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Microsaccade dynamics during covert attention

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Abstract

We compared effects of covert spatial-attention shifts induced with exogenous or endogenous cues on microsaccade rate and direction. Separate and dissociated effects were obtained in rate and direction measures. Display changes caused microsaccade rate inhibition, followed by sustained rate enhancement. Effects on microsaccade direction were differentially tied to cue class (exogenous vs. endogenous) and type (neutral vs. directional). For endogenous cues, direction effects were weak and occurred late. Exogenous cues caused a fast direction bias towards the cue (i.e., early automatic triggering of saccade programs), followed by a shift in the opposite direction (i.e, controlled inhibition of cue-directed saccades, leading to a 'leakage' of microsaccades in the opposite direction).

Keywords: Attention; Eye movements; Fixation; Reaction time

1. Introduction

Ocular fixations often contain 'fixational' eye movements called microsaccades. Microsaccades serve an important purpose in the control of fixation position and binocular disparity (Engbert & Kliegl, 2004). They occur on average about once per second during visual fixation but can be suppressed voluntarily in high-acuity tasks (Bridgeman & Palca, 1980; Findlay, 1974; Winterson & Collewijn, 1976; see Martinez-Conde, Macknik, & Hubel, 2004, for a review). Although microsaccades are not consciously perceived, they can be influenced by attention. Recently, microsaccades were shown (1) to exhibit a characteristic temporal signature of display-change related rate inhibition and enhancement in the Posner (1980) spatial cueing paradigm and (2) to be oriented in the direction of endogenous cues (Engbert & Kliegl, 2003; see also Hafed & Clark, 2002). Here we try to generalize and further specify these previous results by examining the influence and associated time course of endogenous and exogenous cues on microsaccade rate and direction in a spatial attention-shift paradigm adapted from Müller and Rabbitt (1989).

Engbert and Kliegl (2003) reported microsaccade rate inhibition in response to cue-related display changes, starting around 70 ms and reaching a rate minimum at around 150 ms, which was immediately followed by a rate enhancement peaking at approximately twice the baseline rate after about 350 ms, before returning to baseline after about 500 ms (all times are relative to cue onset). Both the shape and the time course of the rate modulation were quite similar to the "saccadic inhibition" effect observed in large saccades after relatively large-scale disruptions of the visual input (Reingold & Stampe, 2002, 2004). In the same study, microsaccade direction was shifted into the cued direction with a time course depending on the type of cue. For endogenous arrow cues the direction effect was observed in a time window corresponding to the rate maximum (i.e.,

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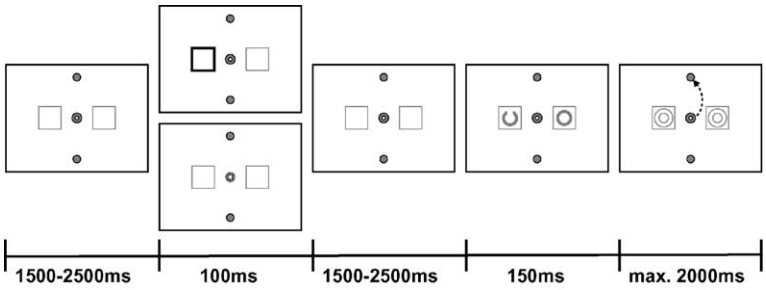

Fig. 1. Sequence and timing of trial events. The sequence of screens is depicted from left to right: (1) pre-cue fixation interval, (2) cue, (3) cue-target interval (4) imperative stimulus, (5) response. The cue screen (2) differed between exogenous and endogenous blocks, as shown in the upper and lower panel, respectively.

300–400 ms), while for endogenous color cues the direction effect occurred later (i.e., 350–600 ms). Direction effects were also stronger for the spatially compatible arrow cues than for purely semantic color cues. Thus, there is evidence for a dissociation of microsaccade rate and direction during endogenous spatial cueing, with direction effects possibly related to the strength of endogenous cues.

In the present study we investigated exogenous and endogenous cueing effects within a single experiment. One central finding of Müller and Rabbitt (1989) was the observation of cue-specific time courses of attention allocation: With peripheral-flash cues attention was allocated faster and stronger than with central symbolic cues. Together with additional findings this was taken as evidence that there are two separate orienting mechanisms, acting at different times after cue onset: Peripheral cues triggered both fast, reflexive (exogenous) orienting and slower voluntary (endogenous) orienting, while central cues triggered only the voluntary (endogenous) orienting mechanism (Müller & Findlay, 1988). Müller and Rabbitt hypothesized that exogenous and endogenous mechanisms add up to determine the net effect of attention. Exogenous orienting had a powerful, but transient response fading 100–300 ms after cue onset, while the more persistent endogenous orienting mechanism came into effect later, that is after about 350 ms; its exact time of onset depended on the time required for cue interpretation. Can microsaccade rate and direction be linked to these different orienting mechanisms? In the Engbert and Kliegl (2003) experiments, microsaccade-rate inhibition following cue presentation was independent of the meaning of the cue and likely a reflexive response to the display change. However, microsaccade direction during the subsequent period of enhancement was modulated by cue meaning. If effects of endogenous and exogenous cues on microsaccade direction differ in their temporal dynamics, then we should see differences during the period of rate enhancement. Specifically, we expected endogenous cues to influence direction later, and possibly to a smaller extent, than exogenous cues. To chart the time courses of exogenous and endogenous orienting of microsaccades, we modified a paradigm introduced by Müller and Rabbitt (1989). They cued participants either centrally (with arrows) or peripherally (with a flash) to shift attention to a peripheral location where a stimulus was presented for comparison with a previously presented one. The manipulation of the cue-stimulus interval allowed them to trace time-differential effects of cue classes on response probabilities. In the present experiment we also cued participants centrally (with color) or peripherally (with a flash) to shift attention covertly to a left or right location where they had to discriminate whether a gap was located at the top or bottom of a Landolt ring (i.e., the imperative stimulus, IS) presented after a variable cue-stimulus interval; the gap location in the IS signalled the direction of the vertical saccade required from the point of fixation to a target at a location orthogonal to IS location (i.e., straight up or straight down from the point of fixation; see Fig. 1). This procedure ensured that covert shifts of attention were orthogonal to overt saccade responses. Clearly, horizontal microsaccades during the critical cue-stimulus interval could not prepare the subsequent vertical saccade required in response to the imperative stimulus.

2. Method

2.1. Participants

Thirty-two undergraduate students from the University of Potsdam received seven Euro for their participation. A session involved 192 test and 32 training trials, plus repetitions of trials during which no steady fixation was held, and lasted for approximately one hour. All participants had normal or corrected-to-normal vision.

2.2. Apparatus

Eye movements were recorded with the video-based Eyelink II system (SR research, Toronto, Canada) with a high spatial resolution (noise <0.01°) at a sampling

rate of 500 Hz. Stimuli were displayed on a 19″ Eye-Q 650 CRT at a resolution of 1024 × 768 and a refresh rate of 100 Hz. A viewing distance of 50 cm was assured by use of a chin rest. A Power Macintosh G4 running Mac OS 9.2 controlled stimulus presentation and eye movement recording by communicating via an Ethernet TCP/IP direct link with an Intel Pentium 4 based Dell Optiplex system, which contained the eye tracker card. The experimental software controlling stimulus display and response collection was implemented in Matlab, using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peters, & Palmer, 2002) toolboxes.

2.3. Stimuli

Display. The fixation spot was marked by a small central disk (0.3° diameter). The two possible locations of the IS were indicated by two square frames (1.24° side length), centered on points on the horizontal meridian 5° to the left and to the right of the fixation spot. The display screen also contained two target spots (0.64° diameter) centered on points on the vertical meridian, 10° above and below fixation. All elements were displayed in gray on a black background.

Cue class. Two classes of cues were used, peripheral flash-cues to trigger both fast exogenous and slow endogenous attention shifts, and central color-cues to trigger endogenous shifts. Central cues were color disks (blue, yellow, white) replacing the fixation spot. For half of the participants, blue was mapped to left and yellow to right IS location, for the other half the mapping was reversed; the white disk served as a neutral cue. Peripheral cues were white flashes (i.e., luminance increments) of one or both lateral frames, on valid or neutral trials, respectively. Cue class was blocked; block order was counterbalanced between participants. Mapping of color to location was practiced in 32 training trials prior to the color-cue block.

Cue conditions. There were three conditions within each cue class: (a) Valid cues (50% of trials) always validly signaled the upcoming location of the IS. (b) Neutral cues (25% of trials) provided temporal information and caused a display change, (c) Finally, in 25% of trials the fixation display remained unchanged (no-cue condition).

Imperative stimulus (IS). The IS was a Landolt ring (diameter: 0.64°; ring width: 0.17°) with the gap pointing either upwards or downwards (gap size: 0.26°).

2.4. Procedure

After the headband was mounted, a nine-point calibration was conducted to align eye and screen coordinate systems. During the experiment, re-calibrations were conducted (a) after every 24th trial, and (b) whenever the eyes were not detected in a central 2° square during a 500 ms pre-trial fixation check. Drift correction was performed after every 6th trial. Two possible trial sequences are depicted in Fig. 1. A trial started with a fixation-spot display, followed by a cue after an interval chosen at random from a uniform distribution of 1500–2500 ms. The cue was displayed for 100 ms. Then, the fixation-spot display was presented again for a variable cue-stimulus interval chosen at random from a uniform distribution of 1500–2500 ms. The IS and a closed ring of the same size as the IS were presented simultaneously at the same distance from fixation in opposite hemifields. Both the Landolt ring and the closed ring were masked by a ring mask after 150 ms. The IS was the signal to perform a speeded saccade from the fixation spot to the top or bottom target spot as indicated by the IS gap location. Reaction time was defined as the time from IS onset until the gaze was detected in a circular area of 2° diameter, centered on the center of the target spot. To encourage subjects to maintain gaze at fixation, an online fixation check was used from the beginning of a trial until appearance of the IS. Whenever gaze left a square with a side length of 5° of visual angle centered on the fixation spot, the trial was discarded and the eye re-calibrated. Discarded trials were repeated in random order after the cue blocks. The size of the fixation check rectangle was chosen to discourage large voluntary saccades to possible IS locations on the one hand and to minimize trial repetitions due to positional displacements caused by microsaccades and drift on the other.

2.5. Data analyses

Pre-processing and microsaccade detection. Trials with pre-IS saccades larger than one degree, eye blinks or other errors during data acquisition were discarded. This led to an exclusion of 468 of a total of 6144 trials (7.6%). Then, microsaccades were determined with the algorithm reported in Engbert and Kliegl (2003), adapted to the 500 Hz sampling rate. Briefly, the time series of eye positions was transformed to velocities using a weighted moving average measure. A threshold defined as six times the median-based standard deviation of the velocity distribution was computed independently for horizontal and vertical components and separately for each trial. Samples exceeding the criterion were classified as microsaccades if the threshold was exceeded for at least four samples and if there was temporal overlap between both eyes. Since the experiment demanded a voluntary saccade at the end of the trial, only samples previous to IS presentation were included in the mean velocity calculation. Trials with saccades greater than 1.5° were discarded from further analyses.

The microsaccade detection algorithm uses a trial-based velocity threshold to account for intra- and

interindividual variability in fixation stability. To evaluate whether the criterion was influenced by cue class (flash, color) or cue type (valid, neutral, none), we conducted a repeated measures ANOVA of the mean criterion measure, defined as the geometric mean of the x- and y-radii of the velocity criterion ellipse (grand mean about 12°/s). This radius-like measure was calculated for all trials. There was no reliable difference between cue conditions, as indicated by the absence of main effects (cue class, $F(1,31) < 1$, $MS_e = 1379.28$, $p = 0.332$; cue type, $F(2,62) = 1.45$, $MS_e = 183.23$, $p = 0.242$) or an interaction (cue class × cue type, $F(2,62) < 1$, $MS_e = 113.80$, $p = 0.579$). Similar results were obtained if the x- or y-radii were analyzed separately. Thus, there was no reliable evidence for a systematic covariation of cue condition and criterion value.

The minimum size of microsaccades detected was 2.8′. The amplitude distribution was positively skewed ($m_3 = 1.64^{\circ 3}$), with a mean (median) of 22.19′ (18.51) and a standard deviation of 14.10′. [1] Although the criterion did not vary between conditions, the mean size of the microsaccades did—it was somewhat larger with flash ($M = 22.5'$) than with color cues ($M = 21.0'$), $F(1,31) = 6.12$, $MS_e = 16.40$, $p = 0.019$. Cue type (valid, neutral, none) did not influence microsaccade amplitude.

Microsaccade rate. Microsaccade rate was calculated individually for each combination of participant, cue class, and cue type. The histogram of microsaccades over cue-aligned sample bins (width = 2ms) was smoothed with an unweighted moving average of width 120 ms, and scaled to a rate-per-second measure. Rates for the corresponding conditions were then averaged across participants.

Microsaccade direction. We used two measures of microsaccade direction. First, raw microsaccade direction was transformed to polar coordinates, and histograms with a bin width of 22.5° were computed for time segments corresponding to periods of microsaccade-rate modulation. Second, each microsaccade was classified according to the congruency of the direction of its horizontal component and the direction of the cue. For trials with directional cues, mean rates of cue-congruent and cue-incongruent microsaccades were computed using the same averaging procedure and parameters as described above.

[1] The empirical mean, median, and standard deviation [min arc] could rather well be recovered ($\widehat{M} = 22.19$, $\widehat{M}d = 18.60$, $\hat{s}d = 14.45'$) by a log-normal distribution with parameters of 2.923 ($sd = 0.005$) for the mean and 0.594 (0.004) for the standard deviation on a log scale. Because the minimum detectable size is restricted by the temporal and spatial resolution of the eye tracker, it is possible that only the large amplitude side of the total distribution was recorded. While this is unlikely to affect the main findings reported below, it could affect the shape of the distribution.

3. Results

3.1. Reaction times and errors (manipulation check)

Reaction times and errors followed the expected pattern. A main effect of cue type (valid, neutral, none) was obtained (reaction time: $F(2,62) = 17.00$, $MS_e = 14009.89$, $p < 0.001$; errors: $F(2,62) = 12.74$, $MS_e = 4.53\text{e}{-3}$, $p < 0.001$). Single comparisons reveal that valid cues led to faster responses and less errors than neutral cues (reaction time: $M = 679$ vs. 720 ms, respectively, $F(1,31) = 4.84$, $MS_e = 22953.31$, $p = 0.035$; errors: $M = 7.6\%$ vs. 11.7%, $F(1,31) = 9.03$, $MS_e = 1.19\text{e}{-2}$, $p = 0.005$). Neutral cues led to faster reactions than the no-cue baseline ($M = 720$ vs. 799 ms, respectively), $F(1,31) = 9.56$, $MS_e = 41230.85$, $p = 0.004$—probably due to the temporal information they provided about IS onset. The difference between the two conditions in error rate ($M = 11.7\%$ vs. 13.4%) was only marginal, $F(1,31) = 3.39$, $p = 0.075$, $MS_e = 5.90\text{e}{-3}$. Thus for each cue type comparison, significant effects in the expected direction were found in at least one of the two measures, and even for the nonsignificant comparisons a numerical trend in the expected direction was observed. Presumably due to the long SOA between cue and IS, leading to endogenously sustained attentional allocation, no effects involving cue class (flash or color) were found in either reaction time or error ($F < 1$ for the interaction of cue class and cue type in both reaction time and errors and for the main effect of cue class in reaction time, $F(1,31) = 2.23$, $MS_e = 5.45\text{e}{-3}$, $p = 0.145$ for the main effect of cue class in errors).

The pattern of cue type effects was similar within each cue class. Reaction time was mainly determined by whether or not a cue was present, whereas error rate was mainly determined by whether or not the cue provided information about IS location. Results of the single comparisons are tabulated in Table 1. In both the flash cue and the color cue conditions, responses were faster with valid and neutral cues than without cues. Within each cue class, responses with valid cues were numerically, but not statistically faster than responses with neutral cues. However, valid cues led to significantly less errors than neutral cues in both the flash and the color cue condition, whereas there was no difference in error rate between the neutral and the no-cue conditions. Taken together, these results suggest that subjects used both flash cues and color cues as intended.

3.2. Microsaccade rate

As shown in Fig. 2, modulation of microsaccade rate in response to any cue presentation (i.e., any display change) closely resembled the signature reported by Engbert and Kliegl (2003). Presentation of both peripheral flash-cues and central color-cues caused an

Table 1
Statistics for pairwise comparisons of cue type within each cue class[a]

Cue class	Cue type	Reaction time (ms)			Errors (%)		
		None	Neutral	Valid	None	Neutral	Valid
Flash	None	–	0.004	0.000[b]	–	0.419	0.007
	Neutral	9.59	–	0.152	0.67	–	0.036
	Valid	23.49	2.15	–	8.47	4.79	–
	Mean	800.90	713.63	680.46	11.95	10.77	7.55
Color	None	–	0.023	0.000[b]	–	0.208	0.000[b]
	Neutral	5.70	–	0.067	1.66	–	0.013
	Valid	33.90	3.60	–	23.52	6.94	–
	Mean	796.44	726.72	676.59	14.90	12.55	7.59

[a] For pairwise comparisons, p-values are listed above, and $F_{(1,31)}$-values below the diagonal. For example, with flash cues reaction times were significantly faster in the neutral than in the no-cue condition, $F_{(1,31)} = 9.59$, $p = 0.004$, whereas there was no corresponding difference in error rate, $F_{(1,31)} = 0.67$, $p = 0.419$.
[b] A tabulated value of $p = 0.000$ means that $p < 0.001$.

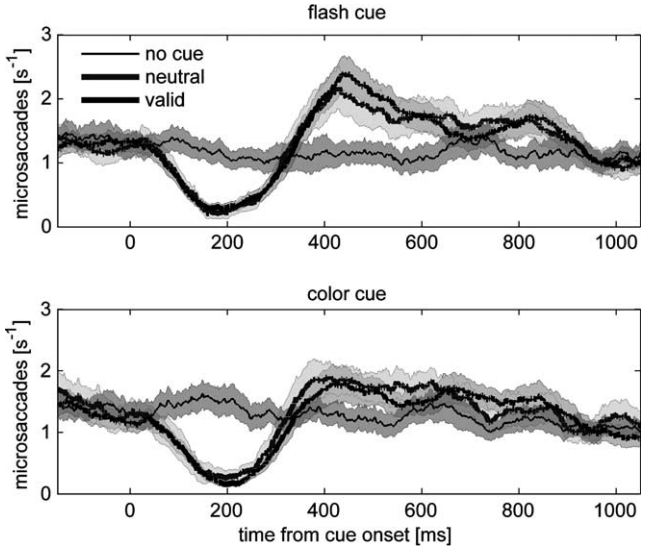

Fig. 2. Changes in microsaccade rate over time as a function of cue class and cue type. Microsaccadic inhibition occurs very soon after a display change and is later followed by a longer period of microsaccadic enhancement. Depicted is the average number of microsaccades per second. Rate was determined individually using a 120 ms rectangular filter and then averaged across participants. Confidence bands of ±1 standard error are shown around the mean rate per condition.

inhibition of microsaccade rate (i.e., a rapid drop that started around 60 ms and reached its minimum at about 190 ms) immediately followed by rate enhancement with a global peak in rate at about 450 ms. The enhancement stayed above the pre-cue baseline at least until about 850 ms. These changes in microsaccade rate were not accompanied by changes in average microsaccade amplitude, which was unaffected by trial events.

The time of the rate minimum was rather stable across participants and cue class, while there was more interindividual variance for the time of the rate maximum. The mean times (and standard errors) for the minimum were 196 (15) ms following flash and 186 (13) ms following color cues. Mean times (standard errors) for the rate maximum were at 446 (23) and 419 (37) ms, respectively. Statistically, there was no difference between flash and color cues in the timing of either the rate minimum or maximum (both t's$(31) < 1$).

Statistical analysis of microsaccade rate focused on four consecutive time windows of equal length (300 ms), one before and three after cue onset, covering the range from −300 to +900 ms. Mean rate was computed for each individual participant for each combination of cue class (flash, color) and cue type (none, neutral, valid), and submitted to a $2 \times 3 \times 4$ repeated measures ANOVA with the factors of cue class, cue type, and time interval. The only significant effects were the effect of time interval, $F(3,93) = 27.55$, $MS_e = 0.65$, $p < 0.001$, the interaction of cue type and cue class, $F(2,62) = 3.52$, $MS_e = 0.25$, $p = 0.036$, and the interaction of time interval and cue type, $F(6,186) = 17.44$, $MS_e = 0.30$, $p < 0.001$. To investigate the latter interaction, two orthogonal contrasts were specified for cue type, one comparing baseline with the combined effect of neutral and valid cues, and the second comparing neutral and valid cues. The cue type × time interval interaction was limited to the first contrast. Thus, there was no evidence that the shape of the rate modulation differed between neutral and directional (valid) cues—any display changes caused the characteristic signature with inhibition followed by enhancement; the rate modulation did not depend on the meaning of the cue. Follow-up analyses confirmed that rates following neutral or valid cues did not differ from baseline in the pre-cue interval ($F < 1$), were significantly lower than baseline in the second ($p < 0.001$), and significantly higher in the third ($p < 0.001$) and even in the fourth interval ($p = 0.002$). The only effect of cue class on the rate modulation was evident in the slight interaction of cue type and cue class, which indicates that the rate enhancement in

the last two time windows following neutral and valid cues is larger with flash than with color cues. Post-hoc comparisons showed that there was one reliable difference associated with cue class, evident in Fig. 2: Microsaccade rates for valid flash and color cues were statistically different in the third time window, around the rate maximum, where the mean rate was higher after flash than after color cues, $t(31) = 2.63$, $p = 0.013$, *mean difference* = 0.33. There was no such difference for the corresponding comparison between neutral flash and color cues.

In summary, microsaccade rate was affected by cue onsets. A quick and short initial period of rate inhibition was followed by a rather long period of rate enhancement. The shape of the rate modulation was independent of whether flashes or colors were used, or whether the cue provided directional information or not, with the exception of a higher rate maximum following flash cues. This last effect, obtained in a post-hoc comparison, is compatible with an interpretation of flashes as stronger cues than colors, but the required triple interaction was not reliable in the overall ANOVA.

3.3. Microsaccade direction

Polar plot histograms. Microsaccade direction was clearly affected by cue class (see Fig. 3). First, a comparison of histograms of microsaccade directions in polar coordinates reveals a tendency for microsaccades to be predominantly directed towards the cued direction in the peripheral-flash condition during a very early time window (i.e., 50–200 ms). [2]

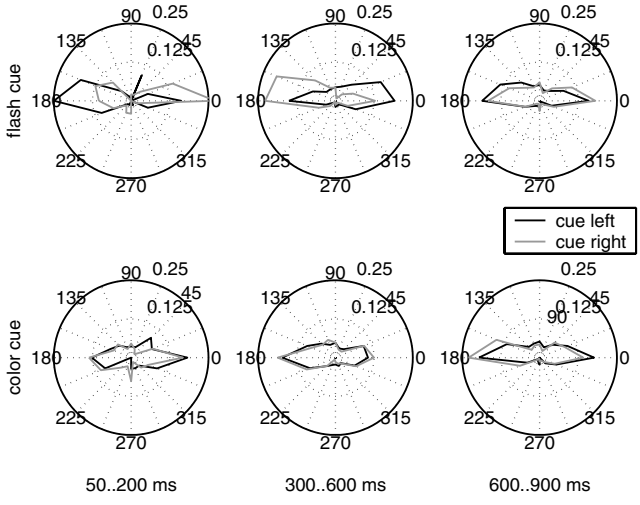

Fig. 3. Microsaccade direction in three post-cue time windows (left column: 50–200 ms; middle column: 300–600 ms; right column: 600–900 ms) for validly cued trials as a function of cue class (top row: flash cues; bottom row: color cues) and cue direction (black line: cue left; grey line: cue right). Plotted in these 'polar histograms' is the relative frequency of microsaccades (per cue direction and time window) in a given direction. Direction is defined by the angle of the polar coordinates of the microsaccade vector. Sixteen equally spaced directional bins were used to produce the histogram.

A little later, 300–600 ms, there was a strong tendency for microsaccades away from the cued location in the exogenous condition. In a yet later time window (i.e., 600–900 ms), a weaker effect away from the cued direction is observed for central color-cues. In contrast, peripheral flash-cues had no influence in the later time window.

Peripheral flash-cues. These results reflect different time courses of the effects of central color-cues and peripheral flash-cues on microsaccade direction. A plot of cue-congruent and cue-incongruent rates as well as the difference between them reveals the qualitative differences associated with cue class more clearly (see Fig. 4).

For valid flash cues, the rates for cue-congruent and cue-incongruent microsaccades diverged early. At around 100 ms, microsaccades pointed predominantly in the cued direction. At 200 ms the effect started to reverse, such that between 250 and 600 ms more microsaccades pointed opposite to the cued direction than in the neutral condition. For microsaccades in the cued direction there was prolonged inhibition from 200 until about 400 ms, and a rebound between 600 and 800 ms; in this time window the rate was again higher for cue-congruent than incongruent microsaccades. There were no cue-congruency effects later than about 850 ms after the cue.

Central color-cues. For color cues, the early cue-congruent effect was absent. The only reliable congruency effect occurred rather late: about 600–700 ms after cue, more microsaccades pointed opposite than in the cued direction. Later in time, congruency effects vanished, and there was no rebound of congruent microsaccades.

Cue congruency analysis. For statistical analysis of microsaccade-cue congruency effects for directional cues, 10 intervals of 100 ms duration were compared: one pre-cue interval (−200; −100 ms) and nine consecutive post-cue intervals, starting at (50; 150) ms post-cue.

For each participant, the number of incongruent microsaccades per cue class was subtracted from the number of congruent microsaccades during each time window, and the resultant differences were submitted to a repeated measures ANOVA involving the factors of cue class and time interval. The main effect of time, $F(9,279) = 3.47$, $MS_e = 4.41$, $p < 0.001$, and the interaction of cue class and time interval were significant, $F(9,279) = 5.85$, $MS_e = 6.00$, $p < 0.001$, while the main effect of cue class failed to reach significance, $F(1,31) = 1.25$, $MS_e = 3.37$, $p = 0.272$.

[2] First inspection of the data suggested that exogenous and endogenous processes had opposing influences on microsaccade direction. To capture the fast-acting exogenous influence before slower top-down processes had a chance to 'hit the brake', we chose a smaller first time window in the direction than in the rate analysis.

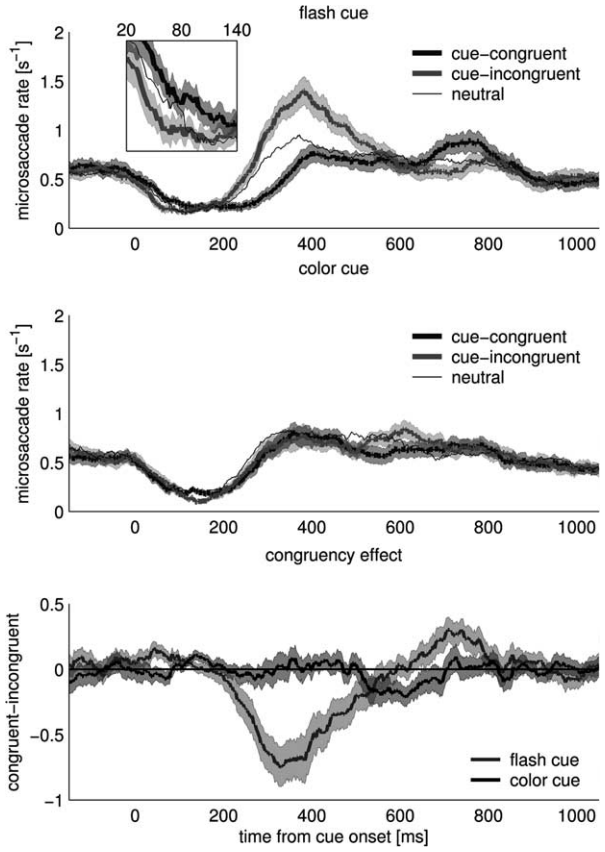

Fig. 4. *Top two panels*: Change of microsaccade rate depending on congruency of their direction with the cued direction, and the type of cue. Rate change in response to neutral cues is also plotted for comparison. *Bottom panel*: Congruency effect as difference in average number of congruent and incongruent microsaccades per time window, plotted separately for endogenous color and exogenous flash cues. Confidence bands of ±1 standard error are shown around the mean rate. An early congruency effect occurs only with flash cues, as is highlighted in the top panel inset, featuring a magnification of the *x*- and *y*-axes for times between 20 and 140 ms (rates between 0.15 and 0.45 s^{-1}).

Follow-up analyses tested whether congruency effects were different from zero for each cue class and time interval. The results are summarized in Table 2, listing the absolute numbers of microsaccades during the intervals, the differences between the number of cue-congruent and cue-incongruent microsaccades, as well as paired-sample *t*- and *p*-values for the differences from zero. In short, during an early time window (50–250 ms), microsaccades following peripheral flash-cues were cue-congruent. For central color-cues, a weaker tendency into the cued direction was observed much later (450–550 ms). Later on there was a strong tendency for microsaccades to point opposite to the cued direction (i.e., they were cue-incongruent). The time interval during which this tendency occurred was earlier, more pronounced, and lasted longer for peripheral flash-cues (350–550 ms) than for central color-cues (650–750 ms). For peripheral flash-cues, a second period of cue-congruency was observed in the 750–850 ms time window. Congruency effects were not significantly different from zero for precue times or during the final 850–950 ms time window in either cue class. [3]

4. Discussion

Exogenous and endogenous cues had a similar effect on microsaccade rate, while they had a strikingly different effect on microsaccade direction. The shape of the rate modulation resembles the one observed by Engbert and Kliegl (2003) or Rolfs, Engbert, and Kliegl (2004). Any display change led to a rapid drop in microsaccade rate, followed by a temporary enhancement. The course of "microsaccadic inhibition" is very similar in all of these studies including the present one, thus it appears to indicate a fast reflex of the oculomotor system to sudden changes in visual input (see Reingold & Stampe, 2002). In the current setting, the enhancement lasted longer than in the Engbert and Kliegl study using the Posner cueing paradigm. Because the longer-lasting enhancement occurred not only with color, but also with flash cues, we suspect that it is at least partly related to processing other than interpretation of the cue—e.g., preparing for IS discrimination, ensuring that fixation is maintained while attention is located elsewhere, or recalling that a saccade orthogonal to the IS had to be performed. Participants reported that the task was rather demanding, so sustained enhancement may be indicative of cognitive load.

The dynamics of the direction of microsaccades differed between flash and color cues. With flash cues, a very fast congruency effect was observed in the cued direction, followed by an effect in the opposite direction, which was again followed by a weaker effect into the cued direction. With color cues, microsaccade-cue congruency effects emerged several hundred milliseconds later, and only a peak away from the cued direction was observed. The direction effect for flash cues has some

[3] *Consistency across participants*. The choice of intervals is somewhat arbitrary and of course critical, because effects reverse over time. We hope that the large number of intervals helps to detect such reversals. The possible fact that some subjects produced extreme difference values in some intervals was addressed by a symbolic recoding of congruency effects such that for each subject in each time window and cue class, a negative difference was coded as −1, a positive difference as +1, and a zero difference as 0. The direction effects were also observed at the coarser, individual level. After peripheral flash-cues, 16 of 32 participants produced more cue-congruent than incongruent microsaccades during the 50–150 ms interval and only 4 of them more incongruent than congruent microsaccades (the remaining participants produced ties); for the 150–250 ms interval the numbers were 12 of 32 vs. 3 of 32. The reverse pattern was obtained for the 350–450 (450–550) ms time window where we counted 4 (9) predominantly congruent and 23 (20) incongruent participants.

Table 2
Statistics for microsaccade direction following valid cues, tabulated by time and cue class

Interval[a] $t_0 \cdots t_1$	Flash				Color			
	MD[b]	$t(31)$[b]	p[b]	N[b]	MD	$t(31)$	p	N
−200 ··· −100	0.22	0.93	0.362	135	−0.16	−0.36	0.719	169
50 ··· 150	0.59	2.71	0.011	83	−0.09	−0.35	0.728	85
150 ··· 250	0.34	2.47	0.019	47	0.25	1.54	0.133	18
250 ··· 350	−0.97	−2.03	0.051	81	−0.03	−0.12	0.908	71
350 ··· 450	−2.97	−4.19	0.000	227	0.47	1.01	0.318	185
450 ··· 550	−1.13	−2.10	0.044	238	0.66	2.24	0.032	161
550 ··· 650	−0.50	−1.00	0.327	188	−0.69	−1.58	0.123	164
650 ··· 750	0.53	1.50	0.143	153	−0.81	−2.31	0.028	178
750 ··· 850	0.91	2.50	0.018	187	−0.22	−0.53	0.600	171
850 ··· 950	0.16	0.32	0.751	157	−0.50	−1.44	0.161	138

[a] Time is given relative to cue onset, i.e., a baseline interval and nine consecutive, non-overlapping time windows following cue-presentation are compared.
[b] MD: mean difference (positive or negative differences indicate that congruent or incongruent microsaccades were predominant, respectively); t-values test difference from zero; $\alpha = 0.05$; N: number of microsaccades observed during the time window.

similarities to results obtained by Rolfs et al. (2004), who report a tendency for microsaccades away from the exogenously cued location during a time window that matches the peak of the incongruency effect reported here. However they did not observe either the early congruency effect or a later rebound of cue-congruent microsaccades. More recently, Rolfs, Engbert, and Kliegl (submitted) obtained an early congruency effect using strong exogenous cues.

The pattern of direction effects for endogenous cues was rather different from the one reported by Engbert and Kliegl (2003) in that they observed an effect into the cued direction, while here it was in the opposite direction (although a slight, but insignificant tendency for a congruency effect into the cued direction following endogenous cues in our data occurred around 450 ms). We interpret these differences as related to one or several of three critical differences between the tasks: First, Engbert and Kliegl used a fairly simple supra-threshold detection task while here the task involved the rather difficult discrimination of an IS. Second, we presented the target vertically below or above the fixation position, thereby separating attention shift and preparation of the response saccade. Third, the on-line fixation check we used introduced a penalty for moving the eye too close to the cued location, which might have caused a tendency for over-correction. Further research is needed to discriminate between these alternative explanations.

How do our results relate to the classic Müller and Rabbitt (1989) findings? We think that our results complement them well. Like Müller and Rabbitt, we observed a fast and transient effect of exogenous cues during an interval about 100–300 ms following cue presentation. Their results suggest that later in time, an endogenous process takes over. Both the peak of the 'incongruency' effect for exogenous cues and the slight (but insignificant) tendency for a congruency effect following endogenous cues in our data occur around 350 ms, i.e. at the time at which Müller and Rabbitt's endogenous process started affecting perception. Note that the direction in which the endogenous process first affects microsaccade direction differs between flash and color cue conditions—it leads to incongruent microsaccades in the former and to congruent microsaccades in the latter. However, the 'incongruency' peak is only delayed in the color cue condition. We think that the most likely explanation is that in our setting there are actually two endogenous processes, one for interpreting cues and initiating an attention shift into the cued direction, and the second related to the task instruction not to move the eyes.

The instruction to keep the eyes at fixation, especially under on-line fixation control conditions, generates an 'executive' attentional control setting to counter-act perceived eye movements. Perceived eye movements are movements of the focus of attention (Deubel, Irwin, & Schneider, 1999; Kowler, Anderson, Dosher, & Blaser, 1995), and not always actual movements of the eye. Over- or miscorrection of an attentional movement by a signal to move the eyes in the opposite direction might actually lead to a shift of the directional distribution of microsaccades in the direction opposite the cued location. The exogenous shift of attention is reflected in the very early effect into the cued direction, while the endogenous corrective mechanism is reflected in the large subsequent incongruency effect, occurring about 200 ms later. With color cues, only endogenous control can be applied. Because colors do not carry explicit directional information, their interpretation takes time—hence the effect on microsaccade direction occurs later. In contrast to earlier results (Engbert & Kliegl, 2003), the effect into the cued direction was only weak (with a tendency for more congruent microsaccades after about 450 ms). We suspect that this is due to the

large inter-individual variability in the time it takes to interpret the meaning of the cue. We also found an effect of the hypothesized second endogenous control process, which counter-acts and over-corrects movements of attention and the eye, and is expressed in the incongruency peak around 700 ms after cue. Taken together, these results can best be integrated if one assumes that reflexive and voluntary orienting mechanisms add to (or subtract from) each other (see also Müller & Findlay, 1988; Müller & Rabbitt, 1989) to produce a net amount of directed attention. Our interpretation is that the effects of conflicting voluntary mechanisms, one responsible for shifting attention, and the other for holding fixation, might add up as well. Our results might thus be relevant for the ongoing debate about the top-down vs. bottom-up control of attention (e.g., Folk, Remington, & Johnston, 1992; Theeuwes, 1991). We show that the effect of endogenous control settings on eye movements can sometimes be stronger, but it also appears later than the exogenous effect of peripheral sudden-onset cues.

What are the implications for our understanding of the physiological aspects of the saccade system? A common assumption in the neurophysiology of saccade control is that saccades elicited by exogenous and endogenous cues differ in the control structures involved (e.g., Guitton, 1991; Guitton, Buchtel, & Douglas, 1985; Hanes & Schall, 1996; Sommer & Tehovnik, 1997; Sommer & Wurtz, 2000). While endogenous cues always seem to involve a pathway from V1 via the frontal eye field (FEF) to the superior colliculus (SC), stimulus-driven saccades can be triggered both by a pathway from V1 via the parietal eye fields to the SC, and by a direct reflexive path from the retina to the SC, causing involuntary saccades. Because rate inhibition occurs very fast in response to stimulus onsets, is observed irrespective of cue meaning or cue class, and the time at which the minimum is reached is relatively invariant across people, it seems to be a stereotyped and automatic reaction, e.g., a sort of orienting reaction (e.g., Pannasch, Dornhoefer, Unema, & Velichkovsky, 2001). Thus the inhibition part of the rate modulation likely reflects workings of the system that is also involved in involuntary saccades. Direction effects are also observed quite early with exogenous cues. We speculate that the more pronounced effects into the opposite direction, which temporally coincide with the later-occurring enhancement part of the rate modulation, are indicative of FEF involvement, because they are affected by task demands such as cue class. Finally, the pattern of interactions between endogenous and exogenous processes could be a behavioral correlate of the influence of top-down (e.g., FEF) and stimulus-elicited input on collicular build-up neurons (e.g., Munoz, Dorris, Paré, & Everling, 2000). We speculate that exogenous cues influence the activity of caudal buildup neurons, whereas real or perceived mislocations of fixation influence the activity of rostral "fixation cells", which are better conceived of as rostral buildup neurons (Krauzlis, Basso, & Wurtz, 2000) and have been shown to be involved in target selection for pursuit and saccades (Krauzlis & Dill, 2002). The present behavioral results therefore complement neurophysiological findings by documenting differential contributions of endogenous and exogenous processes to microsaccade direction. We regard them as further evidence for the close coupling of systems responsible for attention and motor preparation.

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