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The dynamics of microsaccade amplitude reflect shifting of covert attention

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ABSTRACT

Attention flexibly shifts between spatial locations to accommodate task demands. The present study examined if the dynamics of attentional shifting are seen in microsaccades whose direction has been shown to accompany the shifts of covert attention. In a spatial cueing task, the cue predicted the target location on 100%, 75%, or 50% of the trials. The results revealed that microsaccade rate and amplitude were both reduced following cue onset and then rebounded. Both microsaccade rate and amplitude were biased towards the opposite direction of the cue and then returned to the cued direction. Importantly, the cue validity modulated the temporal profile of microsaccade amplitude but had little impact on the temporal profile of microsaccade rate. In line with this, the cueing effect measured with target response accuracy was correlated with the microsaccade amplitude only. These results indicate that the temporal dynamics of microsaccade amplitude reflect shifting of covert attention.

1. Introduction

The eyes are not stationary even when we try hard to maintain gaze. Instead, miniature eye movements occur involuntarily during fixation (Engbert, 2006; Hafed, Chen, & Tian, 2015; Martinez-Conde, Otero-Millan, & Macknik, 2013). The most prominent component of these miniature eye movements is microsaccade, which occur about once per second. Microsaccades bear functional significance, such as helping to correct ocular drift (Ko, Snodderly, & Poletti, 2016) and counteracting visual fading due to neural adaptation when fixating (Martinez-Conde, Macknik, & Hubel, 2004; McCamy et al., 2012).

Although microsaccades are not consciously perceived, they are influenced by external events and attention (Hafed et al., 2015). In Posner cueing tasks, exogenous cues would elicit an initial inhibition in microsaccade rate, followed by a strong rebound. The rate of microsaccades is slightly biased toward the cued location in the inhibition period and largely toward the uncued location in the rebound period (Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Rolfs, Engbert, & Kliegl, 2005). Endogenous cues also elicit an initial inhibition and a subsequent rebound in microsaccade rate (Engbert & Kliegl, 2003), but the rate of microsaccades is biased toward the cued location in the rebound period instead (Engbert & Kliegl, 2003; Laubrock, Kliegl, Rolfs, & Engbert, 2010). These

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findings show that both exogenous and endogenous cues modulate the temporal dynamics of microsaccade rate, although likely in different ways (Laubrock et al., 2005; Meyberg, Sinn, Engbert, & Sommer, 2017).

Researchers in the field have suggested that the deployment of attention is sequential and rhythmic (Fiebelkorn & Kastner, 2019; VanRullen, 2016). For instance, studies in recent years have showed that attention rhythmically shifts between spatial locations (Jia et al., 2017, 2019; Song, Meng, Chen, Zhou, & Luo, 2014) and features (Mo et al., 2019). Rhythmic shifts have been reported for both top-down (Landau & Fries, 2012) and bottom-up attention (Jia, Fan, & Luo, 2021), in both behavioral performance (Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012; Song et al., 2014) and neural activities (Fiebelkorn, Pinsk, & Kastner, 2018; Helfrich et al., 2018; Landau, Schreyer, van Pelt, & Fries, 2015). Critically, it has been shown that attentional shifting is modulated by task demand (Jia et al., 2017, 2019). For example, when cue validity (proportion of trials in which the target appears at the cued location) was manipulated to allocate different proportions of top-down attention to two spatial locations, the attentional shifting became more prominent when the task required a more uniform distribution of attention.

Is there a link between the temporal dynamics of microsaccades and attentional shifting? In a spatial cueing experiment by Laubrock et al. (2005), the microsaccade rate was biased towards the cued direction in the early inhibition period, towards the opposite direction of the cue in the rebound period, and back to the cued direction again later on. This pattern of result implies that attention shifted sequentially between the two locations. However, it is unclear whether this sequential shifting of microsaccade rate is related to behavioral performance (See: Horowitz, Fencsik, Fine, Yurgenson, & Wolfe, 2007; Horowitz, Fine, Fencsik, Yurgenson, & Wolfe, 2007; Kliegl, Rolfs, Laubrock, & Engbert, 2009; Laubrock, Engbert, Rolfs, & Kliegl, 2007) and is influenced by top-down factors like cue validity, which modulates the distribution of spatial attention. If the dynamics of microsaccade rate indeed reflect attentional shifting, changes in microsaccade rate should correlate with behavioral performance (e.g., response time and/or accuracy) and importantly, the dynamics of microsaccade rate should be modulated by top-down factors (i.e., cue validity) known to modulate attentional shifting (Jia, Liu, Fang, & Luo, 2017). In addition to microsaccade rate, previous studies have revealed that microsaccade amplitude varies dynamically following stimulus presentation (Hafed & Ignashchenkova, 2013; Rolfs, Kliegl, & Engbert, 2008; Tian, Yoshida, & Hafed, 2018). The saccade amplitude was proved to be related to attentional shifting (Crawford & Muller, 1992; Deubel & Schneider, 1996). However, the relationship between attentional shifting and the temporal dynamics of microsaccade amplitude has been largely overlooked in previous studies. If the dynamics of microsaccade amplitude also reflect attentional shifting, changes in microsaccade amplitude should correlate with the behavioral performance in attentional tasks and be sensitive to top-down factors (e.g., cue validity).

In the present study, we used a spatial cueing paradigm similar to Jia et al. (2017, 2019) to examine the link between attentional shifting and the temporal dynamics of microsaccades. We presented two placeholders and cued the subject to attend one of them. A target (tilted bar) appeared at one location later on and the participant was required to report the target orientation. The cue predicted the target location on 100%, 75%, and 50% of the trials in three experiments, respectively. We recorded eye movement data and calculated microsaccade rate and amplitude based on the spatial congruency between the microsaccade direction and the cue at each time point. This method allowed us to characterize the temporal profile of microsaccade rate and amplitude and to examine the impact of cue validity. To briefly anticipate the results, the temporal profile of microsaccade amplitude was modulated by cue validity and it accurately reflected attentional shifting.

2. Methods

The research protocols reported here were approved by a local ethics committee at Hangzhou Normal University. Written informed consents were obtained from all participants prior the experiments.

2.1. Participants

The present study recruited a total of 74 volunteers (30 males, 19–25 years old) from Hangzhou Normal University. Twenty-seven, 22, and 25 volunteers participated in the 100%, 75%, and 50% cue-validity experiment, respectively. The sample size was comparable

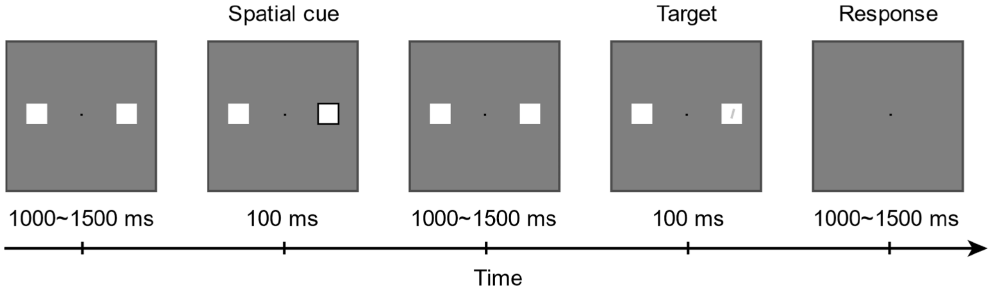

Fig. 1. The sequence of events in a typical trial. A fixation dot flanked by two placeholders (white squares) was first presented on the screen. After 1000–1500 ms, the border of one placeholder turned into black for 100 ms (spatial cue). Another 1000–1500 ms later, the target appeared in one of the placeholders. The target was a bar tilted left or right by 2°. The target was briefly presented for 100 ms, and participants responded with a keypress in 1000 ms. The cue predicted the target location on 100%, 75%, and 50% of the trials in the three experiments, respectively.

to that in previous studies using similar experimental tasks (Engbert & Kliegl, 2003; Laubrock et al., 2005), typically in the 20 to 32 range. All participants were naive with respect to the purpose of the study. They were right-handed, reported normal or corrected-to-normal vision, and had no known neurological or visual disorders.

2.2. Apparatus and tools

The present experiments used MATLAB (The MathWorks) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) to present stimuli and to record behavioral responses. The experiments took place in a dimly lit and sound-proof lab. The participants comfortably seated at a viewing distance of about 70 cm, with their heads stabilized on a chin rest. The visual stimuli were presented on a CRT monitor (resolution: 1024 × 768; refresh rate: 85 Hz) connected to a Windows 7 PC.

2.3. Stimuli and procedure

The spatial cueing task used in the present experiments was similar to that in our previous study on sequential attentional shifting (Jia et al., 2017). The events that occurred on a typical trial are illustrated in Fig. 1. All stimuli were presented against a gray background (23 cd/m^2). A central fixation dot (0.16° × 0.16°; 0 cd/m^2), flanked by two square place holders (4° × 4°; 104 cd/m^2), was first presented for 1000–1500 ms. The distance between the placeholders and the fixation dot was 6°. Then, one of the placeholders was cued by dimming its border to 0 cd/m^2 for 100 ms. Following an inter-stimulus interval of 1000–1500 ms, a target (tilted bar; 1.30°

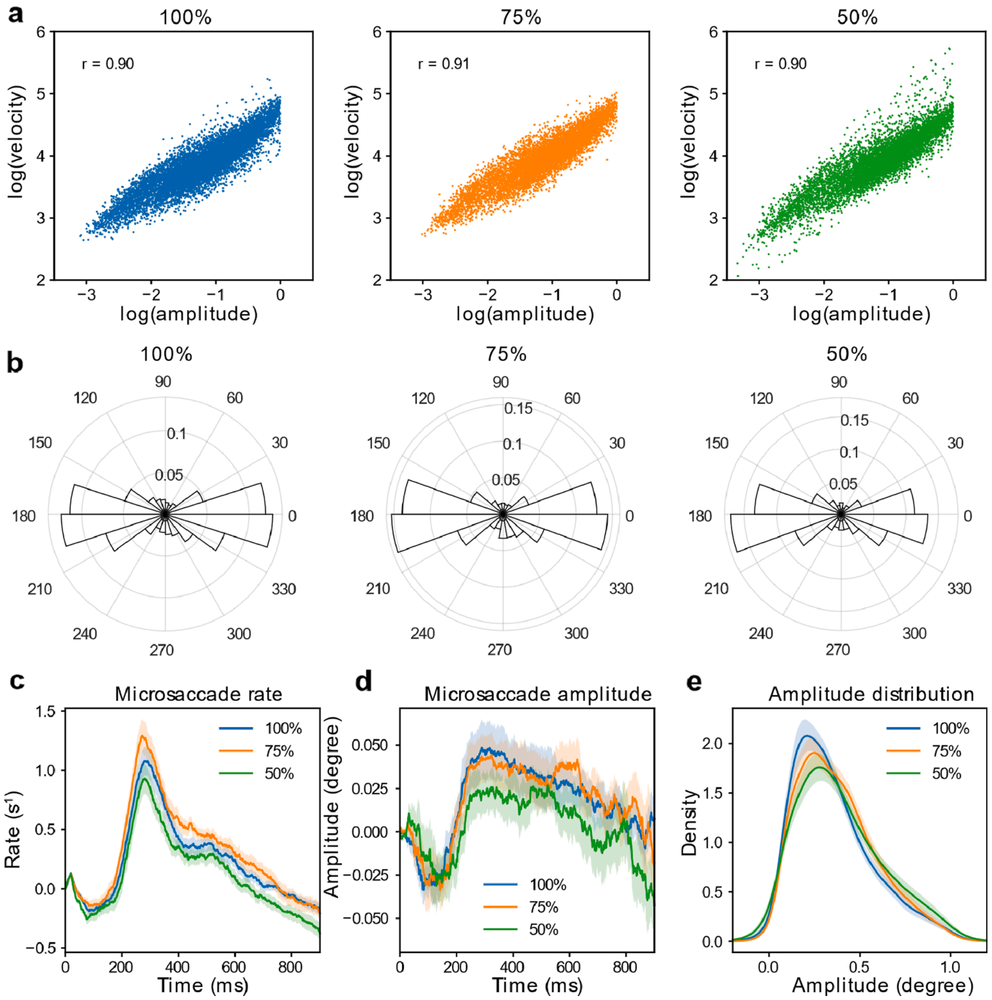

Fig. 2. Properties of the microsaccades in the 100%, 75%, and 50% cue-validity experiments. (a) Microsaccade peak velocity closely correlates with microsaccade amplitude in all three experiments (amplitudes and velocities were natural log-transformed). (b) Most microsaccades had a robust component in the horizontal direction. (c, d) The temporal profiles showed a transient drop at the early phase, followed by a strong rebound, and then a slow return to baseline in microsaccade rate (c) and amplitude (d). (e) The distribution of microsaccade amplitudes in three experiments. The shaded areas in (c-e) represent the standard error of the means (SEMs) across participants.

× 0.13°; 67 cd/m^2) appeared in one of the placeholders for 100 ms. The bar tilted left or right by 2°, and the participants reported the tilt orientation by pressing two keys with their left and right index fingers, respectively. The participant was required to respond to the target within 1000 ms and only target response accuracy was recorded. The next trial started in 1000–1500 ms. The participant was required to maintain fixation throughout the trial.

The present study manipulated cue validity between-subjects to avoid potential carryover effect, and to reduce the length of the experimental tasks. The validity of the spatial cue was 100%, 75%, and 50% in the three experiments, respectively. The participants were informed about the cue validity before each experiment. Each experiment had 400 trials and took about 40 min to complete. Each subject completed 30 practical trials at the beginning of each experiment.

2.4. *Eye movement recording*

Eye movements were recorded binocularly at 1000 Hz with an EyeLink 1000 eye tracker (SR Research, Ottawa). The participant's head was stabilized with a chin rest to maintain good tracking accuracy. The tracker was calibrated with a standard 9-point calibration procedure at the beginning of each experiment and every 50 trials.

2.5. *Microsaccade detection*

Microsaccades were detected with an improved version (Engbert & Mergenthaler, 2006) of the algorithm originally proposed by Engbert and Kliegl (2003). Horizontal and vertical eye positions were mapped onto a velocity space, and a relatively low velocity threshold of 3 standard deviations was used to detect microsaccades (Engbert & Mergenthaler, 2006) as the experimental tasks required the participant to maintain fixation and the eye movements were overall rather small. A temporal overlap between the two eyes, a minimum duration of 5 ms, and an amplitude below 1° were required for a detected saccade to be counted as a microsaccade. Trials that contained saccades larger than 1° were excluded from the analysis. This data cleansing procedure on average excluded 7%, 9%, and 13% of trials from 100%, 75%, and 50% experiments, respectively. As shown in Fig. 2a, the amplitude and peak velocity of the detected microsaccades were highly correlated in all experiments, replicating previous results using the same microsaccade detection algorithm.

2.6. *Microsaccade rate analysis*

A rectangular moving window of 100 ms (stepped in 1-ms) was used to examine microsaccade rate in a 900 ms time window following cue onset (Engbert & Kliegl, 2003; Engbert, 2006; Laubrock et al., 2005). A microsaccade could land in the same or opposite hemifield as the cue. For convenience, we will use "congruent" and "incongruent" to refer to these two types of microsaccades, respectively. The cueing effect was revealed in the rate difference between congruent and incongruent microsaccades.

2.7. *Microsaccade amplitude analysis*

A moving window of 100 ms was also used to examine microsaccade amplitude in a 900 ms time window following cue onset (Engbert & Kliegl, 2003; Laubrock et al., 2005). To quantify microsaccade amplitude in the horizontal direction along which the cue was presented (Fig. 4a), we first projected the vector of each microsaccade to the horizontal meridian. Specifically, the *horizontal amplitude* = *microsaccade amplitude* * cos*(angle)*. We then derived the mean horizontal amplitude for each time bin separately for congruent and incongruent microsaccades. The cueing effect was revealed in the amplitude difference between congruent and incongruent microsaccades.

2.8. *Statistical analysis*

A one-way ANOVA was first performed to compare the target response accuracies across the three experiments. The target could be validly or invalidly cued in the 75% and 50% cue-validity experiments. The target response accuracies for valid and invalid trials were compared with paired t-tests (Bonferroni-corrected). The temporal profiles of microsaccade amplitude and rate were baseline-corrected to the onset of the cue (Barbeito, Tam, & Ono, 1986; Henderson & Luke, 2014; Vergilino-Perez et al., 2012). The rate and amplitude differences between congruent and incongruent microsaccades were examined with paired t-tests, and multiple comparisons were FDR-corrected (Benjamini & Hochberg, 1995). A one-way ANOVA was performed to compare the cueing effect (congruent - incongruent) in microsaccade rate and amplitude across the three experiments. The post-hoc contrasts were corrected as well (with Tukey's HSD). A method proposed by Meng, Rosenthal, and Rubin (1992) was used to compare correlation coefficients; this method is implemented in the *cocor* package of R (Diedenhofen & Musch, 2015). To get a better estimation of the conclusiveness of the present findings, Bayesian statistics (BF10) were also obtained with JASP wherever applicable.

3. Results

3.1. *Cueing effect on target response accuracy*

The overall target response accuracies did not differ significantly across the three experiments (Mean ± SEM: 0.80 ± 0.02, 0.71 ±

0.05, and 0.78 ± 0.03 for the 100%, 75%, and 50% cue-validity experiments, respectively), $F(2,71) = 1.61$, $p = 0.208$, partial $\eta^2 = 0.04$, $BF_{10} = 0.39$. As expected, the response accuracy was higher for valid than invalid trials in the 75% cue-validity experiment (Valid: 0.73 ± 0.05, Invalid: 0.69 ± 0.05), $t(21) = 3.21$, $p = 0.008$, Cohen's $d = 0.69$, $BF_{10} = 10.38$; no difference was observed between valid and invalid trials in the 50% cue-validity experiment (Valid: 0.78 ± 0.04, Invalid: 0.78 ± 0.03), $t(24) = 0.75$, $p = 0.927$, Cohen's $d = 0.15$, $BF_{10} = 0.27$.

3.2. Characteristics of the microsaccades

As is clear from Fig. 2a, the saccade peak velocity linearly correlated with the saccade amplitude following a natural log-transformation, confirming the ballistic nature of saccades (Hafed, Goffart, & Krauzlis, 2009; Martinez-Conde, Macknik, & Hubel, 2000). Most microsaccades had a robust horizontal component, as shown in Fig. 2b. We pooled all microsaccades to examine the temporal profile of microsaccade rate and amplitude. As shown in Fig. 2c, the microsaccade rate dropped transiently, troughed at about 100 ms following cue onset, rebounded and peaked at about 300 ms, and then slowly returned to the baseline level. This temporal profile of microsaccade rate replicated previous observations (e.g., Engbert & Kliegl, 2003; Rolfs, 2009) and demonstrated that the microsaccade detection algorithm in our three experiments was sound. The temporal profile in microsaccade amplitude showed a similar pattern (Fig. 2d). There was a transient drop, followed by a strong rebound, and then a slow return to baseline. Fig. 2e shows the distributions of microsaccade amplitude in the three experiments (smoothed using a normal kernel).

3.3. The cueing effect on microsaccade rate

To investigate the cueing effect, the microsaccades were categorized into congruent and incongruent ones. The congruent ones landed in the same hemifield as the cue, whereas the incongruent ones landed in the opposite hemifield as the cue. As shown in Fig. 3a-c, the temporal dynamics of the cueing effect (congruent - incongruent) in microsaccade rate was similar across the three experiments. The rate did not differ between congruent and incongruent microsaccades in the initial 200 ms. The rate was lower for congruent than for incongruent microsaccades in the 200–500 ms time window. The pattern reversed from about 500 ms following cue onset, and the rate was higher for congruent than incongruent microsaccades.

Three critical time windows were selected to statistically compare the rate of congruent and incongruent microsaccades (i.e., the cueing effect). The first window (80–160 ms) covered the initial drop in microsaccade rate in all experiments, the second window (280–360 ms) covered the rate rebound, and the third window (600–680 ms) covered a period before the rate returned to baseline (see Fig. 2c).

As shown in Fig. 3d, in the first time window, the cueing effect was not significant in any of the three experiments ($p > 0.519$, Cohen's $d < 0.18$, $BF_{10} < 0.30$) and did not differ across the three experiments, $F(2,71) = 0.59$, $p = 0.556$, partial $\eta^2 = 0.02$, $BF_{10} = 0.18$. In the second time window, the cueing effect was significant in all three experiments ($p < 0.019$, Cohen's $d > 0.60$, $BF_{10} > 7.33$), and the cueing effect did not differ across the three experiments, $F(2,71) = 0.27$, $p = 0.766$, partial $\eta^2 = 0.01$, $BF_{10} = 0.14$. In the third time window, the cueing effect was not significant in the 100% or 50% cue-validity experiments ($p > 0.266$, Cohen's $d < 0.28$, $BF_{10} <$

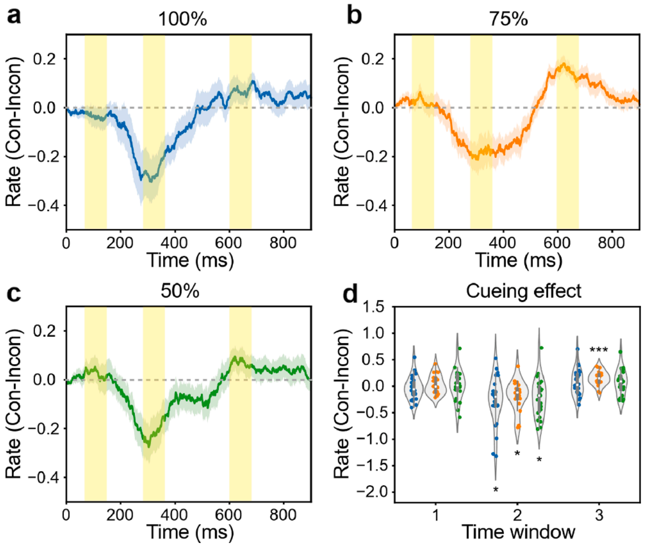

Fig. 3. The cueing effect on the dynamics of microsaccade rate. (a)-(c) The rate difference between congruent and incongruent microsaccades (i.e., the cueing effect) in the 100%, 75%, and 50% cue-validity experiments. (d) A between-experiment comparison of the cueing effect in rate in three time windows (yellow strips in a-c). The shaded areas in (a)-(c) represent the SEMs across participants. * $p < 0.05$, *** $p < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

0.51), but was significant in the 75% cue-validity experiment, $t(21) = 5.23$, $p < 0.001$, Cohen's $d = 1.11$, $BF_{10} = 699.73$. The cueing effect, again, did not differ among the three experiments, $F(2,71) = 1.17$, $p = 0.317$, partial $\eta^2 = 0.03$, $BF_{10} = 0.28$.

These results were consistent with previous observations that the rate is lower for congruent than for incongruent microsaccades about 300 ms following the cue (Galfano, Betta, & Turatto, 2004; Laubrock et al., 2005; Rolfs, Engbert, & Kliegl, 2004), resembling a classic inhibition of return effect (IOR; Galfano et al., 2004; Klein, 2000). However, the cueing effect on microsaccade rate was not modulated by cue validity, implying that the microsaccade rate is immune to top-down attentional control.

3.4. The cueing effect on microsaccade amplitude

Microsaccade amplitudes were projected to the horizontal meridian along which the cue was presented (Fig. 4a). As shown in Fig. 4b-d, the temporal dynamics of the cueing effect (congruent - incongruent) in microsaccade amplitude showed different patterns in the three experiments. As in the analysis of microsaccade rate, three critical time windows were selected to compare the amplitude of congruent and incongruent microsaccades statistically. The three windows were 80–160 ms, 300–380 ms, and 690–770 ms after cue onset.

As shown in Fig. 4e, in the first time window, the cueing effect was not significant in the 100% or 75% cue-validity experiments ($p > 0.118$, Cohen's $d < 0.43$, $BF_{10} < 1.19$), but was significant in the 50% cue-validity experiment, $t(24) = 2.66$, $p = 0.032$, Cohen's $d = 0.53$, $BF_{10} = 3.65$. The cueing effects were significantly different among three experiments, $F(2,71) = 5.98$, $p = 0.004$, partial $\eta^2 = 0.14$, $BF_{10} = 1.00$. Post-hoc contrasts revealed a stronger cueing effect in the 50% cue-validity experiment than that in the 100% cue-validity experiment, $t(71) = 2.67$, $p = 0.025$, Cohen's $d = 0.74$, $BF_{10} = 1.92$, and the 75% cue-validity experiment, $t(71) = 3.23$, $p = 0.005$, Cohen's $d = 0.94$, $BF_{10} = 9.61$. No reliable difference was observed between the 100% and 75% cue-validity experiments, $t(71) = 0.71$, $p = 0.761$, Cohen's $d = 0.20$, $BF_{10} = 0.21$.

In the second time window, the cueing effect was significant in the 100% and 75% cue-validity experiments ($p < 0.018$, Cohen's $d > 0.61$, $BF_{10} > 7.71$), but was not significant in the 50% cue-validity experiment, $t(24) = 0.67$, $p = 0.611$, Cohen's $d = 0.13$, $BF_{10} = 0.26$. The cueing effect did not differ across the three experiments, $F(2,71) = 1.48$, $p = 0.235$, partial $\eta^2 = 0.04$, $BF_{10} = 0.36$.

In the third time window, the cueing effect was not significant in the 100% or 75% cue-validity experiments ($p > 0.306$, Cohen's $d < 0.28$, $BF_{10} < 0.47$), but was significant in the 50% cue-validity experiment, $t(24) = 2.78$, $p = 0.026$, Cohen's $d = 0.56$, $BF_{10} = 4.66$. The cueing effects were significantly different across the three experiments, $F(2,71) = 3.30$, $p = 0.043$, partial $\eta^2 = 0.09$, $BF_{10} = 1.00$. Post-hoc contrasts revealed a stronger cueing effect for the 50% than for the 100% cue-validity experiment, $t(71) = 2.57$, $p = 0.033$,

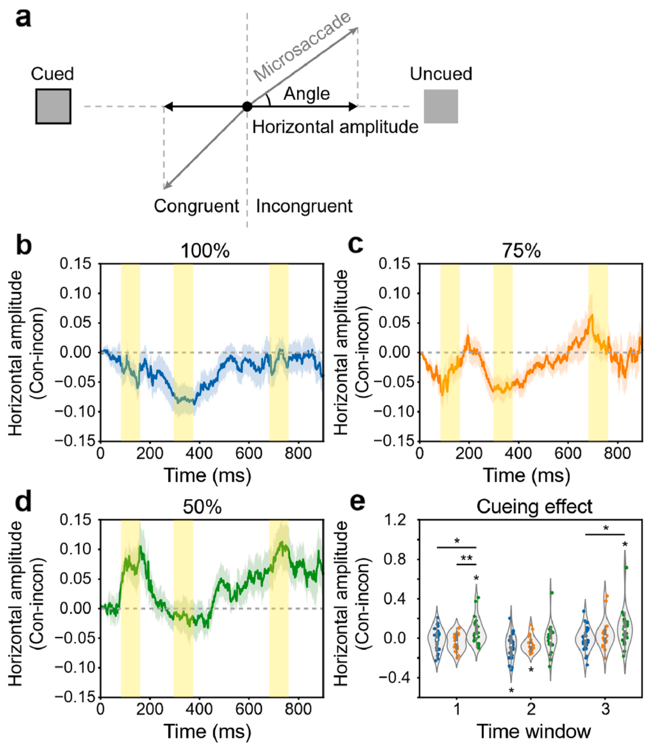

Fig. 4. The cueing effect on the dynamics of microsaccade amplitude. (a) Microsaccade amplitudes were projected to the horizontal meridian. (b)-(d) The amplitude difference between congruent and incongruent microsaccades. (e) A between-experiment comparison of the cueing effect on microsaccade amplitude in three time windows (the yellow strips in b-d). The shaded areas in (b)-(d) represent the SEM across participants. * $p < 0.05$, ** $p < 0.01$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Cohen’s $d = 0.71$, $BF_{10} = 2.19$. The cueing effect did not differ between the 100% and 75% cue-validity experiments, $t(71) = 1.16$, $p = 0.483$, Cohen’s $d = 0.33$, $BF_{10} = 0.33$, or between the 75% and 50% cue-validity experiments, $t(71) = 1.30$, $p = 0.398$, Cohen’s $d = 0.38$, $BF_{10} = 0.30$.

The microsaccade amplitudes were biased towards the opposite direction of the cue in the rebound period, revealing an IOR effect (Galfano et al., 2004; Laubrock et al., 2005; Rolfs et al., 2004). In addition, the 50% cue-validity experiment revealed larger amplitudes for congruent microsaccades before and after the rebound period. This novel observation is consistent with our previous finding that attention would shift between the cued and uncued locations sequentially when cue validity was 50% (Jia et al., 2017, 2019). The temporal dynamics of microsaccade amplitude are modulated by top-down attention, which supports flexible attention sampling to accommodate different task demands (Jia et al., 2017).

3.5. *Microsaccade amplitude reflect attentional shifting*

Our analyses quantified the cueing effect with the difference in rate and amplitude between congruent (directed towards the cue) and incongruent (directed away from the cue) microsaccades. In terms of behavioral performance, the cueing effect was quantified with the difference in target response accuracies for valid and invalid trials, i.e., trials on which the target appeared in the cued and uncued placeholders. If attentional shifting is linked to microsaccade dynamics, the cueing effect in microsaccade rate and/or amplitude (up till target onset) should predict the cueing effect measured with target response accuracy. So, we examined the recovery from IOR (difference between time windows 3 and 2) in microsaccade rate and amplitude and the cueing effect in the target response accuracy. This analysis combined data from 75% and 50% cue-validity experiments to increase statistical power. The cueing effect in target response accuracy did not correlate with that in microsaccade rate, $r = 0.01$, $p = 0.945$, however, it did correlate with the cueing effect in microsaccade amplitude, $r = 0.39$, $p = 0.007$. The latter correlation was statistically stronger than the former correlation, $z = 1.85$, $p = 0.032$ (one-tailed). These results clearly show that the temporal dynamics of microsaccade amplitude reflect attentional shifting.

4. Discussion

The current study investigated the relationship between the temporal dynamics of microsaccades and attentional shifting. In three experiments, the rate and amplitude of microsaccades were initially inhibited by a peripheral spatial cue but quickly rebounded. Both microsaccade rate and amplitude were biased to the opposite direction of the cue in the rebounding period and then returned to the cued direction about 600 ms following cue presentation, exhibiting the classic IOR effect. However, the temporal profile of microsaccade rate was not modulated by cue validity, and it did not correlate with the cueing effect measured with target response accuracy. In contrast, the temporal profile of microsaccade amplitude was modulated by cue validity and correlated with the cueing effect measured with target response accuracy. These findings show that the temporal dynamics of microsaccade amplitude may reflect attentional shifting.

In the present study, the impact of spatial cueing on microsaccades was seen in both microsaccade rate and amplitude. The peripheral spatial cue induced an initial inhibition on microsaccade rate and amplitude (see Fig. 2c-d) in all three experiments. These results were consistent with previous findings that a stimulus change would suppress microsaccades (Hafed & Ignashchenkova, 2013; Valsecchi, Betta, & Turatto, 2007), showing that the experimental tasks and the between-subject design adopted in the present study were sensitive in revealing attentional effects in microsaccades. In the rebound period, both microsaccade rate and amplitude were biased towards the opposite direction of the cue. These results are consistent with previous studies that revealed a close relationship between IOR and microsaccade (Betta, Galfano, & Turatto, 2007; Chica, Lupiáñez, & Bartolomeo, 2006; Galfano et al., 2004). Once attention is disengaged from the cued location, an inhibitory mechanism would kick in to discourage the return of attention to that previously attended location (Klein, 2000; Posner, Rafal, Choate, & Vaughan, 1985). An alternative interpretation is that, in situations where observers are required to maintain fixation, the voluntary control of oculomotor behavior is heightened to counteract automatic oculomotor capture evoked by the peripheral spatial cue (Rolfs et al., 2004). Consequently, microsaccades towards the cue are transiently suppressed. Following the rebound period, both microsaccade rate and amplitude favored the cued direction, showing a sequential switching between the cued and uncued locations.

While microsaccade rate has been found to reflect top-down attentional control (Turatto, Valsecchi, Tamè, & Betta, 2007), little attention has been paid to the microsaccade amplitude. Here, despite the similar temporal dynamics following spatial cueing in microsaccade rate and amplitude, only microsaccade amplitude was modulated by top-down spatial attention (i.e., the cue validity). In the rebound period, the cueing effects were significantly negative only in the 100% and 75% cue-validity experiments (see Fig. 4e). This may be due to the participants exercised strong voluntary control in 100% and 75% cue validities to prevent anticipatory responses toward the target location, leading to a strong suppression in amplitude for microsaccades directed into the same hemifield as the cue. On the contrary, the cue was non-predictive of the target in 50% cue-validity, and thus the task would encourage attentional shifting between the two locations. Consequently, the amplitude of microsaccades directed towards the cue was larger shortly following the cue, but this effect quickly dissipated in the rebound period. Following the rebound period, the microsaccade amplitude was again biased toward the cued location. This attentional dynamics in 50% cue validity was exactly what we observed in a recent EEG study (Jia et al., 2017).

The finding that the directional bias of microsaccade amplitude is directly associated with attentional shifts clearly demonstrates that the amplitude of microsaccade has functional significance in visual attention. Supporting this functional significance, microsaccade amplitude has been found to reflect the information content of visual images (Craddock, Oppermann, Müller, & Martinovic, 2017; Spotorno, Masson, & Montagnini, 2016). Its changes also co-occur with microsaccade rate inhibition (Rolfs et al., 2008). Overall, the present study provides novel evidence that the dynamic changes in microsaccade amplitude reflect attentional shifts.

This sequential deflection between the two locations (Fig. 4e) is consistent with the finding that the rhythmics in microsaccade is coupled with the phase of neural oscillation in the brain and the structural sampling and exploration of the environment (Bosman, Womelsdorf, Desimone, & Fries, 2009). Some researchers have suggested that the onset of the cue resets the phase of ongoing microsaccadic oscillatory rhythms during fixation (Hafed & Ignashchenkova, 2013; Tian, Yoshida, & Hafed, 2016), which resets the phase of sequential attention shifting as well (Benedetto & Morrone, 2017, 2019; Jia et al., 2021; Landau et al., 2015). The present findings are also consistent with a computational model proposed by Engbert (2012) and Engbert, Mergenthaler, Sinn, and Pikovsky (2011), which explains the modulation of display change and attention on microsaccade rate and direction. According to this model, spatial cueing induced an asymmetrical change of the microsaccade potential that generates a pattern of immediate cue-congruent, an intermediate cue-incongruent, and a late cue-congruent microsaccadic direction bias.

Spatial attention and saccades are tightly coupled (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). The present results revealed that microsaccade amplitudes were modulated by spatial cueing and correlated with the cueing effect measured with target response accuracy. Specifically, just before the target appears, the microsaccades that landed in the same hemifield as the cue were larger than those landed in the hemifield opposite to the cue. That is, microsaccades brought the visual target closer to the fovea (Womelsdorf, Anton-Erxleben, & Treue, 2008; Zirnsak, Lappe, & Hamker, 2010). The amplitude of microsaccades may reflect the preparedness of attentional shifts. Previous computational model has suggested that the dynamics of microsaccade are an oculomotor rhythm and do not reflect oscillatory attentional processes (Tian et al., 2016). The present study is partly supported this model as the microsaccade rate was unaffected by top-down attentional manipulation; however, the dynamics of microsaccade amplitude did correlate with top-down attentional manipulation. Previous computational models have exclusively focused on the dynamics of the microsaccade rate and its direction (Engbert, 2012; Tian et al., 2016). The present study demonstrates that the microsaccade amplitude has functional significance in visual attentional shifting. Future computational models should also take microsaccade amplitude into account.

5. Conclusion

The present study examined the temporal dynamics of microsaccade in a spatial cueing task. The results revealed that the temporal dynamics of microsaccade amplitude reflect covert attentional shifting, whereas the temporal dynamics of microsaccade rate may reflect a spontaneous microsaccadic fluctuation modulated by spatial cueing. These observations further demonstrate that the oculomotor system is closely linked to visual attention.

CRediT authorship contribution statement

Xinyu Lv: Investigation, Formal analysis, Visualization. **Suping Cheng:** Supervision. **Zhiguo Wang:** Conceptualization, Formal analysis, Supervision. **Jianrong Jia:** Conceptualization, Formal analysis, Visualization, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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