



Microsaccades as an overt measure of covert attention shifts

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Abstract

Microsaccades, or tiny eye movements that take place during periods of fixation, have long been thought to be random artifacts of the oculomotor system. Here we demonstrate a possible link between microsaccades and covert attention shifts. We designed two psychophysical tasks involving spatial cues that had identical sensory stimuli but differing patterns of attentional benefits and costs. We found that microsaccades, rather than being randomly distributed, had directions that were directly correlated with the directions of covert attention shifts in the two tasks. Our results suggest that microsaccades occur because of subliminal activation of the oculomotor system by covert attention.

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1. Introduction

Microsaccades are tiny eye movements that occur frequently during periods of fixation (Barlow, 1952; Steinman, Haddad, Skavenski, & Wyman, 1973; Zuber, Stark, & Cook, 1965). These movements are referred to as ‘microsaccades’ because they seem to behave very much like larger saccades (Zuber et al., 1965). In other words, microsaccades are rapid eye movements that re-orient gaze. Such gaze re-orientation, however, is so small in the case of microsaccades that it does not cause the foveation of new visual targets when it occurs. Because of that property of microsaccades, these movements have long been thought to be random, involuntary movements (Bell, Davidson, & Scarborough, 1959; Cornsweet, 1956; Steinman et al., 1973) that serve no useful purpose for vision (Kowler & Steinman, 1980; Steinman et al., 1973). In fact, it has been argued that microsaccades may affect vision adversely because of the retinal image smear they cause every time they occur (Kowler & Steinman, 1980; Steinman et al., 1973). On the other hand, it has been shown that the elimination of eye movements during fixation causes the visible world to slowly fade away and eventually disappear (Prit-

chard, 1961). Moreover, recent neurophysiological evidence has shown that microsaccades modulate neural responses in the visual cortex (Leopold & Logothetis, 1998; Martinez-Conde, Macknik, & Hubel, 2000), indicating that these movements may help sustain perception.

Our interest in microsaccades stems from a desire to ‘track’ spatial attention. Eye trackers can measure gaze direction very accurately (Clark, 1975; Cornsweet & Crane, 1973). However, gaze direction is not always correlated with where we ‘look’ with our ‘mind’s eye’. That is, even when a person’s gaze is fixed, attention can shift covertly about the visual field (Egeth & Yantis, 1997; Jonides, 1981; Posner, 1980). Since microsaccades also occur during periods of gaze fixation, we sought to investigate a possible link between these movements and covert attention shifts. In particular, the hypothesis we are putting forward in this paper is that microsaccades may be an *overt* measure of *covert* attention. This hypothesis is based on growing evidence from the psychophysics (Posner, 1980; Sheliga, Riggio, & Rizzolatti, 1994), neurophysiology (Kustov & Robinson, 1996; Matelli, Olivieri, Saccani, & Rizzolatti, 1983), and brain imaging (Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000) literature for a significant overlap between the neural systems that are responsible for controlling overt and covert orienting. Covert attention shifts have been shown to cause activation of the

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superior colliculus (SC), a structure in the brain responsible for saccade generation (Lee, Rohrer, & Sparks, 1988; Wurtz, 1996), as if saccades to the targets of such shifts are planned (Kustov & Robinson, 1996). As will be seen in this paper, our findings suggest that microsaccades result from such activation. We present a theory of microsaccade generation that may help explain much of the observed phenomena associated with microsaccadic eye movements.

To determine whether indeed there is a measurable link between microsaccades and covert attention shifts, we designed two psychophysical tasks in which covert attention shifts were induced by the abrupt onset of peripheral cues (Collie, Maruff, Yucel, Danckert, & Currie, 2000; Egeth & Yantis, 1997). In what follows, we first describe our experimental setup in more detail. We then dispel the view that microsaccades are random by showing that their directions were strongly influenced by the directions of our peripheral cues. We finally establish a stronger link between microsaccades and attention by analyzing behavioral performance and correlating it with microsaccade direction in both of our tasks.

2. Methods

2.1. Psychophysical tasks

The first task used in this study, the ‘pro-cue’ task, consisted of multiple runs of a basic trial sequence (Fig. 1). In each trial, a small white fixation point (FP) and four small white peripheral points (PP) were shown. All four PP’s were at the same eccentricity, which was varied randomly between 4° and 8° from trial to trial. During each trial, a small white cue jumped randomly every 1200 ms to a location halfway between the FP and one of the PP’s. The cue was always visible in a trial. We defined a cue period as the time interval during which the cue remained in a particular location before jumping to another location. So, cue periods were 1200 ms long,

and each trial had several such periods. Moreover, cue location was uniformly distributed across cue periods, so we had roughly the same numbers of cue periods with rightward, leftward, upward, or downward cues across all trials.

After a random number of cue jumps in a trial, or equivalently after a random number of cue periods, the PP that was last cued showed a 200 ms flash of yellowish or greenish color. This happened between 150 and 1200 ms after cue onset, again with the actual time of the flash being varied randomly with a uniform distribution from trial to trial. So, the final cue period in a trial had variable length, and the cue was extinguished at the time of the color flash. Subjects were instructed to always maintain fixation and to report, using mouse buttons, which of the two colors appeared at the end of each trial. Finally, the target colors used in this task were chosen so that on average, subjects correctly responded on 75% of the trials.

The second task in this study, the ‘anti-cue’ task, was identical to the pro-cue task except that the color flash at the end of a trial always happened in the direction opposite the cue. For example, if the final cue in a trial appeared to the right of fixation in this task, then the color flash happened in the leftward PP; if the cue appeared above fixation, then the color flash happened below fixation, and so on for the other cue directions.

It is worth mentioning here that the value of 1200 ms was chosen for the length of our cue periods in order to analyze the patterns of microsaccade occurrences as a function of time from cue onset. It is fairly well known from the literature on attention and peripheral cueing that attention exhibits distinct time courses of benefits and costs when elicited by peripheral cues even up to 1200 ms after the onset of such cues (Collie et al., 2000; Maruff, Yucel, Danckert, Stuart, & Currie, 1999; Nakayama & Mackeben, 1989). We sought to uncover possible parallels for those time courses in microsaccade directions in order to support our claim for a link between microsaccades and attention shifts. It should also

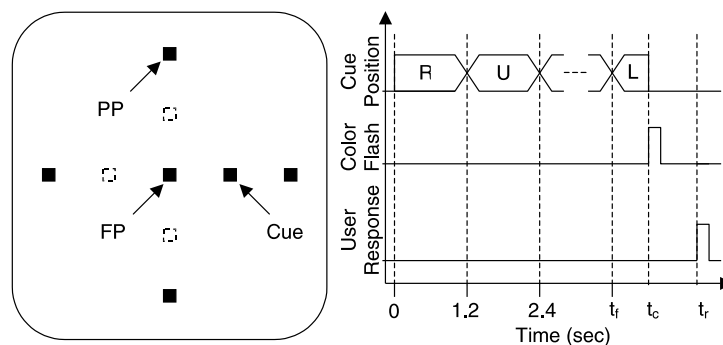


Fig. 1. Methods. The visual display in our tasks included a FP and four PPs. A cue, which was always visible in a trial, jumped to one of four locations (dashed squares) every 1200 ms. After a random number of cue jumps, the PP that was last cued showed a 200 ms color flash. This happened ($t_c - t_r$) ms after cue onset. The cue was extinguished at the time of the color flash. R, U, and L mean right, up, and left, respectively.

be stressed that as far as subjects were concerned, both of our tasks were purely fixation tasks that did not involve any eye movements. In other words, subjects were not aware of any microsaccades that they may have generated in the tasks.

2.2. Experimental procedures

Fourteen subjects (11 females) performed the pro-cue task. These subjects gave informed consent, were naïve to the purposes of the study, and were paid for their participation. All subjects were university students or recent graduates, and their ages ranged from 18 to 26 years. Experimental sessions lasted for approximately 30 min, and subjects participated in two or three sessions each. The first experimental session that a subject participated in consisted of practice followed by three or four sets of 20 trials, and these sets were separated by mandatory 3 min rest periods. Later sessions consisted of four or five sets of 20 trials, again separated by rest periods. Subjects had control over when to start a trial through a mouse button, and they were encouraged to rest in between trials if they ever felt fatigued. Subjects were seated approximately 18 in. away from the display, and they used a chin rest in order to minimize head movements. While the chin rest did not completely eliminate all head movements, whatever movements that remained were fairly slow relative to the eyes' velocity during microsaccades, and they did not introduce any significant errors in our detection of microsaccades. In addition to performing the pro-cue task, four of our subjects performed 20 control trials each. In these trials, subjects generated overt saccades to the jumping cue (Fig. 3(B)).

We collected a total of approximately 2900 trials with the pro-cue task, and these trials contained a total of approximately 6200 cue periods. As mentioned earlier, the cue periods were divided into four roughly equal-sized groups for each of the possible four directions of the cue relative to fixation.

As for the anti-cue task, this task was performed by 13 subjects, three of which were from the pro-cue task group. Ten of the subjects were female, and the total number of trials run for this task was similar to the pro-cue task. The three subjects that performed both tasks performed one task several months before performing the other.

2.3. Microsaccade detection

Eye positions were monitored using a video-based eye tracker (ISCAN, Inc.) with a sampling rate of 240 Hz. Resolution for vertical eye positions was very limited in our eye tracker (approximately 0.11°), so we restricted our analyses to horizontal microsaccades. For these movements, our eye tracker achieved a resolution of

approximately 0.06° . The tracker was calibrated by having subjects look at a five-point calibration display at the beginning of every session. Microsaccades were defined as movements that were less than 1° and that followed the same peak velocity versus amplitude curve as large saccades (Zuber et al., 1965). In a pre-processing stage, raw eye position traces from the eye tracker were smoothed with a median filter (9 samples). Then, simple velocity and size thresholds on horizontal eye position were employed in order to detect microsaccades. In particular, a microsaccade was detected when eye velocity exceeded approximately 8° s^{-1} . This threshold was chosen in order to sufficiently reject noise and select acceptable movements, and it resulted in microsaccades that seemed consistent with what we would have selected by visual inspection of the eye tracker records. We also set a lower threshold for microsaccade size of 0.12° . This threshold was imposed on us by our eye tracker's resolution, and it meant that we did not detect extremely small microsaccades. Incorrectly classified movements were minimized by rejecting movements that were either too short (<3 samples) or accompanied by large vertical components ($>1^\circ$). Finally, pairs of opposing microsaccades with separations less than 750 ms were flagged as physiological square-wave jerks (Feldon & Langston, 1977).

2.4. Data analysis

When subjects first performed our tasks, they had a tendency to move their eyes towards the cue. This tendency was dramatically reduced after practice, with overt eye movements ($>1^\circ$) towards the cue occurring in only 6% of all cue periods. Such periods were discarded from any further analysis. We also eliminated all trials in which subject response times to the color flashes were longer than three seconds, which happened on extremely rare occasions. All analyses were obtained by pooling data from all subjects. Inspection of the data for individual subjects agreed with the findings obtained after pooling.

Data analysis involved measuring and comparing proportions. Statistical confidence intervals were obtained by estimating the standard error of a proportion, p , by $\sqrt{(p(1-p)/n)}$ where n is the number of measurements used to obtain the proportion (Hays, 1973). Graphs of proportions in this paper have error bars showing 95% confidence intervals, so that inferences about the significance of differences between points may be made by inspection. When explicit comparisons are made in the text, we report the value of the Chi-square test statistic that is obtained (Hays, 1973).

This study was approved by the Ethics Review Committee of the Faculty of Education at McGill University.

3. Results

3.1. Patterns of microsaccades: square-wave and single-sided

Horizontal microsaccades were detected and analyzed. We found that microsaccades occurred in approximately one quarter of all trials, with the rest of the trials mainly containing slow drifts that are characteristic of fixation. We also observed that microsaccades either occurred singly—uncoupled microsaccades—or in pairs of opposing movements closely spaced in time—square-wave jerks (Abadi, Scallan, & Clement, 2000; Feldon & Langston, 1977). Typical examples of these two kinds of microsaccade occurrences are shown in Fig. 2. As can be seen from this figure, microsaccades—much like their larger counterparts—cause rapid changes in eye position. Moreover, as shown in Fig. 3(A), microsaccades follow the same peak velocity versus amplitude curve as large saccades (Zuber et al., 1965). This suggests that in terms of movement dynamics, the distinction between microsaccades and saccades is artificial. However, microsaccades do differ from larger saccades in that they are ‘fixation eye movements’—they do not result in the foveation of new visual targets, as is evident in Fig. 3(B). Our goal in this paper was to in-

vestigate whether those ‘fixation eye movements’ reflect covert attention shifts. Sections 3.2 and 3.3 analyze the relationship between microsaccade direction and cue direction in our pro-cue task. The Section 3.4, correlates microsaccade direction with a behavioral measure of attention in both the pro-cue task as well as the anti-cue task.

3.2. Cue direction and square-wave jerks

As mentioned above, microsaccades often occurred in the form of square-wave jerks. We hypothesize that a square-wave jerk, being composed of two microsaccades, reflects two attention shifts: first a shift to the cue and then a shift back to the FP. Abrupt onset of a visual stimulus is known to capture attention (Egeth & Yantis, 1997), so attention is expected to shift to the cue every time this cue appears in a certain location. If our hypothesis is valid, then the leading edges of square-wave jerks are expected to have occurred soon after cue onset and to have been mostly in the direction of the cue. Fig. 4 shows latency distributions of the leading edges of square-wave jerks in our pro-cue task for different cue directions. As can be seen from the figure, most square-wave jerks started within 400 ms from cue onset. Of those, most had leading edges that were in the direction

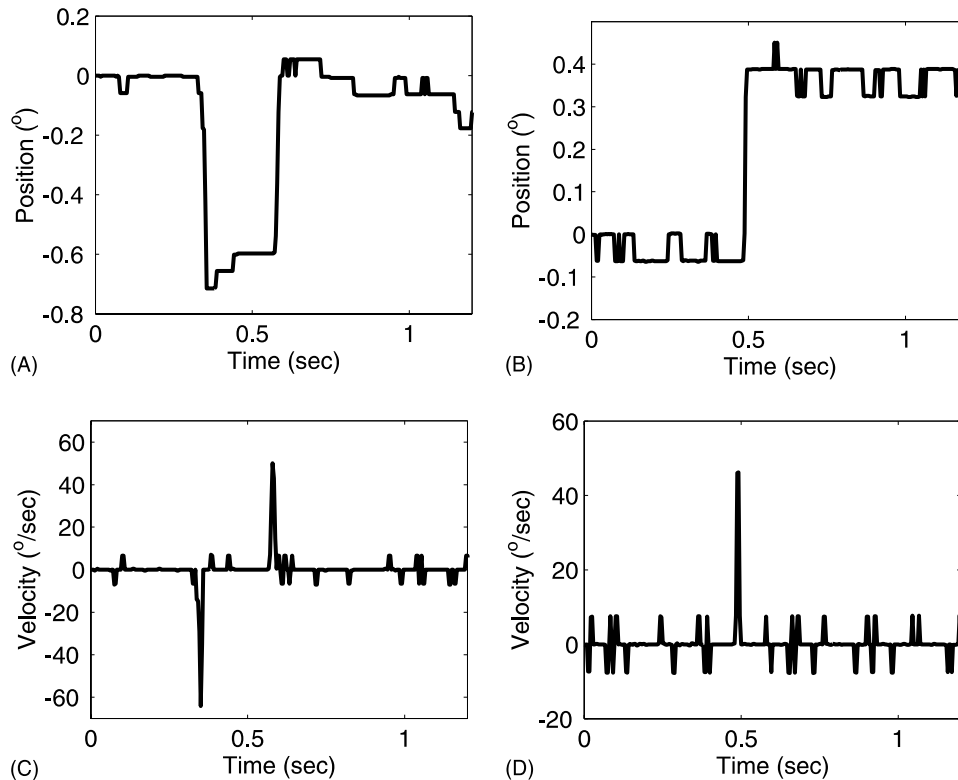


Fig. 2. Patterns of microsaccade occurrences. (A, C) Eye position and velocity traces showing the occurrence of a pair of back-to-back opposing microsaccades. Such a pair is often called a square-wave jerk because of the shape of the eye position trace it results in. (B, D) Eye position and velocity traces showing a typical single-sided microsaccade that is not accompanied by any other microsaccades. Whether single-sided or parts of square-wave jerks, microsaccades—like larger saccades—caused a rapid re-orientation of eye position.

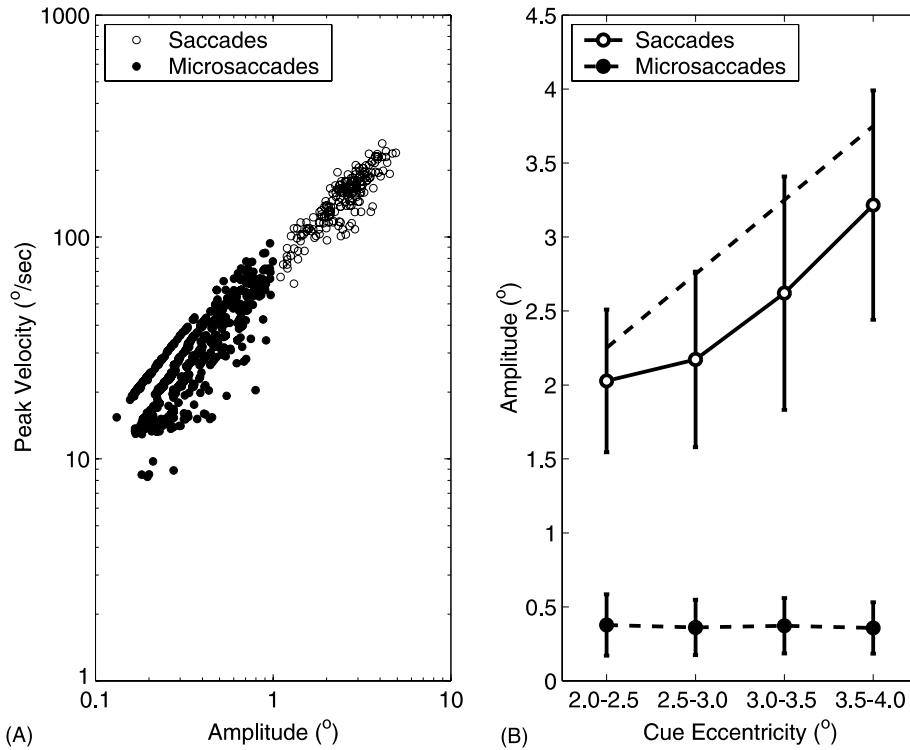


Fig. 3. Saccades and microsaccades. (A) A plot of microsaccade and saccade peak velocity as a function of amplitude. Microsaccades followed the same ‘main sequence’ as that followed by larger saccades (Zuber et al., 1965). (B) Control trials consisted of subjects foveating the jumping cue. The resulting eye movements increased in size with increasing cue eccentricity. Microsaccades on the other hand showed no dependence on cue eccentricity, and they were clearly not overt movements towards the cue. Error bars show standard deviations.

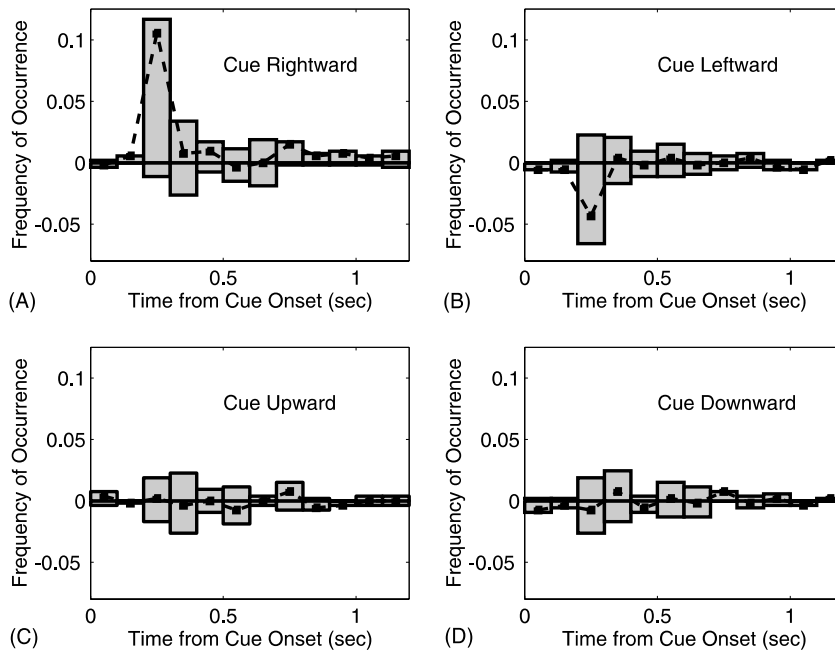


Fig. 4. Square-wave jerk directions were correlated with cue direction. (A, B) Normalized latency histograms of square-wave jerk leading edges for trials in which the cue appeared in a horizontal direction. Positive bars represent counts of rightward movements; negative bars represent counts of leftward movements. Most square-wave jerks started within 400 ms of cue onset and were in the direction of the cue. (C, D) Similar latency histograms but for vertical cues, which had no apparent effect on horizontal square-wave jerks. Dashed lines (in all panels) show the difference between positive and negative bars in each latency bin. Data in all panels were normalized by the total number of horizontal square-wave jerk occurrences across all cue directions.

of the cue. That is, within less than 400 ms from cue onset, we often observed a microsaccade in the direction of the cue followed shortly by another microsaccade in the opposite direction (see also Fig. 7(B) and (C)). Moreover, we observed that the presence of *vertical* cues had no effect on the *horizontal* component of square-wave jerk directions (Fig. 4(C) and (D)), suggesting that square-wave jerks occurred in response to cue onset and that microsaccades are not random events.

We believe that the lagging edges of square-wave jerks reflect attention shifts back to the FP in the pro-cue task. These shifts occurred because the task requirement of maintaining *gaze fixation* resulted in a high salience of the FP. Suggestive evidence for the existence of such shifts during fixation tasks has in fact been reported earlier—with the observed effects sometimes being described as inhibition-of-return mechanisms (Collie et al., 2000; Maruff et al., 1999). Moreover, it is interesting to note that the latencies of the lagging edges of square-wave jerks from the time of occurrence of the leading edges were similar to the latencies of those leading edges from cue onset. This observation is evident in Fig. 5 where it can be seen that the time interval between the two edges of a square-wave jerk varied between approximately 150 and 400 ms, with an average value of approximately 290 ms. Of course it may be argued that the lagging microsaccades of square-wave jerks reflect sensory correction mechanisms that are invoked as a result of the occurrence of the leading microsaccades. This explanation, however, seems to be ruled out by our

analysis of single-sided microsaccades, as will be seen next.

3.3. Single-sided microsaccades as leading/lagging edges of incomplete square-waves

Fig. 6(A) shows the latency distribution of single-sided microsaccades in the pro-cue task. As can be seen, single-sided microsaccades had latencies from cue onset that seemed to exhibit a wider variation than square-wave jerk leading edges (Fig. 4(A) and (B)). However, if one measures the latency distribution of both leading *and* lagging edges of square-wave jerks, one obtains the latency distribution shown in Fig. 6(B), which is expected given the distributions of Figs. 4 and 5. As can be seen, the distributions for single-sided microsaccades and square-wave jerks are very similar. This suggests that, based on latency from cue onset, single-sided microsaccades may represent either the leading or lagging edges of square-wave jerks in which the other edges are successfully suppressed by the brain's fixation system. However, the directions of the lagging edges of square-wave jerks are by definition opposite those of the leading edges. So, microsaccades that were part of a square-wave jerk exhibited a reversal of direction with time from cue onset. If single-sided microsaccades were indeed components of incomplete square-wave jerks, then an analysis of their directions as a function of time from cue onset should reveal a similar reversal.

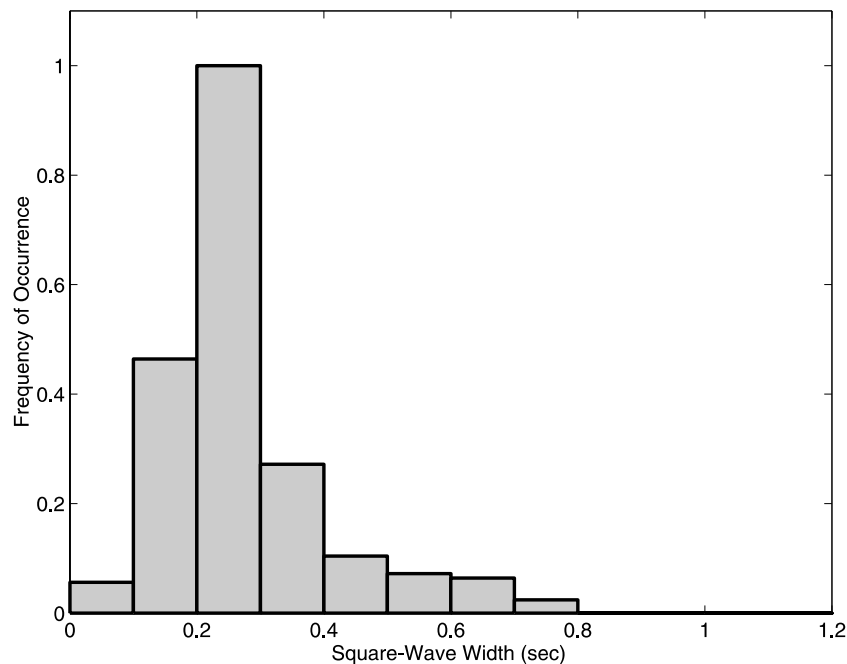


Fig. 5. Normalized histogram of the time interval between the leading and lagging microsaccades of a square-wave jerk. The distribution shown is similar to the distribution of leading microsaccade latencies from cue onset (Fig. 4(A) and (B)).

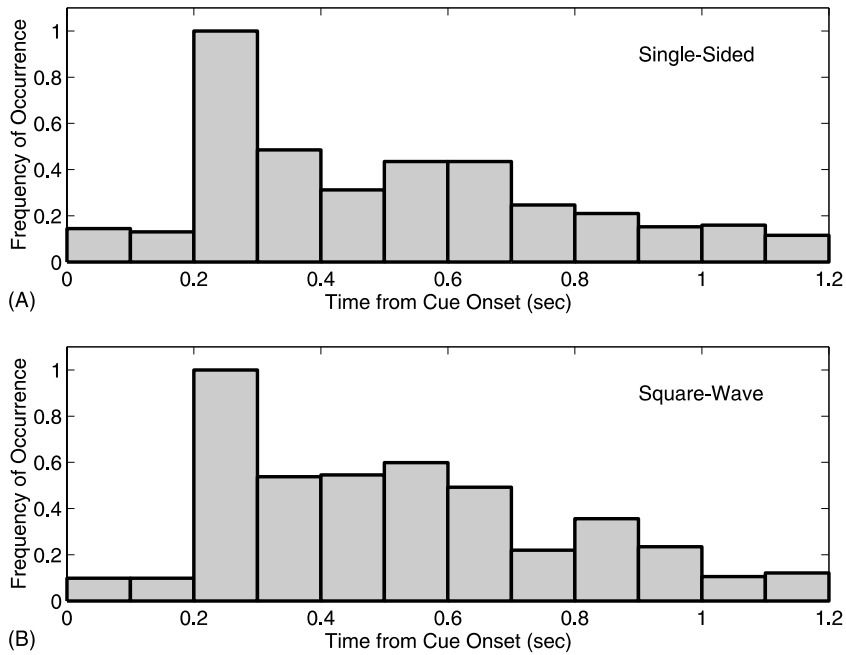


Fig. 6. Single-sided microsaccade latencies from cue onset were similar to those of the components of square-wave jerks. (A) Normalized distribution of single-sided microsaccade latencies from cue onset. (B) Normalized distribution of the latencies of both leading and lagging edges of square-wave jerks.

Fig. 7(A) shows the fraction of single-sided microsaccades that were directed to the right as a function of

the time of occurrence of those movements from cue onset in the pro-cue task. As can be seen, single-sided

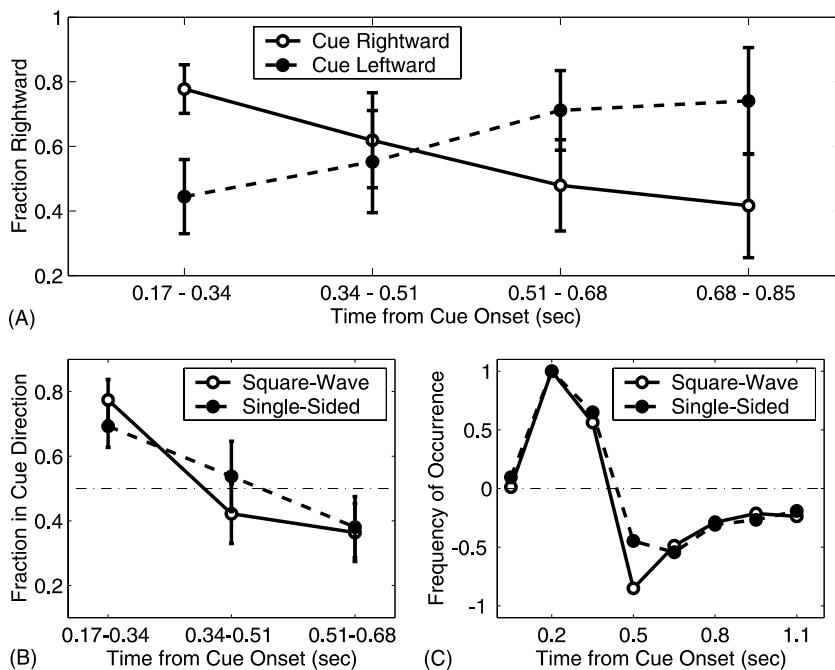


Fig. 7. Reversal of microsaccade directions with time from cue onset. (A) We plotted the fraction of rightward, single-sided microsaccades observed at different times after cue onset. Single-sided microsaccades exhibited a reversal of direction with time from cue onset. (B) Measuring the directions of leading/lagging components of square-wave jerks as a function of time revealed that the reversal observed in (A) for single-sided microsaccades mimicked the inherent reversal in square-wave jerks. (C) Normalized latency histograms for single-sided microsaccades and square-wave jerk components. Positive points count movements in the direction of the cue; negative points count movements away from the cue. Error bars in (A), (B) show the 95% confidence limits for the points plotted.

microsaccades that occurred soon after cue onset were predominantly in the direction of the cue, whereas those that occurred later were in the opposite direction. *Vertical* cues resulted in no similar reversal of *horizontal* single-sided microsaccade direction, again providing evidence that microsaccades are not random movements. So, single-sided microsaccades did appear to represent either the leading or lagging edges of incomplete square-wave jerks. The data in Fig. 7(B) and (C) support this conclusion even further. In particular, Fig. 7(B) shows the fraction of microsaccades that were in the direction of the (horizontal) cue as a function of the time of occurrence of such microsaccades from cue onset. In this figure, data is shown for square-wave jerk components, without classifying pairs of microsaccades as square-wave jerks, as well as for single-sided microsaccades. As can be seen, the reversal of single-sided microsaccade directions was similar to the reversal inherent in square-wave jerks. This is also evident in Fig. 7(C), which shows latency histograms similar to those of Fig. 6 but with microsaccade directions explicitly differentiated. In this figure, positive points show the distributions of movements that were in the direction of the cue up to the third latency bin, and negative points show the distributions of movements that were opposite the cue after the third latency bin. Whether we looked at square-wave jerk components or single-sided microsaccades, we observed more movements in the direction opposite the cue than towards it after the third latency bin. For this reason, we did not present data for either long latency microsaccades in the direction of the cue or short latency microsaccades opposite the cue in this figure.

It may also be observed from Fig. 7(A) that there was a general rightward bias in single-sided microsaccade directions even when the cue was to the left of fixation. This bias could be attributed to our reading direction (Abed, 1991; Singh, Vaid, & Sakhuja, 2000), or it could reflect hemispherical asymmetries in the brain (Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990). Either way, it is similar to rightward *attentional* biases that have been reported earlier (Reuter-Lorenz et al., 1990), an observation that supports our hypothesis that microsaccades reflect covert attention shifts.

3.4. Microsaccade direction and a behavioral measure of covert attention

The evidence provided thus far suggests that *microsaccade direction* behaved in a very systematic fashion in relation to *cue direction* in the pro-cue task. Short latency microsaccades were predominantly directed towards the recently onset cue, and long latency microsaccades were predominantly directed away from this cue. We now wish to ascertain whether this behavior was consistent with the patterns of *covert at-*

tention shifts that took place in our study. In other words, did attention really shift covertly or were microsaccades simply responses to sensory events in our displays? The fact that single-sided microsaccades exhibited a reversal of direction with time from cue onset seems to rule out the possibility that microsaccades were purely sensory reflexes that were elicited by cue onset. Clearly, there were no sensory transients in our displays when long latency microsaccades—whether single-sided or lagging edges of square-wave jerks—occurred. The reversal of single-sided microsaccade direction also rules out the possibility that the lagging edges of square-wave jerks were simply corrective movements that were triggered as a result of the occurrence of the leading edges. This is so because long latency single-sided microsaccades were directed *away* from the cue despite the fact that there were no microsaccades *towards* the cue to correct for. This, added with evidence from the literature that visual transients (such as cue onset) attract attention (Egeth & Yantis, 1997; Posner, 1980), suggests that microsaccades do reflect covert attention shifts.

To further support the above claim, we sought to compare the time courses of microsaccade directions mentioned in this paper with the time courses of attentional benefits and costs on behavioral performance. We did this for the pro-cue task as well as for the anti-cue task. Both tasks involved the appearance of a spatial cue, but the expected patterns of attentional benefits and costs associated with this cue were complementary in the two tasks. In other words, an attention shift to the cue in the anti-cue task was a shift *away* from the location of a color flash, whereas a similar shift in the pro-cue task was one *towards* the location of the flash. Clearly, an attention shift to the cue was expected to hinder performance in one task while improving performance in the other.

Fig. 8(A) shows the time courses of microsaccade directions after cue onset in the two tasks. In this figure, microsaccade directions were defined relative to the cued target—in the direction of the cue in the pro-cue task and opposite in the anti-cue task. Also, microsaccades were not classified as square-wave jerks or single-sided movements because our earlier analysis showed that the relationship between microsaccade direction and microsaccade latency from cue onset was the same whether these movements occurred in pairs or singly. As can be seen from the figure, short latency microsaccades in the anti-cue task were predominantly directed away from the cued target. We believe that these represent exogenous attention shifts to the cue. Longer latency movements were predominantly in the direction of the target, showing a reversal of direction similar to that observed in the pro-cue task (also see Fig. 10). So, microsaccades behaved in a qualitatively similar way in relation to cue onset in both tasks (but see Section 4).

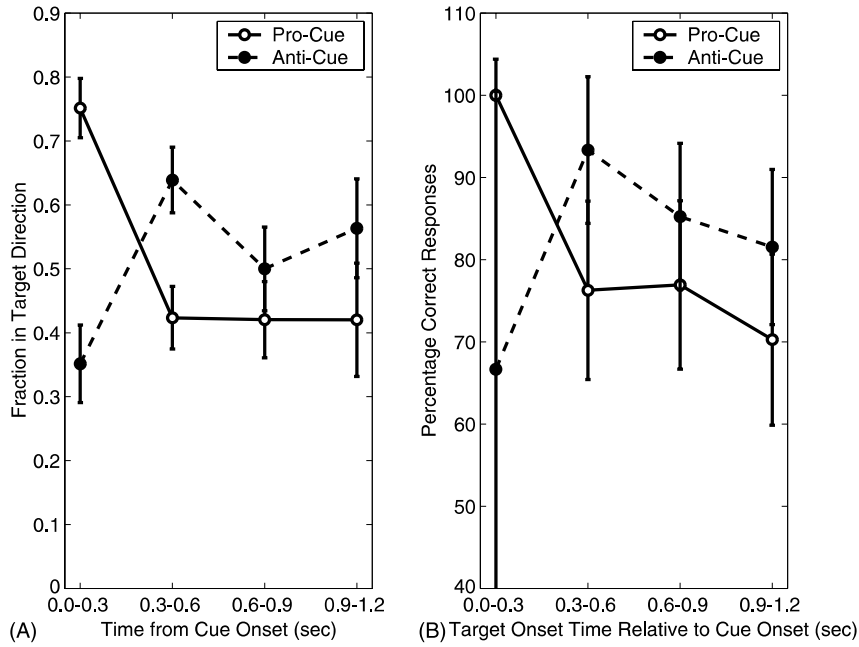


Fig. 8. Time courses of microsaccade directions and behavioral performance. (A) Microsaccades exhibited a similar reversal of direction in the anti-cue task as in the pro-cue task (Fig. 7). However, the tasks were different in the sense that microsaccade directions relative to the cued targets were complementary in the two tasks. (B) This complementary nature was also evident in subjects' behavioral performance in final horizontal trials containing microsaccades. Error bars show 95% confidence intervals.

However, the time courses of their directions relative to the target were complementary.

As mentioned above, a similar complementary nature in the time courses of subject performance in the two tasks was also expected, and evidence for it was indeed

observed, as shown in Fig. 8(B). This figure plots the percentage of correct responses to the target color flashes as a function of the time of occurrence of these flashes from cue onset in trials containing microsaccades. In this figure, we only considered cases in

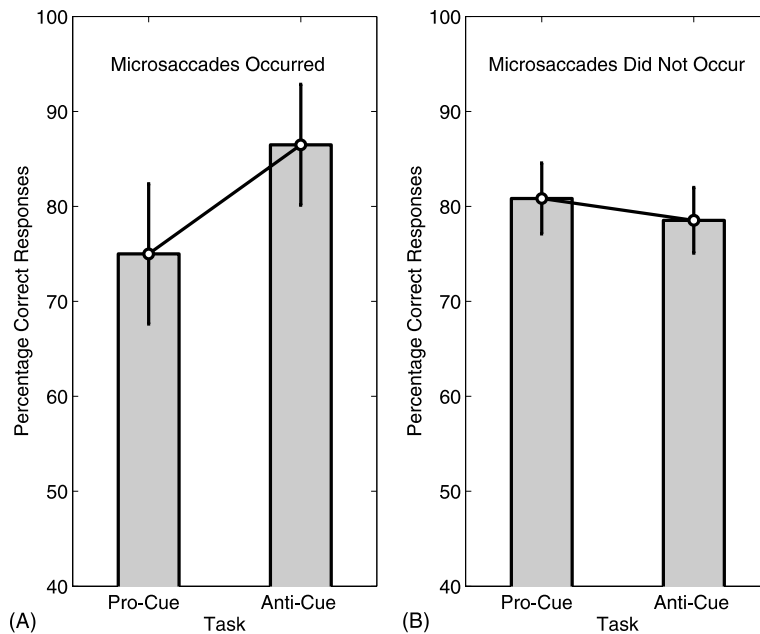


Fig. 9. Correlating microsaccades and attention through measures of behavioral performance. (A, B) For times in which microsaccades were predominantly directed away from the cue (400–1000 ms), performance in the anti-cue task was better than in the pro-cue task. Performance was the same in both tasks when microsaccades did not occur.

which target flashes happened in a horizontal direction, since we were interested in comparing behavioral performance to horizontal microsaccade occurrences. For short latency color flashes in the pro-cue task (0–300 ms), subjects performed very well because the focus of attention had shifted to a location closer to the target. For longer latencies, performance deteriorated. This is expected based on previous work on the dynamics of attentional benefits and costs associated with peripheral cues (Collie et al., 2000; Maruff et al., 1999; Nakayama & Mackeben, 1989). But, what is more interesting is that the time course shown in Fig. 8(B) is surprisingly similar to the time course of reversal of microsaccade directions (Fig. 8(A)). Moreover, for the anti-cue task, we observed an *opposite* effect on subject performance with time from cue onset. Long latency color flashes resulted in increased performance when compared to short latency ones. This increase was again expected based on previous work on the dynamics of covert attention (Collie et al., 2000; Maruff et al., 1999; Nakayama & Mackeben, 1989)—cue onset summoned transient attention *away* from the target at short latencies—and it was mirrored by a reversal of microsaccade directions, now from being away from the target at short latencies to being towards the target at longer latencies.

We analyzed behavioral performance further in Fig. 9. In particular, we assessed the performance of subjects in trials in which color flashes happened between 400 and 1000 ms from cue onset. These times were chosen because they covered the period in which microsaccades (Figs. 7 and 8(A)) exhibited a marked reversal of roles between the two tasks. Also, these times covered the period in which attentional costs (benefits in the case of the anti-cue task) associated with peripheral cues were expected to set in (Collie et al., 2000; Maruff et al., 1999; Nakayama & Mackeben, 1989). Fig. 9(A) shows a result similar to that shown in Fig. 8(B): performance was worse in the pro-cue task than in the anti-cue task in trials containing microsaccades ($\chi^2 = 5.02$; $p < 0.05$). In trials in which microsaccades *did not* occur (Fig. 9(B)), there was no appreciable difference between the two tasks, suggesting that attention may not have shifted during those trials.

4. Discussion

This paper presented evidence that microsaccadic eye movements reflect covert attention shifts. We employed a spatial cueing paradigm to elicit covert attention shifts, and we observed two main forms of microsaccade occurrences: square-wave jerks and single-sided microsaccades. The time courses of microsaccade directions suggest that square-wave jerks corresponded to attention shifts towards the cue in our tasks and then back to fixation. Single-sided microsaccades seemed to represent

single edges of square-wave jerks for which the other edges were successfully suppressed. Analysis of subject performance in our two tasks revealed evidence that the time course of subject performance was correlated with the time course of microsaccade directions, suggesting that attention shifts are associated with microsaccades. In the following paragraphs, we briefly discuss several issues that relate to our work, starting with methodology and then moving on to potential practical and theoretical implications.

First, concerning our methodology, we employed an upper threshold on microsaccade size of 1° , with larger movements being viewed as regular, overt saccades. Some would argue that this threshold is excessively large and that the movements we studied were, therefore, not ‘microsaccadic’ in nature. However, we would like to argue otherwise. In particular, we believe that the issue of differentiating between microsaccades and regular saccades is better resolved by the functional role of these movements than by their size. This is so because based on movement dynamics alone (Fig. 3(A)), putting a threshold on the maximum possible size of a microsaccade is arbitrary. This arbitrariness is exemplified by the fact that this threshold is variable in the existing literature on microsaccades. Some authors have used a threshold of $10'$ of arc (Steinman et al., 1973) whereas others have used a threshold of 2° (Martinez-Conde et al., 2000). Bridgeman and Palca (1980) have acknowledged the fact that the maximum size of microsaccades is a matter of definition, and Winterson and Collewijn (1976) reported microsaccades as large as $33'$ of arc even though they suggested that microsaccades are movements that are less than $10'$ of arc. Having said that, it should be noted that the main common feature in all of the above examples and others is that the movements studied were made *during fixation*. This is also true in our case. Given this, we believe that our threshold of 1° for maximum microsaccade size was conservative enough to control for or ensure fixation. It is interesting to note, however, that, despite this threshold, most (84%) of our microsaccades were actually less than 0.5° or $30'$ of arc in size, which is well within the range that many authors have used to define microsaccades. It is also interesting to note that our results still hold with different upper and lower thresholds on ‘microsaccade’ size than the ones we used in this paper. In particular, we tried replicating our analyses for movements that were only in the range of 0.12 – 0.5° as well as for movements that were only in the range of 0.5 – 1° . In both cases, the same basic observations that we presented in this paper were made.

We now move on to the potential utility of our work. Our results suggest that microsaccades may be used as an overt measure of covert attention shifts. Even though covert attention has been measured indirectly in the past (see for example Carrasco, Penpeci-Talgar, & Eckstein,

2000; Egeth & Yantis, 1997; Jonides, 1981; Nobre et al., 2000; Posner, 1980; Weichselgartner & Sperling, 1987; Yeshurun & Carrasco, 1998), no obvious observable parameter exists for tracking covert attention overtly. The practical implications of the existence of such a parameter are numerous. In particular, any application that involves monitoring how people ‘look’ at their visual environment may use such a parameter whenever the locus of spatial attention is misaligned with gaze direction. Microsaccades may perform the role of such a parameter. However, we only related the *directions* of microsaccades with those of covert attention. So, based on the evidence provided in this paper, microsaccades only provide limited information about the allocation of covert spatial attention. While future studies could reveal that microsaccade amplitude¹ is related to the amplitude of attention shifts, microsaccade direction alone may be useful if combined with image-based measures of salience in order to yield a statistical model of attentional allocation.

Our work also has important theoretical implications. In particular, no convincing explanations exist in the literature as to how and why microsaccades are generated. Our results, however, suggest that microsaccades may arise as a result of subliminal activation of the oculomotor system by covert attention shifts. In what follows, we briefly argue why our theory of microsaccade generation is plausible.

First, microsaccades have the same dynamics as larger saccades (Zuber et al., 1965). This led Zuber et al. (1965) and others to conclude that microsaccades are generated by the same system responsible for saccade generation. So, one can now ask whether the organization of the oculomotor system as we know it can allow for the existence of influences of covert attention shifts on motor programming. There is a large body of evidence pointing to such influences, but perhaps the clearest evidence comes from direct recording in the SC during tasks involving covert attention shifts (Kustov & Robinson, 1996). The SC is known to contain a spatial map of motor space (Lee et al., 1988). Neurons in this map exhibit patterns of mutual inhibition such that saccades are generated when neurons in a certain area of the map win in a winner-take-all competition with neurons representing the foveal or fixation zone (Hafed & Clark, 2000; Munoz & Istvan, 1998). When attention shifts to a peripheral target, neurons in the sensory and motor layers of the SC encoding the position of that target exhibit transient activity (Kustov & Robinson, 1996) that we believe acts to weaken the neural responses in the collicular fixation zone. This in turn re-

duces the strength of the excitatory signals that are known (Gandhi & Keller, 1997) to project from this zone to brainstem omnipause neurons, which act as the gating mechanism for saccades (Everling, Paré, Dorris, & Munoz, 1998). This reduction may be just enough to momentarily shut down or reduce the activity of these neurons, thus allowing the transient activity on the SC to move the eyes. It is interesting to note here that malfunctioning omnipause neurons have already been suggested as the cause of microsaccadic flutter, which is a disorder of microsaccades characterized by fast oscillations of back-to-back movements (Ashe, Hain, Zee, & Schatz, 1991). As for the sources of attentional signals in the SC, the SC is known to receive projections from the lateral intraparietal area (LIP) (Paré & Wurtz, 1997) and the frontal eye fields (FEF) (Sommer & Wurtz, 1998), areas in which the salience of spatial locations seems to be encoded (Fuster, 2000; Kusunoki, Gottlieb, & Goldberg, 2000).

The above description of microsaccade generation can explain why microsaccades, despite being referred to in general as *involuntary* eye movements (Bell et al., 1959; Cornsweet, 1956; Martinez-Conde et al., 2000), may be suppressed voluntarily (Steinman, Cunitz, Timberlake, & Herman, 1967) and during ‘high acuity’ visual tasks (Bridgeman & Palca, 1980; Winterson & Collewijn, 1976). Such tasks require focused attention, which in our view means fewer microsaccades. Also, it has been argued that microsaccades are “busy work” and that they may affect vision adversely (Steinman et al., 1973). However, it is well known that stabilization of retinal images causes fading of vision (Pritchard, 1961), and as mentioned by Martinez-Conde et al. (2000), the fact that slow control on its own can prevent retinal image stabilization (Steinman et al., 1973) does not rule out the possibility that microsaccades also help in performing this role. Recent neurophysiological evidence suggests that microsaccades do indeed play an important role in ‘refreshing’ retinal images in order to maintain perception (Leopold & Logothetis, 1998; Martinez-Conde et al., 2000). It is still, however, unclear what events elicit microsaccade generation. If the role of microsaccades is indeed to help maintain perception, then our results suggest that the visual system achieves such maintenance by making use of the existing infrastructure for oculomotor control to periodically generate microsaccades.

One final note concerns the differences between the two tasks we ran. It was mentioned that microsaccades behaved in a qualitatively similar manner in the two tasks (Fig. 8(A)). However, closer inspection of the patterns of microsaccades reveals differences that cannot be attributed to sensory mechanisms—since the two tasks had identical sensory stimuli. In particular, microsaccades were generally less frequent in the anti-cue task than in the pro-cue task. Also, Fig. 10 shows the data in Fig. 8(A) with a finer time resolution and with

¹ Our data do suggest that microsaccade amplitude could reveal valuable information related to the attention shifts that took place in our tasks, but we cannot make any explicit conclusions here without further experimentation.

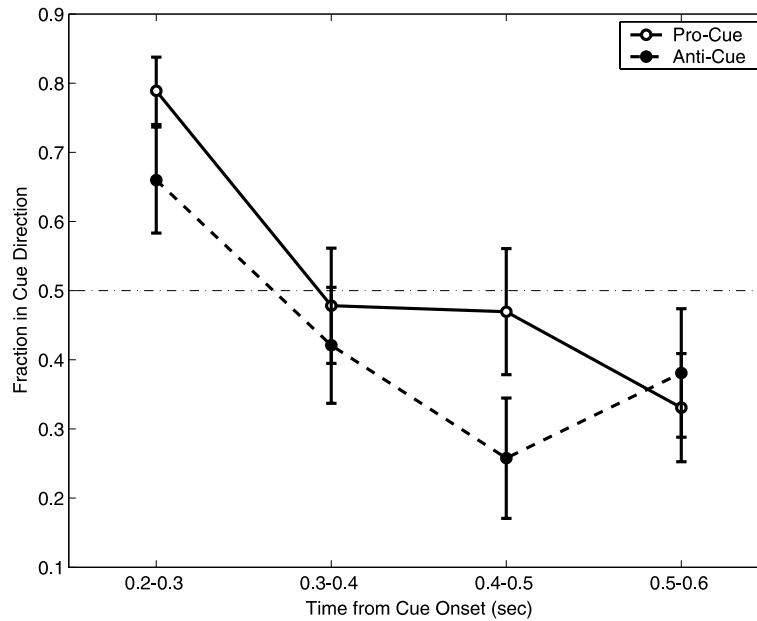


Fig. 10. Changing the requirements on attention modified the time course of microsaccade occurrences after cue onset. We plotted the fraction of microsaccades in the direction of the cue at different latencies from cue onset for both tasks. There were fewer microsaccades in the direction of the cue at short latencies in the anti-cue task than in the pro-cue task. Moreover, at 400 ms, we were equally likely to observe movements towards the cue or away from it in the pro-cue task, whereas there was a clear bias away from the cue in the anti-cue task. Error bars show the 95% confidence limits for the points plotted.

microsaccade directions defined relative to *cue* direction rather than *target* direction. Notice that between 200 and 300 ms from cue onset, there were fewer microsaccades in the direction of the cue in the anti-cue task than in the pro-cue task. Also, by 400 ms, there was a clear bias of microsaccade directions *away* from the cue in the anti-cue task, whereas we were equally likely to observe a movement towards the cue or away from it in the pro-cue task (clear reversal in the pro-cue task was evident at longer latencies). We believe that the *salience* of various stimuli differed in our two tasks, and it was salience, not just sensory information, that influenced microsaccade directions. Our results as they stand suggest that microsaccades at the very least reflect exogenous attention shifts (Egeth & Yantis, 1997; Jonides, 1981; Posner, 1980). While we believe that our tasks had endogenous (Egeth & Yantis, 1997; Jonides, 1981; Posner, 1980) components of attention to them, future experiments with symbolic cues can reveal in a clearer fashion the influences of endogenous attention shifts on microsaccades.

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