performed by Valsecchi and Turatto (2007) was precluded because the peak in the microsaccadic rate was not clearly identifiable on the single-participant plots for the auditory-unimodal condition. We conducted an analysis producing a surrogate sample through jackknifing. The analysis did not show a shorter latency for the auditory-unimodal condition as compared to the attended auditory-bimodal condition using the correction introduced by Ulrich and Miller (2001) $F(1,12) = 49.192$, $p_{corr} > 0.05$.

The peak microsaccadic frequency in standard epochs, i.e. the frequency in the 100-ms wide time window where the maximal microsaccadic frequency was measured, was submitted to a two-way repeated-measures ANOVA with Attended Modality (auditory vs. visual) and Condition (unimodal vs. bimodal) as factors. The main effect of Attended Modality $F(1,12) = 18.256$, $p < 0.001$, of Condition $F(1,12) = 9.454$, $p < 0.01$ and the two-way interaction $F(1,12) = 31.264$, $p < 0.01$ were significant. Moreover, further tests showed that the peak amplitude in the auditory unimodal case was lower than in all of the other three cases (all ps < 0.001).

We also observed that the peak microsaccadic frequency in response to bimodal standard stimuli was slightly higher in the attend visual as compared to the attend auditory condition. This difference, however, only approached significance $t(12) = 1.834$, $p = 0.0914$.

As for oddball stimuli, in all conditions the microsaccadic response presented a prolonged inhibition. On the basis of the results of Experiment 1, showing that the critical difference between standard and oddball epochs was observed in the time window corresponding to the maximum rebound in response to standard stimuli, and in order to maximize the power of our analysis, we chose to performed a paired-t test for each cell of the Attended Modality × Condition design confronting the microsaccadic frequency in oddball and standard epochs in the time window of the peak rebound elicited by standards. In all four cases the frequency in response to oddball stimuli was lower than in response to standard stimuli (all ps < 0.01, uncorrected).

In addition, the baseline level of microsaccadic frequency, i.e. the microsaccadic frequency in the window centered on the time of stimulus presentation, seemed to be higher in the case of unimodal-attended auditory epochs. In this case we also decided to limit the analysis to standard epochs, where we could obtain a better estimate given the higher number of averaged epochs. In principle the frequency of microsaccades in response to standard and oddball epochs should be the same in this time window, given that the upcoming stimulus has not been processed yet. We entered the microsaccadic frequency in standard epochs at

0 latency into a two-way repeated-measures ANOVA with Attended Modality (auditory vs. visual) and Condition (unimodal vs. bimodal) as factors. The main effect of Attended Modality $F(1,12) = 24.003$, $p < 0.001$, of Condition $F(1,12) = 8.365$, $p < 0.014$, and the two-way interaction $F(1,12) = 22.357$, $p < 0.001$ were significant. As in the case of the peak frequency, the microsaccadic frequency was different in the auditory unimodal condition as compared to the remaining three conditions (all ps < 0.001).

Finally, we analyzed the overall frequency of microsaccades within the whole epoch. The values were entered into a three-way repeated-measures ANOVA with Type of Stimulus (oddball vs. standard), Attended Modality (auditory vs. visual) and Condition (unimodal vs. bimodal) as factors. The effect of Attended Modality $F(1,12) = 7.355$, $p < 0.019$ and the Attended Modality × Condition interaction $F(1,12) = 8.925$, $p < 0.011$ were significant. All other effects and interactions were not significant (all ps > 0.05). This indicates that for both standard and oddball stimuli, the overall frequency of microsaccades was higher when the auditory modality was attended and the presentation was unimodal.

Discussion

A clear picture emerges from the results of Experiment 2. First of all, the average response to oddball stimuli was independent from modality, with a prolonged inhibition and without a clearly identifiable rebound. This is consistent with the hypothesis that the microsaccadic behavior in response to oddball stimuli is mainly driven by modality-independent control mechanisms.

Moreover, a comparison between the data of Experiment 1 and those reported by Valsecchi et al. (2007) and Valsecchi and Turatto (2007) led us to hypothesize that standard auditory stimuli induced a more limited modulation of microsaccadic frequency as compared to visual stimuli. This impression was confirmed by the observation of a smaller amplitude in the peak microsaccadic frequency in Experiment 2 when only auditory stimuli were presented as compared to the epochs in which a visual stimulus was presented alone or in combination with an auditory stimulus. As for now, it is difficult to find an explanation for this difference. First of all, we should observe that no parametric study has been conducted to associate the amplitude of the modulation of microsaccadic frequency to the intensity of the stimulation. We suspect that, at least within the visual modality, the microsaccadic response could be maximal within a wide range of stimulus intensity, given that Valsecchi et al. (2007) found that the microsaccadic rebound had the same amplitude when stimuli consisted of a luminance onset or a simple hue change, although the latency of the rebound was slightly longer in the case of simple hue changes. Nonetheless, we can not exclude that the amplitude of the microsaccadic modulation might change with stimulus intensity in the auditory modality, but the intensity of stimuli can not easily be matched on an absolute scale across modalities (Marks, Szczesiul, & Ohlott, 1986; Gescheider, 1988). The smaller amplitude of the microsaccadic modulation obtained with unimodal auditory stimuli than unimodal visual stimuli could however be the result of a more limited weighting of the auditory input as compared to the visual input in the SC.

The same reasoning holds for the overall frequency of microsaccades too. We have shown that the frequency of microsaccades averaged along the whole epoch was higher in the unimodal-attended auditory condition as compared to the unimodal-attended vision condition. This difference could depend on the intensity of the stimuli we used or on the relative efficiency of the visual and auditory modalities in driving the microsaccadic response. In any case, on the basis of what we found, we can conclude that the continuous presentation of stimuli that generate a more evident inhibition-rebound modulation of microsaccades might induce a generalized inhibition of microsaccades. It is interesting to note that the Engbert & Mergenthaler (2006) model of microsaccade generation proposes that the frequency of these fixational eye movements is controlled in an homeostatic way in relation to the amount of retinal slip. The hypothesis is consistent with our observation that a more limited rebound is produced when the baseline microsaccadic frequency is higher.

Finally, it interesting to note that the amplitude of the microsaccadic rebound was slightly higher for bimodal stimuli when the subjects attended to the visual modality as compared to when they attended to the auditory modality. This observation is intriguing, since it could indicate that the microsaccadic response to standard stimuli was modulated by the fact that participants attended to the modality preferentially driving the microsaccadic response or the weaker one. We must however notice that our manipulation of modality-selective attention was probably not very powerful, given that target stimuli were generally rare in both modalities, whereas target stimuli consisting of a frequent stimulus in the unattended modality and of a rare stimulus in the attended modality were comparatively less probable. Experiment 3 was specifically devised in order to ascertain whether the attended modality could influence the microsaccadic response to bimodal standard stimuli.

Experiment 3

In Experiment 3 we directly addressed the question of whether the attended modality could influence the response to standard stimuli in a bimodal oddball task. The results

from Experiment 2 are suggestive of a possible modality-specific modulation of microsaccadic frequency in response to standard stimuli, but the trend was not significant.

In Experiment 2 the way we manipulated attention to the different modalities in the bimodal condition may have been weak. This could be due to two different reasons. First of all, when a stimulus was a target in the attended modality, most of the times it was a rare stimulus also in the unattended modality. This was necessary, otherwise, had we randomized the position of the rare stimulus in the series independently for the two modalities, the proportion of bimodal oddballs would have been to low to yield a sufficient number of epochs per participant. Second, since the stimuli changed from bimodal to unimodal or vice-versa after each block, the saliency of the stimuli in the unattended modality might have increased, given that they were repeatedly switched on and off. In Experiment 3 we decided to present only bimodal stimuli in order to make the unattended modality less salient, and to increase the total number of epochs in order to have a more stable measure of the microsaccadic behavior.

Methods

Participants

Twelve participants volunteered for Experiment 3 (nine female, mean age = 21.8). All of the participants reported normal or corrected-to-normal vision and hearing and were naïve as to the purpose of the study. Informed consent to participation was obtained from all participants, in accordance with the Declaration of Helsinki.

Stimuli

Stimuli were the same as in the bimodal condition of Experiment 2.

Procedure

Each participant underwent two sessions, in separate days, each containing 192 series of stimuli. In each session, participants were asked to silently count either the rare tones or the rare circles, and to report the number of oddball stimuli after each block of 12 series. Stimulation was always bimodal (the auditory and the visual stimulus were presented simultaneously).

A bimodal oddball, i.e. the simultaneous presentation of a rare stimulus in both the auditory and the visual modality was delivered in 62.5% of the series. In 12.5% of the series the oddball stimulus was presented only in the attended modality, in 12.5% of the series a rare stimulus was presented only in the unattended modality and in the remaining 12.5% of the series only standard stimuli were presented. As in Experiment 2, the number of stimuli per series was eight, and the oddball stimuli could be presented in a random position between the second and the seventh in the series. This yielded an overall target frequency of less than 10%. The rate of presentation of the stimuli was 1/s.

Table 2 Average and minimum number of artifact-free epochs per subject, in each cell of the experimental design of Experiment 3

	Attended sound		Attended vision	
	Mean	Minimum	Mean	Minimum
Oddball	98.3	66	94.1	41
Standard	802.6	607	786.7	587

Eye movement recording and microsaccade detection

Eye movements were recorded with the same equipment as in Experiment 1. Microsaccades were detected using the same procedure as in Experiment 1. Epochs containing blinks and/or saccades with an amplitude exceeding 1.5° were discarded from the analysis.

Results

The number of artifact-free epochs collected for each participant is reported in Table 2. None of the participants was discarded from the analysis. The evolution of microsaccadic frequency is depicted in Fig. 3. Not surprisingly, given

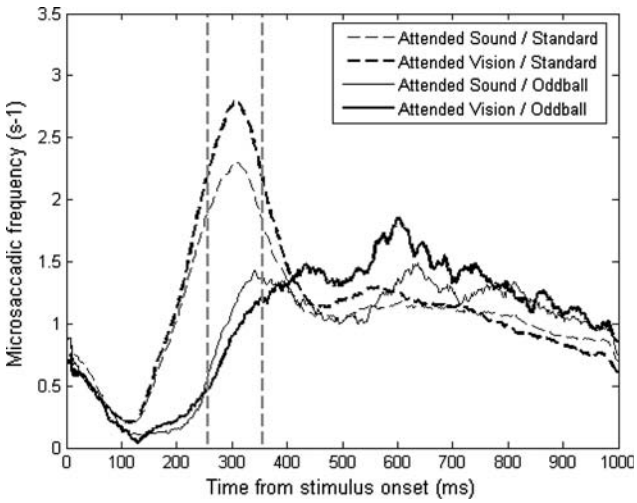

Fig. 3 Evolution of microsaccadic frequency in Experiment 3, in response to oddball and standard stimuli. *Thick lines* correspond to the session where the visual channel was attended and *thin lines* correspond to the session where the auditory channel was attended. The vertical *dashed lines* delimit the time window of interest centered on the peak microsaccadic rebound. The plots were constructed calculating the frequency of microsaccades in a 100 ms wide time window moving in 2 ms steps

that the experimental paradigm was almost identical, the overall pattern was similar to the one observed in the bimodal condition of Experiment 2. In particular, the standard stimuli induced the usual biphasic modulation of microsaccades, featuring an early inhibition and a subsequent rebound phase, whereas the presentation of oddball stimuli elicited a prolonged inhibition of microsaccades without a clearly identifiable rebound phase. However, the difference between the rebound amplitude as a function of the attended modality was more evident than in Experiment 2.

Given that the latency of the rebound phase in response to standard stimuli, as calculated by inspection of Fig. 3, was substantially identical in the two conditions (306 and 308 ms post stimulus onset for the attended-visual and in the attended-auditory conditions, respectively), we decided to use a single time window of interest (WOI), centered on 306 ms post stimulus onset, for both conditions. First, we entered the frequency of microsaccades in the time WOI into a two-way repeated-measures ANOVA with Type of Stimulus (oddball vs. standard) and Attended Modality (auditory vs. visual) as factors. The effect of Type of Stimulus $F(1,11) = 27.932$, $p < 0.001$ and the two-way interaction $F(1,11) = 20.728$, $p < 0.001$ were significant. Two paired-sample t tests were performed to confront the microsaccadic frequency in response to standard and oddball stimuli between attend-auditory and attend-visual conditions in the time WOI. The test was not significant in the case of oddball epochs $t(11) = 1.459$, $p = 0.172$, whereas it was significant in the case of standard stimuli $t(11) = 2.517$, $p < 0.028$.

Finally, we analyzed the overall frequency of microsaccades. A two-way repeated-measures ANOVA with Type of Stimulus (oddball vs. standard) and Attended Modality (auditory vs. visual) as factors revealed only a significant effect of Type of Stimulus $F(1,11) = 6.636$, $p < 0.025$.

Discussion

The results of Experiment 3 indicated that, as compared to what happens in the case of oddball stimuli, under bimodal stimulation the microsaccadic response to standard stimuli is modulated in a functionally different fashion by the orienting of attention to a sensory modality. Specifically, the response to bimodal oddball stimuli was mainly characterized by the usual prolonged inhibition regardless of the attended modality, whereas the rebound phase in response to standard stimuli showed a higher amplitude when the participants attended to the visual modality as compared to when they attended to the auditory modality.

The smaller amplitude of the response to bimodal standard stimuli when the auditory modality was attended seems to indicate that attending to the modality preferentially driving the microsaccadic response produces a more effective modulation of microsaccadic frequency than when the lesser effective modality is attended.

The fact that the difference in the amplitude of the rebound in response to bimodal standard stimuli as a function of the attended modality was significant in Experiment 3, whilst only a tendency in this direction was observed in the bimodal condition of Experiment 2, suggests that removing the unimodal presentation from the experimental design was effective in reducing the saliency of the unattended modality. The increased reliability of the effect might be related to the fact that we increased of about 35% the number of epochs per participants as compared to Experiment 2, thus making our measures more stable.

General discussion

Valsecchi et al. (2007) demonstrated that microsaccades can be used as a tool to investigate the brain's response to rare targets in a visual oddball paradigm. They showed that oddballs induced a prolonged microsaccadic inhibition, whereas standards induced a biphasic inhibition-rebound modulation of microsaccades. Their results suggested that the microsaccadic response to oddballs would reflect the intervention of a top-down inhibitory component associated with stimulus categorization and target detection. By contrast, the response to standards would be mainly driven by reflex-like oculomotor reactions. In a following study Valsecchi and Turatto (2007) showed that even the response to standard stimuli can be controlled by a cortical network, which left open the possibility that even this aspect of the microsaccadic response may be modulated by cognitive factors.

We reasoned that if the prolongation of the microsaccadic inhibition reflects the higher-level stages of target analysis (i.e. stimulus categorization and target detection) rather than the analysis at perceptual stages, it should be possible to observe the same effect regardless of the specific sensory modality. To test this prediction we used the auditory modality because there was evidence (Rolfs et al., 2005) that auditory stimuli, like visual stimuli, can induce a biphasic modulation of microsaccadic frequency, which strongly suggested a connection between the auditory system and the microsaccade-generating structures.

The results of Experiment 1 and of the unimodal-attended auditory condition of Experiment 2 confirmed our hypothesis: the prolonged inhibition of microsaccades first described in a visual oddball task by Valsecchi et al. (2007) was indeed produced independently from the modality of stimulation, which strengthens the point that this effect is related to the categorization phase of the stimuli. Moreover, the fact that this effect was observed with auditory stimuli presented binaurally through earphones (during static

visual stimulation) strongly suggests that in our oddball paradigm neither the focusing of visuospatial attention nor the focusing of auditory spatial attention can be an antecedents of the prolonged microsaccadic inhibition in response to rare targets.

Overall, the data from the three experiments seem to indicate that the microsaccadic response to oddball stimuli is similar regardless of the attended modality and regardless of whether the presentation is unimodal or bimodal. On the contrary, the response to standard stimuli, which is not task-relevant, seems to vary as a function of the modality in which the stimuli are presented under unimodal stimulation, being also modulated by the attended modality under bimodal stimulation.

In general, the fact that, as compared to standard stimuli, the microsaccadic behavior in response to oddball stimuli was less sensitive to the modality of the stimuli and to the attended modality is coherent with the findings from electrophysiological studies of the intermodal oddball paradigm. These findings indicate that the earlier task-independent components elicited by rare stimuli, such as the Mismatch Negativity, are strongly modality-specific (Besle, Fort & Giard, 2005; Brown, Clarke & Barry, 2006; Brown, Clarke & Barry, 2007). On the contrary, later ERPs which more selectively index the task-related processing of rare targets, such as the P300 (Verleger, 1988; Donchin & Coles, 1988; Kok, 2001), seem to be much less modality-specific. These studies, however, were not conducted using both unimodal and bimodal stimuli and manipulating the attended modality, so that no direct comparisons can be made.

It is worth noting that the differential modulation between oddball and standard epochs is most evident around 300 ms post stimulus onset, but is already evident before 200 ms post stimulus onset. Thus, the onset of the target-related effects in microsaccadic frequency seems to occur earlier than is commonly observed in ERPs, where only modality-specific effects (N1 or Mismatch Negativity, e.g. Näätänen et al., 1978) are commonly found before 200 ms latency.

The modulation of the microsaccadic response to bimodal standard stimuli as a function of the attended modality was rather small. However, it is important to note that in Experiments 2 and 3 the target stimulus was often a rare event in both modalities, which could have weakened the attention selectivity to the task-relevant modality. Moreover, it has been demonstrated (Busse, Roberts, Crist, Weissman & Woldorff, 2005) that the presentation of a relevant stimulus in one modality can enhance the sensory processing of the stimulus in an unattended modality as long as they are presented synchronously. That is tantamount to say that in our task the sensory processing of the stimuli in the unattended modality could have been enhanced given that at the same time relevant stimuli were presented in the attended modality. Hence, one may hypothesize that stronger attentional effects should be observed if the participants were shown two interleaved streams of asynchronous unimodal stimuli, e.g. auditory–visual–auditory–visual and so on, and were asked to selectively attend to one of the two modalities.

Unfortunately the present data do not allow us to establish whether the auditory stimuli are less effective in driving the microsaccadic behavior as compared to the visual ones. Data from Valsecchi and Turatto (2007) showed that a luminance onset generates the same response as a color hue change, indicating that at least for visual stimuli no clear relationship exists between the microsaccadic response and stimulus intensity. No such claim can be made as far as the auditory modality is concerned. In any case, a parametric study of the relationship between stimulus intensity and microsaccadic modulation was beyond the scope of the present study. In principle, we can not exclude that attending to different streams of stimuli presented synchronously within the same modality could modulate the response to standard stimuli in the oddball paradigm, as we found when participants attended to different modalities. To test this hypothesis, however, one would need to create two stimuli within the same modality, which can clearly induce a different microsaccadic inhibition-rebound response, but there are currently no indications that this is feasible.

It is worth noting that the modulation of microsaccadic frequency we observed is consistent with the variety of response patterns observed in the SC cells. Perrault, Vaughan, Stein & Wallace (2005) found that the response of about 45% of the multisensory neurons in the cat SC did not vary as a function of visual stimulus intensity, and about 48% of the multisensory neurons did not show a dynamic range in response to auditory stimuli. Moreover, for those stimuli showing a dynamic range in their response, they found that only 18% showed superadditivity when an highly effective stimulus was coupled with a stimulus from another modality, meaning that the neuron's response was higher than the one predicted by the sum of the two unimodal responses, all of the other cells showed subadditivity. These observations are compatible with our findings showing that the microsaccadic response to bimodal standard stimuli was mainly driven by the most effective (i.e. visual) modality and was not affected by the presentation of a synchronous less efficient stimulus (a sign of subadditivity).

Our observation that the microsaccadic response to bimodal standard stimuli was also modulated by the attended modality is consistent with the finding that the multisensory response in the macaque SC neurons is supported by cortical structures such as the Anterior Ectosylvian Sulcus and the rostral Lateral Suprasylvian

Sulcus (Jiang, Wallace, Jiang, Vaughan & Stein, 2001; see Stein, Wallace, Stanford, & Jiang, 2002, for review). Selective lesions of those structures largely abolish the superadditivity of the cells' response, which becomes equal to the sum of the response generated by the single modalities. Although we did not find superadditivity in the microsaccadic response, this suggests the possibility that the multisensory response properties to of the SC cells which control microsaccadic execution are not hard-wired in the subcortical circuits and could be modulated in a flexible way.

To summarize, we have shown that, like the later evoked potentials (e.g., P300) triggered by the presentation of oddballs, the microsaccadic response to oddball stimuli is not modality specific. This supports our claim that this response might be an index of higher-order cognitive mechanisms driving the brain's response to rare targets in the oddball task (Valsecchi & Turatto, 2007). Finally, we showed that the microsaccadic response to standard stimuli is not entirely reflex-like, being sensitive to the task relevance of the different unimodal components of bimodal stimuli.

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