Research Article

Fixational Eye Movements Are Not an Index of Covert Attention

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ABSTRACT—*The debate about the nature of fixational eye movements has revived recently with the claim that microsaccades reflect the direction of attentional shifts. A number of studies have shown an association between the direction of attentional cues and the direction of microsaccades. We sought to determine whether microsaccades in attentional tasks are causally related to behavior. Is reaction time (RT) faster when microsaccades point toward the target than when they point in the opposite direction? We used a dual-Purkinje-image eyetracker to measure gaze position while 3 observers (2 of the authors, 1 naive observer) performed an attentional cuing task under three different response conditions: saccadic localization, manual localization, and manual detection. Critical trials were those on which microsaccades moved away from the cue. On these trials, RTs were slower when microsaccades were oriented toward the target than when they were oriented away from the target. We obtained similar results for direction of drift. Cues, not fixational eye movements, predicted behavior.*

People's eyes are never completely still. Even when one is fixating on a small point in space, one's eyes are in constant motion. There are three types of fixational eye movements: tremor, drift, and microsaccades (for a recent review, see Martinez-Conde, Macknik, & Hubel, 2004). Fixational eye movements may arise, in part, from noise in the oculomotor system, but they are also known to maintain direction of gaze and prevent image fading due to neural adaptation (Cornsweet, 1956; Martinez-Conde, Macknik, Troncoso, & Dyar, 2006). Recently, several researchers have proposed that fixational eye movements (specifically, microsaccades) are related to shifts in attention

(Engbert, in press; Engbert & Kliegl, 2003; Hafed & Clark, 2002).

Researchers have known for more than a century that the focus of attention can be separated from ocular fixation. This can be demonstrated using a cuing task (Posner, 1980). Observers maintain central fixation while a cue indicates the likely location of a peripheral stimulus, to which they make a speeded response. Observers are faster to respond if the cue is valid (indicating the actual location of the stimulus) than if the cue is invalid, uninformative, or absent. This *validity effect* illustrates that attention can shift to a location without a change in overt gaze. The premotor theory of attention (e.g., Sheliga, Craighero, Riggio, & Rizzolatti, 1997) holds that attentional shifts made during fixation are accompanied by a cancelled saccade plan. Studies have demonstrated that there is significant activation of oculomotor areas of the brain during attention tasks (Nobre, Gitelman, Dias, & Mesulam, 2000), suggesting that the act of shifting attention may leave telltale traces in oculomotor activity. These traces might be reflected in the direction of microsaccades made during fixation.

This idea is supported by the work of Engbert and Kliegl (2003), who found that microsaccades recorded during fixation in a cuing task tended to be biased in the cued direction. Other researchers have reported microsaccades both toward and away from the cued direction (Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Rolfs, Engbert, & Kliegl, 2004). Hafed and Clark proposed that cue-consistent microsaccades are driven by attentional shifts, whereas microsaccades in the opposite direction, often occurring later in the postcue interval, reflect corrective movements toward the center of the fixation point. Galfano et al. pointed out that the timing of microsaccades away from the cued direction is consistent with inhibition of return, in which perceptual processing of a cued location is first enhanced, then inhibited (Briand, Larrison, & Sereno, 2000). These results are all consistent with there being a relation between the direction in which attention is oriented and the direction of microsaccades during

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fixation. However, Tse, Sheinberg, and Logothetis (2002, 2004) have shown that abrupt onsets, widely held to capture attention, do not affect the spatial distribution of microsaccades.

The proposal that microsaccades are linked to attentional shifts is compelling. If true, it may resolve long-standing debates about the cause and purpose of microsaccades (e.g., Ditchburn, 1980; Kowler & Steinman, 1980). Furthermore, a link between microsaccades and attentional shifts would allow researchers with a sufficiently sensitive eyetracker to explicitly measure the direction of attention. Unfortunately, the existing findings do not resolve this debate. Studies to date have shown only that, under appropriate conditions, average microsaccade direction is correlated with cue direction. Microsaccades are not produced on every trial, so the correlation relies on a small proportion of trials. The effect is weaker with color cues than with arrow cues (Engbert & Kliegl, 2003), and rapid display changes can obliterate the effect altogether (Rolfs et al., 2004; Tse et al., 2002). More important, there is no direct evidence that microsaccades have any impact on performance in cuing tasks.

To put the point another way, a quarter-century of attention research has shown that cues can direct attention. In these studies, an attentional shift has been demonstrated by the validity effect, defined as better performance on validly cued trials than on invalidly cued trials. Recent work indicates that, under some circumstances, a cue can also bias the distribution of microsaccades in the direction of the cue. What is not known is whether there is a direct, predictive relation between microsaccade direction and attention.

In the present study, our goal was to directly test the link between attention and microsaccades in order to determine whether the direction of microsaccades can be used as an explicit measure of the direction of attention. If it can, then the direction of microsaccades on a given trial (if they occur) should be at least as predictive of performance as the direction of the cue. If the relation between cues and microsaccades were perfect, then one would be unable to test this hypothesis; fortunately, it is not. In Engbert and Kliegl's (2003) data, for example, 35 to 39% of microsaccades (depending on condition) moved *away* from the cue. If microsaccade direction is a marker for attention, then these trials represent cases in which attention went the wrong way (perhaps because of faulty cue processing or imprecise control of attention). Conveniently, such hypothetical "attentional mistakes" provide an opportunity. If microsaccades reflect attentional deployment, then on these mistake trials, attentional benefits should go with the microsaccade, not the cue. If the microsaccade on a mistake trial points toward the target, the cue is pointing away from the target. If there is a direct relation between microsaccades and attention, invalid cues would be associated with faster responses than valid cues on such trials.

Microsaccades might still have an effect on behavior even if they did not produce a validity effect analogous to the cue-validity effect. It is possible that a slight shift in eye position toward the target, even a shift smaller than 1°, would improve performance. If so, the tendency for microsaccades to move in the cued direction might reflect a (possibly unconscious) strategy on the part of the observer to bring the fovea closer to the expected target location. If this is the case, reaction times (RTs) should be faster overall when microsaccades point to the target, regardless of cue direction.

Our method was to classify each trial according to whether the microsaccade (or microsaccades) observed on that trial were directed toward or away from the target. In the standard cuing paradigm, trials are classified as valid or invalid according to whether or not the cue predicted the eventual location of the target. We made the same classification, but on the basis of microsaccade direction, and looked for a "microsaccade-validity effect": faster responses on trials with valid microsaccades (oriented toward the target) than on trials with invalid microsaccades (oriented away from the target). The critical trials were those on which the cue and microsaccade direction disagreed, as well as trials on which the cue provided no information (control trials, on which either no cue was presented or the cue was neutral).

We adapted the cuing task used by Engbert and Kliegl (2003) and adopted their algorithm for identifying microsaccades. Because the critical trials for our purposes were those on which the direction of the cue and microsaccades differed, and Engbert and Kliegl showed that these directions are correlated, we required many more trials per observer in order to have sufficient data to test our hypothesis. Thus, we elected to run a small number of observers for more than 2,500 trials each. Additionally, Engbert and Kliegl used only two response conditions, a saccadic left/right localization response and a manual detection response. We suspected that the results might depend on response mode (e.g., the link between attention and microsaccades might be different for saccadic and manual responses). However, response modality was confounded with detection versus localization (or number of response alternatives) in Engbert and Kliegl's design, so we added a condition in which subjects made manual left/right localization responses; this condition was designed to be more comparable to the saccade condition.

To this point, we have discussed only microsaccades because they have been the subject of claims in the literature. However, we see no reason why other components of fixational eye movements, such as drift, might not also be biased by shifts of attention. In addition to analyzing microsaccades, we use the same strategy to analyze the effects of fixational eye movements more generally.

METHOD

Observers

Three observers (ages 23–40 years) each completed 10 experimental sessions. Observers E.M.F. and R.E.H., both experi-

enced with the eyetracker, completed one practice session before data collection. Observer D.E.F., who was not familiar with the eyetracker, completed three practice sessions before data collection. Both E.M.F. and R.E.H. were nearsighted (uncorrected for this experiment; both required correction of 3.5 diopters or less); D.E.F. did not require correction. At the 75-cm test distance, both the calibration and test stimuli were clear to all observers. Observers D.E.F. and E.M.F. are authors of this article; R.E.H. was naive as to the purpose of the experiment.

Apparatus

Stimuli were presented on a LACIE electron22blueIV 21-in. color monitor running at 160 Hz with a resolution of 1024 × 768 pixels. Screen width was 40 cm, or 28°. Head position was stabilized with a bite bar and forehead rest. Displays and data collection were controlled with custom-built software developed using Matlab 6.5 (Release 13) and the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997) and running on an AMD Athelon XP 1800+ computer with a Matrox Millenium G550 video card under Microsoft Windows 98. Position of the right eye was monitored using a Fourward Technologies Generation 6.3 dual-Purkinje-image eyetracker. The accuracy of our system, measured under the testing procedures described later in this section, is better than 10 min arc. Horizontal and vertical eye position were recorded at 200 Hz. Viewing was binocular.

Eyetracker Calibration Procedure

The eyetracker was calibrated to the observer before each testing session. Fifteen white dots (0.23°, 16.7 cd/m^2) were presented sequentially in a 5 × 3 grid spanning the monitor. When each dot appeared, observers were to fixate it and then press a joystick button. After 100 ms of eye-position recording, the dot disappeared, and the next dot appeared 250 ms later. Once all 15 points had been sampled, eyetracker output was fitted with a bivariate quadratic polynomial using a least squares method. A dot location was repeated if the standard deviation of eye position for that location exceeded 3 times the mean standard deviation across locations or if the predicted eye position was outside a criterion range from the known pixel location. A calibration was considered "good" when it met these two criteria and the R^2 of the fitted function was at least .99. The final fit was used in the experiment to determine fixation accuracy and in the analyses to determine eye position throughout the trial.

Experimental Design and Procedure

In all conditions, observers made a speeded response. In the saccade condition, the task was to make a saccade in the direction of the target. In the manual localization condition, the task was to indicate where the target appeared by pressing either the "z" (left) or "/" (right) key. In the manual detection condition, the task was to press the space bar when the target appeared.

Each session consisted of one block of 84 trials per condition, in random order. Cue type (valid, invalid, neutral, or no cue) was randomly selected on each trial. Each block included 48 valid trials and 12 of each other type. The cues were 0.61° × 0.98° white chevrons. On the valid and invalid trials, there was a single chevron, the closed end of which was positioned at either the left or the right end of the fixation cross (see Fig. 1). On the neutral trials, two chevrons appeared, one on the left and one on the right side of the fixation cross. On no-cue trials, the fixation cross remained on the screen during the cue phase. The target appeared equally often to the left and right of fixation in each cue condition.

Before each trial began, a small (0.25°) white dot was displayed at the center of the monitor. When the observer was fixating the dot, he or she pressed a key. This initiated data collection from the eyetracker. If the observer's eye position was within 1° of the center of the dot for 1,000 ms, the trial began. Otherwise, the system beeped and waited for the observer to indicate refixation. The trial began with presentation of a 0.73° white plus sign at the center of the monitor for a variable time ranging from 1,500 to 2,000 ms. The plus sign was followed by the cue (or continued to be displayed in no-cue trials) for 2,000 to 2,500 ms. At cue offset, the target was presented, centered 12.4° to the left or right of fixation. The target was a 0.73° white disc. It remained visible until the observer made the appropriate response (depending on condition), or for a maximum of 1,000 ms.

Observers were instructed to maintain fixation throughout each trial during the two keyboard-response blocks and until the target appeared in the saccade block; a saccade of 1.5° or greater
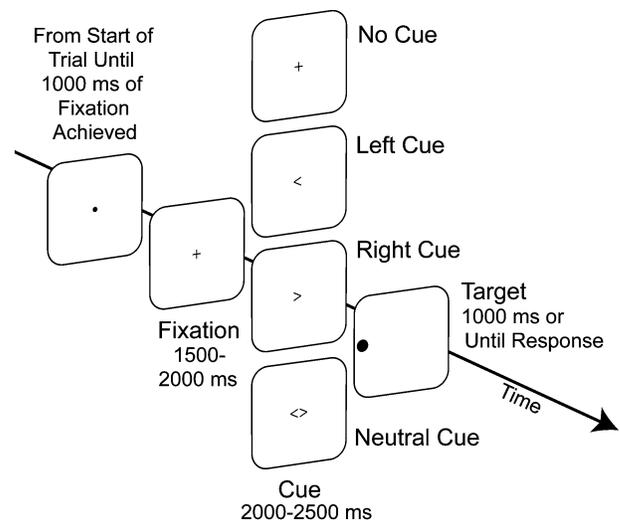

Fig. 1. Trial sequence. Observers began a trial by fixating the dot. A key press initiated presentation of the fixation cross, which was followed by the cue phase and then the target phase. Three types of cues or no cue could be presented during the cue phase. The target was presented until the observer's response, or for a maximum of 1,000 ms. The trial illustrated would be a validly cued trial if the left cue were presented and an invalidly cued trial if the right cue were presented.

after the target appeared was considered a response on saccade trials. Trials were recycled if the eye moved 1.5° or farther from the center of the fixation cross at any time in keyboard-response blocks or prior to target onset in saccade-response blocks, or if the eyetracker signaled a loss of tracking.

Data Analysis

We analyzed each observer's data separately. Median RTs and confidence intervals based on the standard error of the median were computed for each condition.

Eye-position data were analyzed using Engbert and Kliegl's (2003) algorithm. For each trial, we converted eye positions to velocities using a five-sample (25-ms) moving average, then derived a median-based standard deviation estimator. A microsaccade was defined as at least three consecutive samples (15 ms) for which average velocity exceeded the standard deviation by a factor of 6.0. Standard deviations were computed using only data gathered before the target appeared.[1] We assigned a direction to each microsaccade by computing the angle θ between the position of the initial sample and the center of gravity of subsequent samples (i.e., the averaged x- and y-coordinates of each point sampled during the microsaccade); an angle of 0 indicated a horizontal shift to the right. Microsaccades for which θ was between $-\pi/2$ and $\pi/2$ were labeled "right pointing"; the remainder were labeled "left pointing."

Each trial with at least one microsaccade within a specified interval (see Results) was classified according to microsaccade direction. When more than one microsaccade was detected in the interval, we used three different classification methods: the average direction of all microsaccades in the interval, the direction of the first microsaccade in the interval, and the direction of the last microsaccade in the interval. We present results obtained using the direction of the first microsaccade, but all three classification methods produced similar results.

In addition to analyzing microsaccades, we analyzed average eye position. We computed the average eye position during the fixation phase and categorized each trial on the basis of whether the average eye position during a specified cue-phase interval (see Results) was to the left or to the right of the average fixation location.

RESULTS

Observers were highly accurate in their responses. There were no errors in the saccadic localization condition, nor any anticipations in the manual detection condition. In the manual localization condition, accuracy was greater than 97.0% for all observers.

It would be difficult to interpret microsaccade-validity effects if observers did not show a standard cue-validity effect (valid

RTs < invalid RTs). As Figure 2 illustrates, our observers demonstrated classic cue-validity effects in both manual-response conditions. D.E.F. and E.M.F. also showed this pattern in the saccadic localization condition, but R.E.H. did not. It is not clear why she did not show a validity effect in this condition,
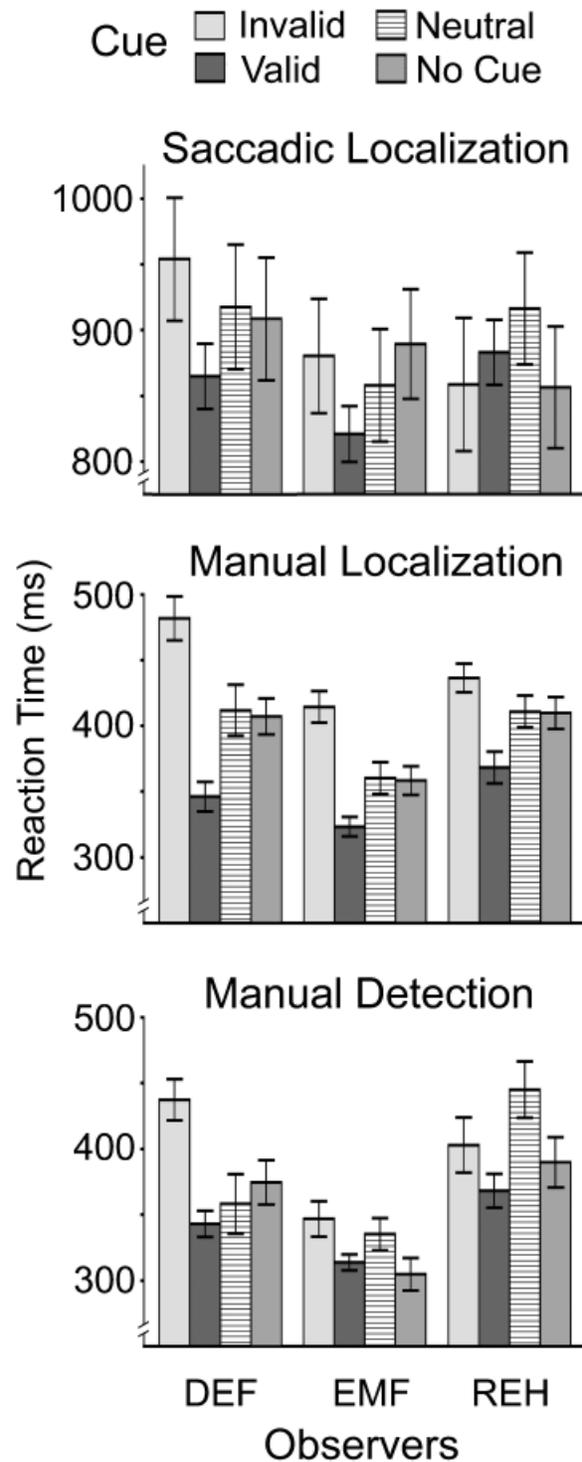

Fig. 2. Median reaction time by cue type and response mode for each observer. Error bars indicate 95% confidence intervals based on the standard errors of the medians.

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[1] We also analyzed the data from the complete trial; excluding the target phase did not noticeably affect the results.
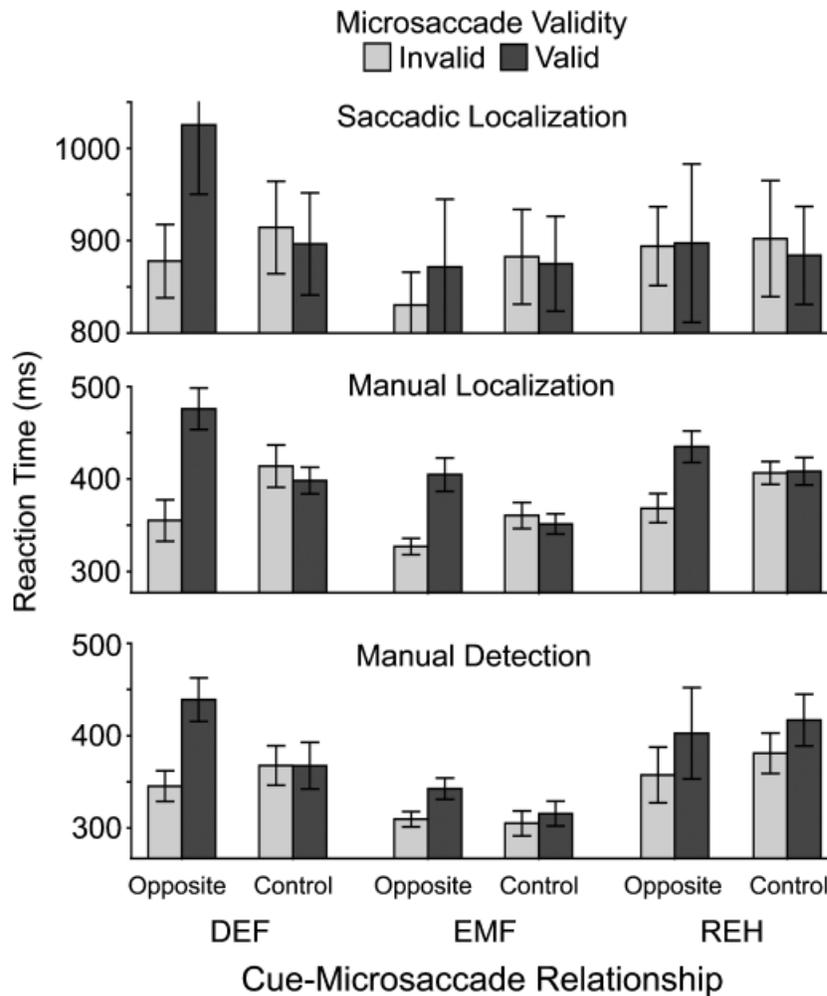
Fig. 3. Median reaction time as a function of response condition, cue-microsaccade relationship, and microsaccade validity for each observer, computed over 2,000 ms following cue onset. ''Opposite'' refers to trials on which the microsaccade and the cue pointed in opposite directions (thus, invalid-microsaccade trials were also validly cued trials, and valid-microsaccade trials were invalidly cued trials). ''Control'' refers to trials with no cue or a neutral cue. Error bars indicate 95% confidence intervals based on the standard errors of the medians.

given that her accuracy did not suffer. Her data from this condition are not discussed further.

We next looked at the ability of microsaccade direction to predict RT. When the cue and the microsaccade agreed, we observed significant microsaccade-validity effects. However, because these were also cue-validity effects, these data do not address our hypothesis. Figure 3 depicts RTs as a function of microsaccade validity on informative trials, that is, trials on which the directions of the cue and microsaccade did not match and control (i.e., no-cue and neutral-cue trials) trials. In most cases, valid microsaccades led to longer RTs than invalid microsaccades. The direction of the cue, not the microsaccade, predicts attentional facilitation.

One problem with this analysis is that it summarizes data across the cue-to-target period. Overall, microsaccades in this interval were biased against the cue direction (see Table 1). However, as noted in the introduction, microsaccade direction might not be driven by the same factors throughout the cue period. Galfano et al. (2004) claimed that early postcue microsaccades tend to move toward the cue, whereas later microsaccades move away from the cue (see also Hafed & Clark, 2002). In previous studies, researchers have selected analysis windows by eyeballing the data. We computed the size of the microsaccade-validity effect (invalid RT − valid RT) within a 400-ms moving boxcar window and selected the window with the greatest difference for each observer for each task. In this analysis, valid-microsaccade RTs were faster than invalid-microsaccade RTs in the saccadic localization condition for all 3 observers, but the difference was significant only for E.M.F. In the other two response conditions, valid-microsaccade trials

TABLE 1

Proportion of Microsaccades in the Cue Direction Within 2,000 Ms After Cue Onset

| Observer | Response condition | | |
	Saccadic localization	Manual localization	Manual detection
D.E.F.	.45	.37*	.42
E.M.F.	.45	.40*	.44*
R.E.H.	.29*	.27*	.27*

Note. Asterisks indicate proportions significantly different from .50 by chi-square test.

produced RTs that were either slower than or indistinguishable from those on invalid-microsaccade trials.

Although existing claims in the literature focus on microsaccades (Engbert & Kliegl, 2003; Hafed & Clark, 2002), it may be that attentional shifts are manifest in the drift component of fixational eye movements as well. For a simple test of this hypothesis, we repeated our analyses, classifying trials by the shift in average eye position from the fixation phase to the cue phase. The results were similar to those of the microsaccade analyses. When the eye drifted away from the cue, invalid trials produced faster RTs than valid ones. This pattern was broken only in R.E.H.'s saccade condition.

As with the microsaccade analyses, however, it was possible that we were averaging over different phases of the oculomotor response to an attentional shift, thereby masking any real effect. Accordingly, we computed eye-position shift in 400-ms moving boxcars across the cue phase, selecting those boxcars in which the validity effect (invalid RT – valid RT) was largest. The results did not differ substantially from those when the entire cue phase was used. Except for R.E.H.'s saccade condition, RTs on valid trials were never faster than RTs on invalid trials.

Finally, we evaluated the possibility that microsaccades work to improve performance without directly reflecting attention. If that is the case, RTs should have been faster when the microsaccade moved toward the target than when it moved away. Figure 4 plots the microsaccade-validity effect (the advantage for having a microsaccade pointing toward the target, rather than away from it) as a function of cue validity. If microsaccades improved performance, these validity effects should have been uniformly positive. However, the microsaccade-validity effects were either negative or quite small.

DISCUSSION

In this study, shifts in fixational eye movements did not reflect the direction of attentional shifts (as assessed by the validity effect). When fixational eye movements moved away from the cue, attentional facilitation went with the cue, not the eye. These data categorically contradict the hypothesis that fixational eye movements can predict attentional benefits. Note that we are not
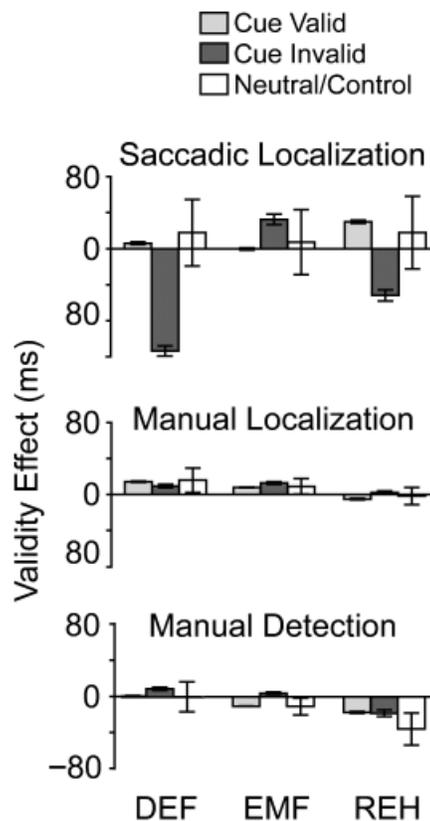

Fig. 4. Microsaccade-validity effects (reaction time on invalid-microsaccade trials minus reaction time on valid-microsaccade trials) as a function of cue validity. Each panel represents data from a different response condition. Error bars indicate 95% confidence intervals based on the standard errors of the medians.

reporting a null result. In most cases, valid microsaccades actually led to slower RTs than invalid microsaccades. Under some circumstances, the distribution of microsaccade directions and attention may be correlated, but this is only because they are both driven by an antecedent variable, the cue.

We anticipate two objections to our conclusions. First, in the saccadic localization condition (within a certain temporal window), microsaccades in the future target direction did predict faster RTs, even when the cue pointed the other way. If we had run only this condition, we might have taken this result as evidence that microsaccade direction reflects covert attention. However, in the context of the manual-response conditions, it seems more likely that the microsaccades in this case reflected motor preparation, rather than attentional facilitation. When observers were prepared to saccade leftward, for example, responses were faster when the target appeared on the left than when it appeared on the right. In the manual localization condition, which was identical except that the response was made with the hand rather than the eye, the opposite effect was observed.

The idea that microsaccades reflect motor preparation may explain some other findings in this area as well. Kliegl and his colleagues (Engbert & Kliegl, 2003; Rolfs et al., 2004) have reported that microsaccade rate is suppressed immediately

following a cue, and then rebounds. Horwitz and Albright (2003) replicated this finding in monkeys, though they did not see a change in the directional distribution of microsaccades. Following Rolfs, Laubrock, and Kliegl (2006), we propose that the microsaccade rate inversely reflects saccade preparation activity, because saccades and microsaccades rely on the same neural mechanisms. Thus, microsaccade suppression following a cue indicates preparation of a saccade in the cued direction. If the observer is instructed to fixate, this program must be canceled, leading to a rebound in the microsaccade rate. Under some conditions, the direction of microsaccades in the rebound phase might be primed by the direction of the canceled saccade.

Second, one might object that we analyzed the wrong time interval. Early microsaccades might indicate shifts in the cued direction, and later microsaccades might indicate either corrections toward fixation (Hafed & Clark, 2002) or inhibition of return (Galfano et al., 2004). The precise time interval in which microsaccades ought to reflect the distribution of attention is not obvious. Our solution to this problem was to select for each observer the time interval that maximized the microsaccade-validity effect. Except in the saccadic-response condition, the largest microsaccade-validity effects were still either zero or negative. We have also performed the same analysis using the window with the highest proportion of microsaccades pointing in the cued direction; in this analysis, the data uniformly followed the pattern in Figure 3. Our data suggest that there is no systematic relation between microsaccade direction (or fixational eye movements in general) and attention. In fact, microsaccades have very little effect on performance in this task, even apart from their relation to attention, as shown in Figure 4.

Attention and eye movements are intimately related (Craighero, Nascimben, & Fadiga, 2004; Gersch, Kowler, & Dosher, 2004; Peterson, Kramer, & Irwin, 2004), and there is substantial overlap in the underlying neural pathways (Corbetta, 1998; Schall, 2004). Nevertheless, they can be functionally separated. Tse et al. (2002, 2004) demonstrated that abrupt onsets captured attention, but did not elicit directional microsaccades (or drift). This finding is in agreement with our conclusions. However, the current study makes two important advances over the work of Tse et al. First, like Engbert and Kliegl (2003), they reported associations between cues and RT, on the one hand, and between cues and fixational eye movements, on the other. We directly analyzed the relation between fixational eye movements and RT. Second, Tse et al. (2004) used a very different methodology than Engbert and Kliegl did (Engbert & Kliegl, 2003; Rolfs et al., 2004). In contrast, we attempted to mimic the procedures and stimuli of Engbert and Kliegl as closely as possible, so our findings cannot be dismissed on that account.

The goal of this experiment was to determine whether microsaccades can serve as a window into the distribution of attention. Unfortunately, they cannot. Instead, researchers should view microsaccades as a window into oculomotor preparation (Rolfs et al., 2006).

REFERENCES

Brainard, D.H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*, 443–446.

Briand, K.A., Larrison, A.L., & Sereno, A.B. (2000). Inhibition of return in manual and saccadic response systems. *Perception & Psychophysics*, *62*, 1512–1524.

Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences, USA*, *95*, 831–838.

Cornsweet, T.N. (1956). Determination of the stimuli for involuntary drifts and saccadic eye movements. *Journal of the Optical Society of America*, *46*, 987–993.

Craighero, L., Nascimben, M., & Fadiga, L. (2004). Eye position affects orienting of visuospatial attention. *Current Biology*, *14*, 331–333.

Ditchburn, R.W. (1980). The function of small saccades. *Vision Research*, *20*, 271–272.

Engbert, R. (in press). Microsaccades: A microcosm for research on oculomotor control, attention, and visual perception. *Progress in Brain Research*.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research*, *43*, 1035–1045.

Galfano, G., Betta, E., & Turatto, M. (2004). Inhibition of return in microsaccades. *Experimental Brain Research*, *159*, 400–404.

Gersch, T.M., Kowler, E., & Dosher, B. (2004). Dynamic allocation of visual attention during the execution of sequences of saccades. *Vision Research*, *44*, 1469–1483.

Hafed, Z.M., & Clark, J.J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research*, *42*, 2533–2545.

Horwitz, G.D., & Albright, T.D. (2003). Short-latency fixational saccades induced by luminance increments. *Journal of Neurophysiology*, *90*, 1333–1339.

Kowler, E., & Steinman, R.M. (1980). Small saccades serve no useful purpose: Reply to a letter by R. W. Ditchburn. *Vision Research*, *20*, 273–276.

Laubrock, J., Engbert, R., & Kliegl, R. (2005). Microsaccade dynamics during covert attention. *Vision Research*, *45*, 721–730.

Martinez-Conde, S., Macknik, S.L., & Hubel, D.H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews Neuroscience*, *5*, 229–240.

Martinez-Conde, S., Macknik, S.L., Troncoso, X.G., & Dyar, T.A. (2006). Microsaccades counteract visual fading during fixation. *Neuron*, *49*, 297–305.

Nobre, A.C., Gitelman, D.R., Dias, E.C., & Mesulam, M.M. (2000). Covert visual spatial orienting and saccades: Overlapping neural systems. *NeuroImage*, *11*, 210–216.

Pelli, D.G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442.

Peterson, M.S., Kramer, A.F., & Irwin, D.E. (2004). Covert shifts of attention precede involuntary eye movements. *Perception & Psychophysics*, *66*, 398–405.

Posner, M.I. (1980). Orienting of attention. *Quarterly Journal of Experimental Psychology*, *32*, 3–25.

Rolfs, M., Engbert, R., & Kliegl, R. (2004). Microsaccade orientation supports attentional enhancement opposite a peripheral cue: Commentary on Tse, Sheinberg, and Logothetis (2003). *Psychological Science*, *15*, 705–707.

Rolfs, M., Laubrock, J., & Kliegl, R. (2006). Shortening and prolongation of saccade latencies following microsaccades. *Experimental Brain Research*, *169*, 369–376.

Schall, J.D. (2004). On the role of frontal eye field in guiding attention and saccades. *Vision Research*, *44*, 1453–1467.

Sheliga, B.M., Craighero, L., Riggio, L., & Rizzolatti, G. (1997). Effects of spatial attention on directional manual and ocular responses. *Experimental Brain Research*, *114*, 339–351.

Tse, P.U., Sheinberg, D.L., & Logothetis, N.K. (2002). Fixational eye movements are not affected by abrupt onsets that capture attention. *Vision Research*, *42*, 1663–1669.

Tse, P.U., Sheinberg, D.S., & Logothetis, N.K. (2004). The distribution of microsaccade directions need not reveal the location of attention. *Psychological Science*, *15*, 708–710.