

Microsaccadic modulation of response times in spatial attention tasks

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Abstract Covert shifts of attention are usually reflected in RT differences between responses to valid and invalid cues in the Posner spatial attention task. Such inferences about covert shifts of attention do not control for microsaccades in the cue-target interval. We analyzed the effects of microsaccade orientation on RTs in four conditions, crossing peripheral visual and auditory cues with peripheral visual and auditory discrimination targets. Reaction time was generally faster on trials without microsaccades in the cue-target interval. If microsaccades occurred, the target-location congruency of the last microsaccade in the cue-target interval interacted in a complex way with cue validity. For valid visual cues, irrespective of whether the discrimination target was visual or auditory, target-congruent microsaccades delayed RT. For invalid cues, target-incongruent microsaccades facilitated RTs for visual target discrimination but delayed RT for auditory target discrimination. No reliable effects on RT were associated with auditory cues or with the first microsaccade in the cue-target interval. We discuss theoretical implications on the relation about spatial attention and oculomotor processes.

Introduction

The Posner cueing task is probably the most frequently used experimental paradigm in spatial attention research

(Posner, 1980; Posner, Davidson, & Snyder, 1980). It is built on the premise that we can separate the focus of attention from the point of ocular fixation. So-called covert shifts of attention are induced by cues that are either presented at the point of fixation or in the periphery at the future location of the target. The cues can be valid, neutral, or invalid with respect to the eventual location of the target. Classic results are response latency (RT) benefits for valid cues and RT costs for invalid cues relative to neutral cues. Moreover, peripheral cues typically exert their influence faster and more strongly than central cues (Müller & Rabbitt, 1989). This is interpreted as reflecting a high degree of automatic ‘attention grabbing’ by peripheral cues.

Obviously, the absence of *overt* eye movements during a cue-target interval is critical for attributing response-time benefits and costs to *covert* shifts of attention. To this end, researchers typically used cue-target intervals (CTIs) that are too short to allow programming and execution of a saccade (i.e., shorter than 200 ms). Nevertheless, as our eyes are always in motion, there are small overt fixational eye movements during any CTI, that is even when we attempt to fixate our eyes. Customarily, one distinguishes three types of fixational eye movements: tremor, drift, and microsaccades (Barlow, 1952; Ditchburn & Ginsborg, 1953; Ratliff & Riggs, 1950). Here, we are concerned only with microsaccades. These occur up to several times per second and are very fast movements with saccade-like properties but with amplitudes of less than one degree. Microsaccades may result in robust changes in visual perception (e.g., Clowes, 1962; Deubel & Elsner, 1986; Ditchburn, 1955; Donner & Hemilä, 2007; Elsner & Deubel, 1986; Laubrock, Engbert, & Kliegl, 2008; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006; Rattle & Foley-Fisher, 1968; Zuber & Stark, 1966), and their orientation is reliably correlated with the direction of spatial attention shifts.

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Microsaccades are oriented *in* the direction of cues (Engbert & Kliegl, 2003) in a restricted time window following central informative cues. In contrast, orientation effects in response to peripheral cues show more fluctuation over time and are dependent on the experimental paradigm. First, they are oriented in the direction of the cue, then opposite to the cue direction, and finally back in cue direction (e.g., Laubrock et al., 2005, 2008; Rolfs, Engbert, & Kliegl, 2004, 2005; see also Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; for an overview see Engbert, 2006).

Matters are further complicated by strong systematic fluctuations of microsaccade rate. For example, in response to any sudden-onset event (such as a visual or an auditory cue), the rate quickly declines from the baseline rate of 1–0.2 Hz and then raises back to the baseline level or twice the baseline rate (e.g., Rolfs et al. 2005). Weak cues (e.g., color vs. arrows as central cues) induce a slower development of this pattern (Engbert & Kliegl, 2003). Also, with densely scheduled visual events, microsaccades may be driven to low rates that prevent any meaningful statistical analysis (Tse, Sheinberg, & Logothetis, 2002, 2004; Rolfs et al., 2004).

In summary, on the one hand, there is a solid empirical link between perceptual events and the rate of microsaccades as well as between spatial attention and the direction of microsaccades. On the other hand, the relation between these microsaccadic effects and a prime measure of spatial attention research, response latency, is unclear at best. Indeed, Horowitz, Fine, Fencsik, Yurgenson, and Wolfe (2007a, b) doubted that there is any relation to RTs at all and concluded that microsaccades are irrelevant for an understanding of processes subserving spatial attention. Laubrock, Engbert, Rolfs, and Kliegl (2007) raised various methodological problems with this perspective and demonstrated an, admittedly weak, relationship between cue-congruency of microsaccades and subsequent RT after statistical control of the cue-RT relation. In their reply, Horowitz et al. (2007, p. 368) allowed that “this finding may be of use in elucidating the neural circuitry underlying attention and oculomotor control” but that “the very weakness of that relationship indicates that microsaccades cannot be used as a reliable index of spatial attention.”

Before we close the book on this question, there are several reasons why we propose to search for conditions under which the relation may be stronger than observed so far. First, we do not expect a perfect relation between microsaccade direction and spatial attention. For example, we certainly expect a cue validity effect in trials without microsaccades. Second, if a microsaccade occurs, the cue validity effect may depend on whether or not a microsaccade in the CTI is congruent or incongruent with the target. Finally, the strength of the relation may depend on whether the microsaccade occurred after the cue or before the target.

Plausibly, effects of microsaccade direction on RTs may be more likely for the last than the first microsaccade in a CTI. For example, Rolfs et al. (2006) reported longer RTs for trials in a delayed-saccade task with microsaccades occurring just before the go signal that is when they occurred close to the response. For a memory-guided condition, they also reported a facilitative effect for microsaccades early after target definition. Such differential time-dependent effects may cancel systematic microsaccadic effects on RT. This article reports microsaccade-related modulation of RTs from four experiments employing unimodal (visual and auditory) and crossmodal spatial attention tasks. The original report of these data in Rolfs et al. (2005) focused only on microsaccade rate and orientation; it did not detail how RTs relate to the time of occurrence, direction, and frequency of microsaccades in the CTI.

Methods

Materials and methods

Methods will be outlined in a condensed form. The four experiments differed in the type of cue-target combination: visual cues and visual targets (VV), visual cues and auditory targets (VA), auditory cues and visual targets (AV), and auditory cues and auditory targets (AA) in experiments 1–4, respectively.

Participants

A total of 112 undergraduate students (28 in VV; 31 in VA; 25 in AV; 28 in AA) were paid or received study credit for their participation. Participants had normal or corrected-to-normal vision, reported normal hearing, and were in good health. The 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). Visual stimuli were presented on a 19-inch EYE-Q 650 Monitor (1,024 × 768 resolution; frame rate 100 Hz). Auditory stimuli were presented through Sennheiser HD 520 II headphones.

Visual stimuli were presented on a gray background. The fixation spot was a small ring (diameter 0.8°; inset 0.1°) in dark gray color. Each of the four experiments

reported here implemented one of the four combinations of cue and target modality (visual or auditory). No other variables were manipulated between experiments.

Visual cues were white circles flashing for 100 ms 12.7° to the left or to the right of the fixation spot along the horizontal axis. Auditory cues were 70 dbA noise bursts (duration 82 ms), monaurally played to the left or right ear.

Visual targets were either green or red squares (width 0.8° ; eccentricity 12.7° to the left or to the right of the fixation point along the horizontal axis). Auditory targets were monaurally presented 70 dbA sinusoidal tones differing in tone pitch (440 or 880 Hz). Depending on cue location and cue validity, target stimuli were presented either to the left or to the right. All targets were presented for a maximum time of 500 ms or until the participant's response. False responses triggered a combined 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 a key training, linking “red” and “green” (VV and AV) or “high pitch” and “low pitch” (VA and AA) to the up and down arrow keys, respectively, participants performed five randomly ordered practice trials introducing the task and 120 test trials.

A standard 9-point (grid) calibration of the eye tracker was performed and validated before the first and after every 15th test trial. Every fifth trial, and if fixation was not correct at the beginning of a trial, a drift correction was carried out.

Figure 1 illustrates trial sequence for each of the four experiments. Participants were required to look at the fixation spot during the whole trial. After some 1,000–1,500 ms, a cue was presented. After cue presentation plus an additional

1,000–1,500 ms of fixation, the target appeared. Participants made speeded manual responses discriminating which of two alternative targets, a green versus a red square (VV and AV) or a low- versus a high-pitch tone (VA and AA), occurred. Incorrect responses were followed by an error feedback; correct responses directly initiated the next trial.

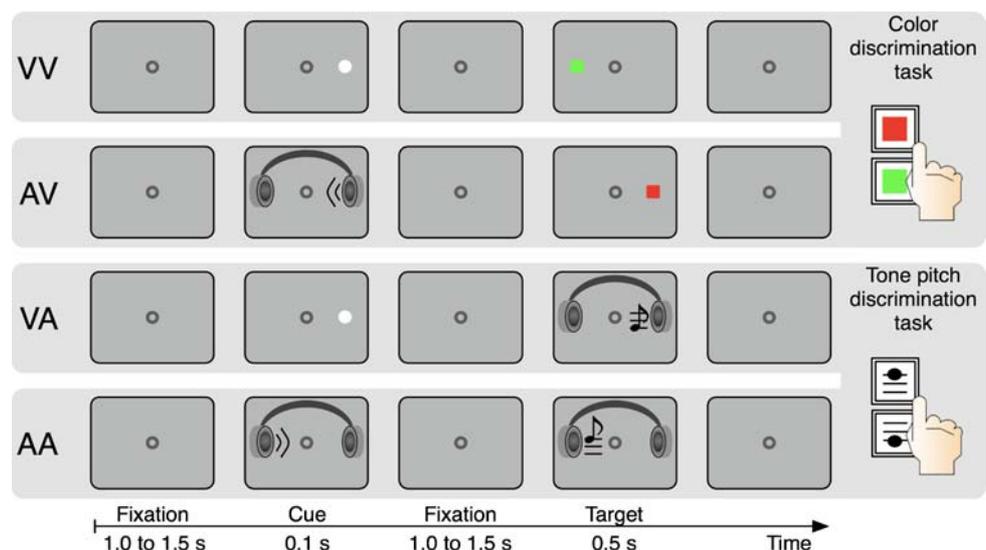
Cue position (left or right) as well as target alternative (red vs. green or low pitch vs. high pitch) had equal probability over the 120 trials. Thirty trials of every combination of cue position and target alternative included 24 trials with a valid cue and six trials with an invalid cue (80% cue validity). Trials were presented in a pseudo-random order, with a maximum of three subsequent trials with the same cue position, cue validity, and target alternative.

Data analyses

Trials with incorrect responses were discarded as were trials including blinks after cue onset or saccades larger than 1° of visual angle. Moreover, a few trials had to be excluded due to technical problems with the eye-tracking system. Finally, we also excluded trials with RTs longer than 2 s (i.e., 87 of 21,797 trials; 0.4%); there were no fast responses (i.e., minimum RT was 228 ms).

Using an improved version (Engbert & Mergenthaler, 2006) of the algorithm proposed by Engbert & Kliegl (2003), microsaccades were detected in 2D velocity space. Velocity thresholds (6 median-based SD of eye velocity in a given trial, independently estimated for horizontal and vertical components) and minimum duration (6 ms, or three data samples) were used and a binocularity criterion (temporal overlap of microsaccades in the two eyes) was applied. Only microsaccades occurring in the time window from cue onset to 100 ms after target onset were considered.

Fig. 1 Trial procedures in the four cue-target combinations. VV visual cue, visual target; VA visual cue, auditory target; AV auditory cue, visual target; AA auditory cue, auditory target. Responses were always spatially compatible (*top* high tone and red color, *bottom* low tone and green color) (color in online version)



Obviously, with an 80:20 ratio of valid to invalid cues, most microsaccades were associated with valid trials. Such an imbalance between experimental conditions leads to serious loss of power in conventional ANOVA statistics. This loss of statistical power has been shown to be substantially less severe for linear mixed-effects models (LME; Baayen, 2008; Quené & van den Bergh, 2004; Pinheiro and Bates, 2000). Moreover, these statistics are very well suited to statistically control for individual differences between subjects, both with respect to differences in the number of microsaccades and differences in overall RT.

Data were analyzed with LMEs, specifying cue validity (CV) and the number of microsaccades (MN) in the CTI (i.e., 0, 1 or at least 2) and the mean RT of subjects as random effect. For MN we used repeated contrasts (i.e., 0 vs. 1 and 1 vs. 2+) or Helmert contrasts (absence vs. presence and 1 vs. 2+) and tested the cue validity effect (CVE) as nested within these contrasts of MN. These analyses were carried out for each of the four cue-target combinations. In a second set of LMEs, we constrained the analyses to trials with 2 or more microsaccades. For these trials, we specified the effect of microsaccade target congruency (MTC) as nested within levels of CV. The MTC analyses were carried out twice. First, we sorted trials into congruent or incongruent MTC categories depending on the orientation of the last microsaccade, i.e., the microsaccade that was closest to the RT. Then, we sorted the same trials according to the orientation of the first microsaccade in the CTI, i.e., the microsaccade that was closest to the cue. Thus, any systematic differences in RT between these effects must arise solely from differences in target congruency between first and last microsaccades in trials.

We also report a number of control analyses for selected aspects of the main results: (1) we document the cue validity effect for trials without microsaccades and for trials with a single microsaccade. (2) We checked the effects of other features of microsaccades besides their orientation on RT. In particular, we analyzed effects of the time of occurrence in the CTI (either cue-locked or target-locked), of the amplitude and the peak velocity of the microsaccade, and of the number of microsaccades in the CTI.

We used the *lmer* program of the *lme4* package (Bates, 2008) in the R environment (R Development Core Team, 2007). Descriptive statistics and graphics were prepared mainly with the *reshape* (Wickham, 2007a) and *ggplot2* packages (Wickham, 2007b).

Results

Effects of cue and target types on number of microsaccades

Across all conditions, an average of 2.0 microsaccades occurred per CTI (SD = 1.6; range = 0–13). This distribu-

tion is highly skewed to the right with 20, 25, 23, 15, 10, and 4% of trials containing 0–5 microsaccades, respectively, and covering 97% of all trials. The number of microsaccades was significantly smaller for visual than for auditory cues ($b = 0.40$, SE = 0.17, $t = 2.3$) and for visual than for auditory targets ($b = 0.44$, SE = 0.17, $t = 2.6$). Thus, ignoring between-subject differences, we observed the smallest number of microsaccades in the VV-condition ($M = 1.6$), followed by VA and AV conditions (M s = 2.1 and 1.9), and the AA condition ($M = 2.4$).

Effects of the number of microsaccades on RT

The first set of analyses asks whether the number of microsaccades in the CTI has benefits or costs for visuo-spatially or audio-spatially cued discrimination of visual and auditory target and whether this effect interacts with cue validity. To this end, we distinguished between trials with zero, one, and two or more microsaccades (see Table 1). Figure 2 displays the interactions for each cue-target combination.

For the overall LME, we crossed Helmert contrasts for number of microsaccades (0 vs. 1 or 2+ and 1 vs. 2+), cue validity, type of target, and type of cue. Four main effects or contrasts are visible in Fig. 2. First, there is a cue validity effect ($b = -54$ ms, SE = 4 ms, $t = -12.2$). Second, there are faster responses to visual than auditory targets (i.e., VV, AV vs. VA, AA; $b = 94$ ms, SE = 29 ms, $t = 3.3$). Third, we observe *microsaccade-related slowing*, as RTs were longer for trials with one than with no microsaccade ($b = 19$ ms, SE = 6 ms, $t = 2.9$) There are also three significant two-factor and two significant three-factor interactions relating to the patterns of means in Fig. 2. All of these involve the contrasts coding for occurrence of microsaccades, and three of the five involve both microsaccade occurrence and cue validity, suggesting that microsaccades modulate effects of attention. In particular, microsaccade-related slowing is greater with visual than with auditory cues ($b = -29$ ms, SE = 13 ms, $t = -2.2$), especially if two or more microsaccades are observed in a trial ($b = -35$ ms, SE = 17 ms, $t = -2.1$). Microsaccade-related slowing is also more pronounced with invalid than with valid cues ($b = -13$ ms, SE = 7 ms, $t = -1.9$). If only a single microsaccade occurs, its effect on cue validity is stronger with auditory than with visual targets ($b = -31$ ms, SE = 14 ms, $t = -2.2$), in fact, in the absence of microsaccades there is no cue validity effect with auditory targets. Finally, the increase in the cue validity effect with more than one as compared to a single microsaccade is limited to visual cues ($b = 49$ ms, SE = 19 ms, $t = 2.6$).

For ease of interpretation, we carried out separate analyses for each cue-target combination (i.e., for each of the four panels) with two repeated contrasts for number of microsaccades (i.e., 0 vs. 1; 1 vs. 2+).

Table 1 Means (M), standard errors (SE), and number of trials (N) for spatial discrimination RTs broken down by cue/target condition, number of microsaccades in cue-target interval, and cue validity

EXP	NM	Cue validity					
		Invalid			Valid		
		M	SE	N	M	SE	N
VV	0	586	17	125	528	7	605
	1	596	16	154	560	8	622
	2+	698	17	251	617	8	933
VA	0	683	23	81	689	11	382
	1	774	21	134	712	10	493
	2+	779	16	278	698	7	1172
AV	0	580	19	89	517	7	367
	1	599	17	111	535	7	446
	2+	628	12	268	592	6	1054
AA	0	675	29	63	639	13	252
	1	695	25	108	613	10	441
	2+	661	12	321	615	6	1293

Data are from Rolfs et al. (2005); NM number of microsaccades in cue-target interval; VV visual cue/visual target condition, VA visual cue/auditory target condition, etc., with number of subjects in parentheses; 0, 1, 2+ number of microsaccades in CTI

Visual cues and visual targets (VV)

Valid cues led to shorter RTs than invalid ones ($b = -62$ ms, $SE = 7$ ms, $t = -8.5$). The presence of a single microsaccade did slow down RTs ($b = 24$ ms, $SE = 11$ ms, $t = 2.1$) and two or more microsaccades led to even longer RTs than one microsaccade ($b = 40$ ms, $SE = 10$ ms, $t = 3.9$). Interactions between cue validity and contrasts on number of microsaccades were not significant.

Visual cues and auditory targets (VA)

The cue validity effect was significant ($b = -48$ ms, $SE = 10$, $t = -4.9$), as was the increase in RT from zero to one and the change in RT from one to two or more microsaccades ($bs = 65, 32$ ms, $SEs = 17, 13$ ms, $ts = 3.8, 2.4$). Both increases in RT with increase in number of microsaccades were stronger for invalid than valid cues ($b = -42, -27$ ms, $SE = 16, 12$ ms, $t = -2.6, -2.2$). Note that there is no cue validity effect for the zero-microsaccade case. Thus, here is an example where the presence of the microsaccade looks like a precondition for a cue validity effect.

Auditory cues and visual targets (AV)

Again, cue validity was significant ($b = -51$ ms, $SE = 8$ ms, $t = -6.5$). There were numerical, but not statistically reliable increases in RT with increases in number of microsaccades for this cue-target combination ($bs = 14, 16$ ms, $SEs = 13, 10$ ms, $ts = 1.0, 1.6$). Interactions were not significant.

Auditory cues and auditory targets (AA)

Cue validity led also to significantly shorter RTs in this condition ($b = -54$ ms, $SE = 10$ ms, $t = -5.4$). Neither the contrasts for number of microsaccades, nor their interactions with cue validity approached significance (all $ts \leq 1.0$). Despite the non-significance of the critical interaction, the results suggest that, as with VA, cue validity was weaker in the absence than the presence of microsaccades and, indeed, cue validity was not significant for trials without a microsaccade in an alternative post-hoc LME ($b = -38$ ms, $SE = 23$ ms, $t = 1.7$), but obviously, there was a clear numerical trend in the expected direction.

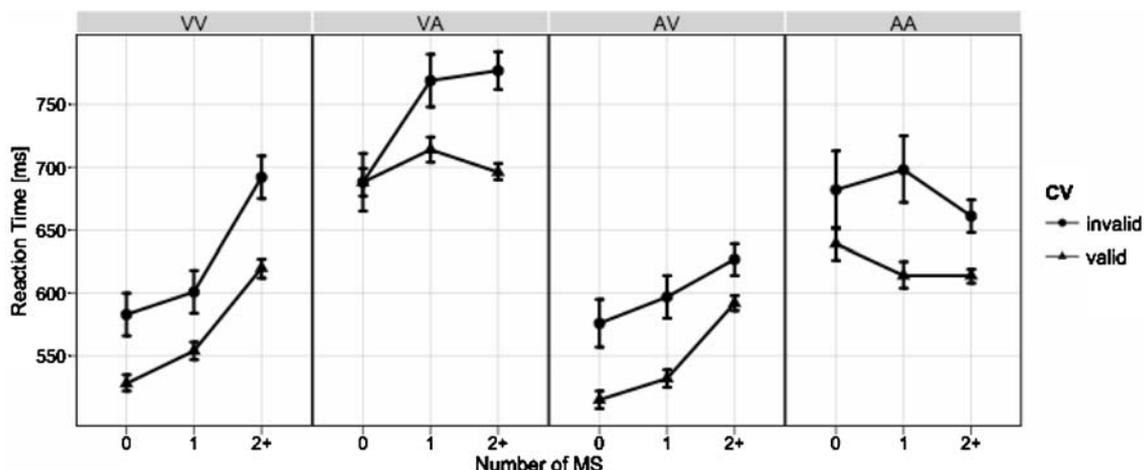


Fig. 2 RTs as a function of cue validity and number of microsaccades (0, 1, or 2 or more) in cue-target interval for each of the four cue-target combinations (VV visual cue, visual target; VA visual cue, auditory

target; AV auditory cue, visual target; AA auditory cue, auditory target). Error bars are 1 SE

Intermediate summary

Aside from the expected main effect of cue validity and the presumably task-specific main effect of type of target, there are two noteworthy consistencies across the four conditions relating to the nature of cue and the nature of the target, respectively. First, microsaccade occurrence more strongly affected reaction time in conditions with visual than in those with auditory cues. In the visual-cue conditions, microsaccade occurrence also modulated visual-cue validity effects, which were stronger with than without microsaccades. Second, a statistically reliable cue validity effect was present for visual targets irrespective of cue type and for auditory targets following auditory cues, but required at least one microsaccade for *auditory targets* following visual cues. Thus, there is some evidence for a functional role of microsaccades in a spatial attention tasks with visual cues and auditory targets.

Effects of cue validity and the congruency of microsaccade direction with target location on RT

Previous research on the functional role of microsaccades in spatial attention tasks highlighted the impact of spatial cues on the direction of microsaccades (i.e., they tend to be oriented in cue direction with central cues and for a large part of the CTI opposite to the cue direction with peripheral cues, see “Introduction”). The focus of the following analyses is on the impact of the microsaccade direction on the subsequent RT. Therefore, we classified microsaccades according to whether they are congruent or incongruent with the target (MTC). Moreover, in the case of two or more microsaccades, we have to decide which one to select for the analyses. The expectation was that the last microsaccade in the CTI, that is the one closest to the manual response would be most likely to affect RT. As a control, but also because it is the one closest to the cue and represents the limiting case for long-term effects on RT, we also carried out all analyses using the direction of the first microsaccade as a classification criterion.

There were 1,184, 1,450, 1,322, and 1,614 microsaccade pairs in conditions VV, VA, AV, and AA, respectively. The average times of occurrence after cue in the four conditions were 349, 394, 364, and 374 ms, respectively, for first microsaccades and 875, 1,022, 953, and 1,004 ms for last microsaccades; the corresponding times relative to target occurrence were $-1,007$, -991 , $-1,017$, $-1,030$ ms for first and -481 , -363 , -428 , -400 ms for last microsaccades. The pattern of means, standard errors, and number of trials for the four conditions, broken down by CV and MTC is shown in Table 2. The left part contains results when MTC is based on the first microsaccade in a CTI and the

Table 2 Means (M), standard errors (SE), and number trials of spatial discrimination RTs broken down by cue/target condition, cue validity and target congruency of first and last microsaccade in cue-target interval

MTC based on			First MS			Last MS		
EXP	CV	MTC	M	SE	N	M	SE	N
VV	Invalid	inc	694	22	144	733	26	116
		con	704	27	107	668	22	135
	Valid	inc	596	11	382	598	9	494
		con	632	11	551	640	13	439
VA	Invalid	inc	797	20	152	762	21	127
		con	758	24	126	793	22	151
	Valid	inc	693	10	529	694	9	608
		con	702	9	643	702	9	564
AV	Invalid	inc	649	20	135	613	14	129
		con	607	14	133	642	19	139
	Valid	inc	596	9	541	589	8	545
		con	588	8	513	596	9	509
AA	Invalid	inc	671	19	153	646	16	177
		con	653	16	168	681	19	144
	Valid	inc	615	8	661	609	7	624
		con	616	8	632	621	8	669

Data are from Rolfs et al. (2005). MS microsaccade in cue-target interval; VV visual-cue/visual target condition, VA visual-cue/auditory target condition, etc.; CV cue validity; MTC microsaccade target congruency; N Number of trials

right part displays the same RTs when they are based on the last microsaccade. Figure 3 also displays this information in the top and bottom row of panels.

The overall LME revealed the already reported effects of cue validity and type of target. For an understanding of the interactions detailed in the panels of Fig. 3, separate LMEs were conducted for each cue-target combination, once based on the target congruency of the last microsaccade in the CTI and once based on the first microsaccade. The key results reflecting microsaccadic modulation of cue validity effects were obtained for visual-cue conditions (VV, VA) when MTC was based on the last microsaccade in the CTI. For each condition, we specified MTC as nested within invalid and valid cues in an LME.

Visual cues and visual targets (VV) for last CTI microsaccade

In the VV-condition (first panel of Fig. 3), there is a significant reduction of the RT cost associated with invalid cues when the last microsaccade in the CTI was in the direction of the target ($b = -48$ ms, $SE = 19$ ms, $t = -2.5$). The increase in RT for valid cues was not significant ($b = 10$ ms, $SE = 10$ ms, $t = 1.0$).

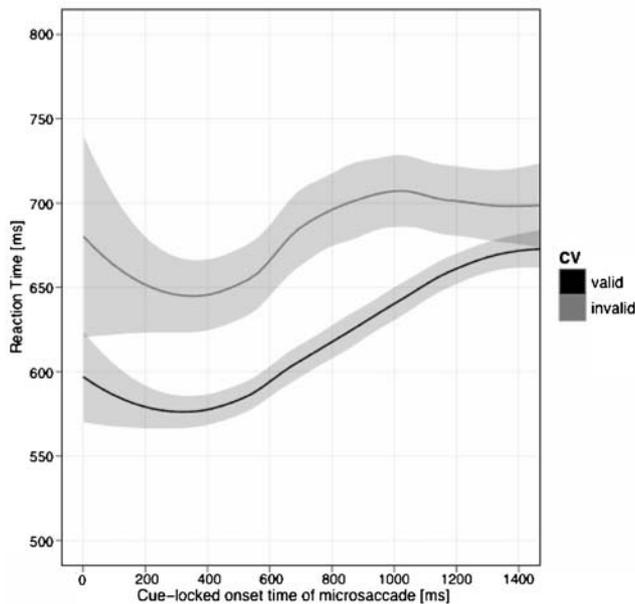


Fig. 4 Reaction time as a function of onset of last microsaccade (including also single microsaccades) in cue-target interval; time is locked to cue. Data are collapsed across four experiments. Smoothing is based on local polynomial regression fitting (Loess method, degree = 2) with a span of 0.75 [i.e., the proportion of the points with tricubic weighting proportional to $(1 - (\text{dist}/\text{maxdist})^3)^3$]; bands represent 95% confidence intervals

Discussion

In all conditions we obtained the expected cue validity effects, i.e., faster RTs after valid than invalid cues that preceded the target by about 1 s. The absolute RTs indicate that peripheral color discrimination and pitch discrimination as implemented here are very difficult tasks. Therefore, the stability of the cue validity effect across a long CTI is compatible with Krummenacher, Müller, and Geyer's (2008) suggestion that, in difficult discrimination tasks, facilitation of cued locations decays less strongly than in detection tasks due to the need of spatial attention to analyze the target. Obviously, these results are a necessary condition for establishing additional and interactive effects of microsaccade time and orientation on RT. As a general disclaimer, we note that systematic effects of microsaccade parameters and RT are of a correlational nature. Thus, they may exert such an influence directly or they could both be indicators of a common third variable, such as, for example, transient fluctuations of vigilance or heart rate.

Microsaccade-related slowing

If there is no microsaccade during the CTI, responses are faster than in the case of microsaccade occurrence. Betta

and Turatto (2006) also reported that faster responses are associated with a reduction in microsaccade rate. In the present data, this microsaccade-related slowing is only observed when one of the task elements—cue or target—is visual. It is more pronounced with visual than with auditory cues, and especially so when more than one microsaccade occurs during the cue-target interval. Note that for visual cues, cue-congruent microsaccades are in the majority for single microsaccade trials, whereas cue-incongruent ones dominated trials with two or more microsaccades. Thus, if a second microsaccade follows a cue-congruent one, its direction is likely to be opposite to the cue, possibly because attention is not focused on the potential target location. Most relevant for the theme of this special issue are the interactions of microsaccade occurrence with cue validity. Microsaccade-related slowing is greater with invalid than with valid cues, and this modulation is stronger for visual than for auditory cues. Furthermore, in the visual-cue/auditory target condition, the cue validity effect depended on the presence of microsaccades. Although some of these effects were not expected, they clearly suggest that microsaccades are related to attention.

Microsaccade time of occurrence

Whether and how microsaccades influence RT depends on when in the cue-target interval they occur. Early in the trial, microsaccade rate and direction are clearly influenced by the cue. Responses are generally faster, when a microsaccade occurred in that period (Fig. 4). Such microsaccades could indicate a heightened state of attentiveness following the cue. However, microsaccades in general and microsaccades late in the trial in particular slow down responding. Thus, detection and/or discrimination of the target and/or the preparation of a manual response are more difficult when microsaccades happen close before target presentation.

Effects of microsaccade target congruency

Microsaccade direction modulated the cue validity effect (CVE) under very specific conditions. The target congruency of microsaccades interacted with cue validity in two conditions using informative visual peripheral cues and visual or auditory discrimination targets. Microsaccades congruent with a visual discrimination target significantly reduced RT after invalid visual cues and increased RT after valid visual cues. Microsaccades congruent with auditory targets increased RT, independent of cue validity. These MTC effects were reliable if congruency was based on the last microsaccade in the cue-target interval; the effects were not reliable when congruency was based on the first microsaccade of the cue-target interval. The effects also depended

on visual cues; conditions using auditory cues in combination with visual or auditory targets did not exhibit such a modulation of RT. In our opinion, prior research does not afford a solid basis for the prediction of such a complex three-factor interaction. In fact, we were rather surprised to find this pattern of results. In particular, given our earlier results (e.g., Laubrock et al., 2007), we had expected an effect of the *first* microsaccade in the trial. Although the observed numerical direction of this effect is as predicted (Fig. 3, bottom row), it is far from being statistically significant. Instead, the pattern of microsaccade target congruency effects related to the *last* microsaccade in the trial is often in the opposite direction.

RT costs of target-congruent microsaccades

Microsaccades following valid visual cues led to slower RTs when they were congruent with visual or auditory targets. This relationship held for the last microsaccade in the cue-target interval. Slowing due to microsaccades occurring close to saccadic responses has been interpreted as the consequence of mutually inhibitory motor programs rivaling for expression (Rolfs et al., 2006). In this case, a dependence of slowing on microsaccade direction remains possible due to global interactions that spatially bias the competing processes (Rolfs, Kliegl, & Engbert, 2008; Rolfs, Laubrock, & Kliegl, 2008). However, slower RTs have also been associated with higher microsaccade rates in a task requiring manual responses to visual targets presented in the fovea (Betta & Turatto, 2006). These authors offered several explanations for their results. First, lower microsaccade rates may result from higher levels of arousal or orienting in time, and both would be associated with faster responses. Second, microsaccades might be affected by the preparation of a manual response itself. That is, the selection of a manual response may affect oculomotor activity directly. These explanations, however, suggest that slowing may be largely independent of microsaccade direction. Our results suggest a qualification of this idea, showing that microsaccade target congruency plays a significant role for manual RTs in visual and auditory discrimination tasks. We propose that biased microsaccade directions indicate the engagement of the oculomotor system, resulting in conflicting roles of microsaccades in the discrimination tasks: general interference with manual response preparation, and facilitation of visual discrimination due to correlated attentional benefits. The combination of these tendencies may have resulted in the pattern of results reported here.

RT benefits of target-congruent microsaccades following invalid visual cues

From the earlier report on these and other data, we know that microsaccades orient opposite to peripheral cues dur-

ing most of the CTI in the VV-condition (Rolfs et al., 2004, 2005). We have interpreted such effects as a consequence of the attempt to counteract oculomotor capture by a peripheral visual cue. In a comment on an interesting observation by Tse et al. (2003), we speculated that this tendency may actually cause attention to spread away from the cue (Rolfs et al., 2004). This tendency to counteract capture is much more pronounced for visual than auditory cues. In fact, with auditory cues we only observed the effect when attention was guided to a visual target (Rolfs et al., 2005), thus, involvement of *visual* attention may be a precondition. Obviously, if the spreading of attention were tied to the visual modality, we would expect an RT benefit only for visual but not for auditory targets. Apparently, the RT benefit of this attention spreading can be strong enough to almost compensate RT costs associated with an invalid cue.

Inhibition of return

We speculate that the present results may also be taken to reflect a more general attentional mechanism—namely inhibition of return (IOR). Inhibition of return (Posner & Cohen, 1984) describes the finding that initial cueing benefits become cueing costs during the course of a trial: detection of a target at the cued location is enhanced only with relatively short cue-target SOAs (ca. 100–300 ms), whereas with longer SOAs it is impaired, as if the target location was inhibited. IOR explanations of cue-induced effects on microsaccade direction were reported by Betta, Galfano, and Turatto (2007) and Galfano et al. (2004). There are two parallels between the current results and IOR: first, the majority of cue-incongruent microsaccades (or target-congruent microsaccades following invalid cues) occurred in trials with more than a single microsaccade. Second, the majority of (visual) cue-congruent microsaccades was found in trials with a single microsaccade only, corresponding to the fact that the size of the cueing benefit is typically larger than the size of the IOR effect. Thus, microsaccades may mimic covert movements of the ‘attentional spotlight’ (i.e., towards the cued and away from this location), and follow the same temporal dynamics as attention (facilitation & inhibition) in the spatial attention task.

For visual targets, a cue validity effect was also observed for trials without microsaccades. Thus, microsaccades are not necessary for cue validity effects on RT. To be sure, nobody would have been more surprised than us, if it had been different; we never entertained such a hypothesis, but recent discussions come close to suggesting that we postulate such a deterministic link (Horowitz et al., 2007a, b). Surprisingly, the cue validity effect for auditory target discrimination could only be established for trials involving microsaccades. Across the four experiments reported here, the rate of microsaccades increased when visual attention

was less important to solve the task. Therefore, we speculate that microsaccade occurrence is an indicator of dedicating resources to the auditory domain, resulting in reliable attentional effects while relaxing the oculomotor fixation system at the same time.

LME versus ANOVA

We close with a methodological note. The effects and interactions relating to the absence/presence of microsaccades in the CTI were far from significant in traditional ANOVA statistics (i.e., removing subjects from the analysis when they had missing design cells, computing the average for each subject in each design cell, and running the ANOVA over these means). Why is this so? One problem relates to the experimental design aspect that valid cues are presented four times as often as invalid cues. This difference in power is completely ignored in the traditional ANOVA statistics. As matter of fact, when we removed all data of subjects who had incomplete design cells in the analyses of the effect of number of microsaccades on RT (amounting to a drop from 10,043 to 7,266 trials), but analyzed the remaining unaggregated trials with LME, the pattern of means of Fig. 2 and with two exceptions the significant effects were still obtained. Of course, this is not very surprising because the cell means of subjects with few data will be shrunken towards the estimated population mean (“borrowing strengths”) in linear mixed-effects models. For further evidence about the statistical power of linear mixed-effects models in the face of unbalanced designs, we point to recent eye-movement research in reading, recovering effects that led to mixed interpretations in traditional ANOVA statistics (Kliegl, Risse, & Laubrock, 2007) and demonstrating that this procedure allows the simultaneous assessment of a much larger number of variables in quasi-experimental designs than traditional repeated-measures multiple regression analyses (Kliegl, 2007). Thus, linear mixed-effects models or generalized linear mixed models are clearly the method of choice for the analysis of inherently unbalanced designs such as those relating to spatial attention tasks or of studies facing frequent missing at random cases, as is typical of eye-movement research. It may be worth while revisiting some other data sets with this statistical tool, especially if the authors had argued the null hypothesis.

Conclusion

The general question following this report is: how can we explain the RT costs and benefits associated with target-congruent microsaccades? We don’t have a decisive answer yet, but obviously, more than one process has to be involved to generate such a diverse pattern. During the long

cue-target interval, the task of the participants is not only to maintain attention at the location it has shifted to in the expectance of the discrimination target, but also to ensure visual fixation. Maintenance of attention must be assumed, because it is well known that, at least with uninformative peripheral cues, inhibition of return develops over time, leading to a reduced likelihood of detecting a target at the cued location and hence to cueing costs. Inhibition of return has also been observed for microsaccades (Betta et al., 2007; Galfano et al., 2004). These attentional dynamics will likely involve saccade-preparation mechanisms. Another process at a somewhat lower level might also contribute, namely, prevention of visual fading, which is considered a prime function of microsaccades (Ditchburn, 1980; Engbert & Mergenthaler, 2006; Gerrits & Vendrik, 1974; Martinez-Conde et al., 2006). Whether and how these higher-level processes (attention shifts, maintenance of attention, maintenance of fixation, and oculomotor preparation) and the lower-level process of prevention of fading contribute to the pattern of effects needs to be addressed experimentally. To the least, our re-analyses show that more than one process needs to be considered.

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