Shift and deviate: Saccades reveal that shifts of covert attention evoked by trained spatial stimuli are obligatory

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The premotor theory of attention predicts that motor movements, including manual movements and eye movements, are preceded by an obligatory shift of attention to the location of the planned response. We investigated whether the shifts of attention evoked by trained spatial cues (e.g., Dodd & Wilson, 2009) are obligatory by using an extreme prediction of the premotor theory: If individuals are trained to associate a color cue with a manual movement to the left or right, the shift of attention evoked by the color cue should also influence eye movements in an unrelated task. Participants were trained to associate an irrelevant color cue with left/right space via a training session in which directional responses were made. Experiment 1 showed that, posttraining, vertical saccades deviated in the direction of the trained response, despite the fact that the color cue was irrelevant. Experiment 2 showed that latencies of horizontal saccades were shorter when an eye movement had to be made in the direction of the trained response. These results demonstrate that the shifts of attention evoked by trained stimuli are obligatory, in addition to providing support for the premotor theory and for a connection between the attentional, motor, and oculomotor systems.

When we interact with our complex daily environment, there are numerous potential actions that can be performed. Selecting and executing the responses that are most appropriate in a given context—for instance, a grasp or an eye movement—is key to successful goal-directed behavior. The premotor theory of attention claims that attentional shifts are involved in preparing and executing a response, irrespective of the response modality (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). More explicitly, this theory states that whenever a motor response is prepared, there is an automatic shift of covert attention to the location to which the motor response is programmed.

Indeed, there is ample evidence that the programming of an eye movement is associated with a shift of covert attention (Deubel & Schneider, 1996; Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel & Theeuwes, 2007). For instance, performance on a letter identification task is higher at the location of a subsequent eye movement than at other locations (Deubel & Schneider, 1996; Van der Stigchel & Theeuwes, 2005). Moreover, the link between attention and manual movements has been revealed by studies that have shown superior visual discrimination for locations close to the target of a goal-directed manual movement (Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; Deubel, Schneider, & Paprotta, 1998; Schiegg, Deubel, & Schneider, 2003).

A recent study by Dodd and Wilson (2009) provided additional evidence for the premotor theory by showing that learning to associate an arbitrary central cue with a horizontal motor movement influenced target detection of stimuli presented on the horizontal plane. Participants initially performed a target detection task in which a nonpredictive cue (a blue or green color patch) appeared at fixation prior to a left/right target; unsurprisingly, reaction time to detect the target was unaffected by the cue. The initial session was followed by a training session in which participants were trained to associate the colors blue and green with left and right space: A color patch was presented on each trial, and the participants were required to execute a motor movement (a directional response, using a joystick) to the left or to the right, depending on the color of a central cue. After this training session, the participants again performed the target detection task with a nonpredictive blue or green cue. Now, however, when the association of the central cue was congruent with the target location (as dictated by the previous training session), the participants were faster to respond to targets, relative to when the association of the cue and target was incongruent. This indicates that a shift of attention occurred to the target location, even though the cue was nonpredictive. According to the authors, the shifts of attention evoked by

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an arbitrary central cue were completely obligatory and were caused by the learned spatial properties of the central cue, in a manner similar to the automatic shifts of attention evoked by central numbers (Dodd, Van der Stigchel, Leghari, Fung, & Kingstone, 2008; Fischer, Castel, Dodd, & Pratt, 2003), arrows, and directional words (Hommel, Pratt, Colzato, & Godijn, 2001; Pratt & Hommel, 2003).

The present study investigated whether the shifts of attention evoked by trained spatial stimuli are truly obligatory by using an extreme prediction of the premotor theory: If attention is the common mechanism underlying the execution of both manual and eye movements, an obligatory shift of attention evoked by a central cue learned using manual movements should be reflected in an eye movement executed in the presence of this cue. This effect would then be caused by a common attention mechanism underlying both response modalities.

EXPERIMENT 1

In Experiment 1, we used the same methodology as Dodd and Wilson (2009), but in the pre- and the posttraining blocks, participants had to make an eye movement to a target presented either above or below fixation. If the training session caused individuals to associate color with space, leading to an obligatory shift of attention in the direction consistent with the color, this should be reflected in an eye movement in the posttraining block. More explicitly, we expected that the eye movement trajectory to the target presented on the vertical meridian would be influenced by the obligatory shift of covert attention as evoked by the presence of the central cue. Eye movement trajectories have been shown to deviate from a location in space where attention is allocated (Sheliga et al., 1994; Van der Stigchel, Meeter, & Theeuwes, 2007). A horizontal shift of covert attention would therefore be reflected in a deviation of the vertical eye movement trajectory, although the participant would be unaware of this.

During the training, the participants learned an association between colors and motor movements, as well as an association between colors and the shifts of attention that accompanied motor movements. The activation of a specific response program by the nonpredictive cue

would then be accompanied by a covert shift of attention in the posttraining block, reflected in a deviation of the eye movement trajectory. Note that both the manual and the eye movement tasks did not require a covert shift of attention to the left or to the right, since the target always appeared on the vertical meridian. Therefore, training effects or carryover effects were unlikely. If, indeed, a trajectory deviation was observed in the posttraining block, this would show that the shifts of attention evoked by the central cue were completely obligatory.

In the pre- and posttraining blocks, there were three possible intervals between the presentations of the cue and the target (100, 500, and 800 msec). Dodd and Wilson (2009) observed training effects for all three intervals, but in their study, all responses were performed in the same horizontal plane. In the present study, motor responses were made in the horizontal plane in the training phase but were made in the vertical plane in the pre- and posttraining blocks. It was therefore difficult to predict whether consistent training effects would be observed at all intervals.

Method

Participants

Fourteen undergraduate students at the University of Nebraska, Lincoln, volunteered in exchange for course credit. All the participants had normal or corrected-to-normal vision and were naive as to the purpose of the experiment. All persons gave their informed consent prior to their inclusion in the study.

Apparatus

Eye movements were recorded by means of a video-based eyetracker (SR Research, Canada). The EyeLink II system has a 500-Hz temporal resolution and a spatial resolution of 0.025°. An eye movement was considered a saccade either when the movement velocity exceeded 35°/sec or when the movement acceleration exceeded 9,500°/sec². The participants performed the experiment in a soundattenuated and dimly lit room.

Procedure

The experiment consisted of three blocks of trials, and all the participants completed the blocks in the same order. These will be outlined in turn.

Pretraining block. See Figure 1 for an overview of a typical trial sequence. At the beginning of each trial, a white circle (1° in diameter) was presented at the center of the screen. Following a period of 500 msec, the color of the fixation circle changed from white to

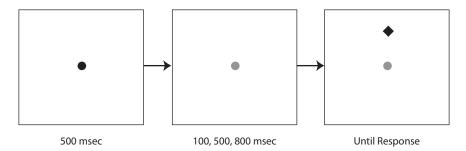


Figure 1. Sequence of a typical trial in the pretraining and posttraining blocks of Experiment 1. At the beginning of each trial, a white circle was presented at the center of the screen. Following a period of 500 msec, the color of the fixation circle changed from white to either blue or green. After a stimulus onset asynchrony of 100, 500, or 800 msec, a white diamond-shaped stimulus was presented either directly above or below the central circle. This element was the target for the eye movement, which had to be made as quickly as possible.

either blue or green. The participants were informed that the color of the fixation circle was irrelevant to their task and did not predict the location of the upcoming target. After a variable stimulus onset asynchrony (SOA) of 100, 500, or 800 msec, a white diamond-shaped stimulus ($1.25^{\circ} \times 1.25^{\circ}$) was presented either directly above or below the central circle. This element was the target for the eve movement, which was to be made as quickly and as accurately as possible. The distance between the target and the central circle was 6.5°. The participants were instructed to fixate the center fixation point until the onset of the target and to then move their eyes to the target location. It was stressed that one had to make a single accurate saccade toward the target element. The participants heard a short error tone when the saccade latency was higher than 600 msec or shorter than 80 msec. Each target location and color of the fixation circle was equally probable. The participants were explicitly informed that the color of the fixation circle was not predictive in the task.

Training block. During the training block, no eye movement had to be made. Rather, the display consisted solely of the fixation circle, which started off white and then turned blue or green following a period of 500 msec. The participants were instructed to fixate on this circle for the entire block and to make a directional response using a Gravis Destroyer joystick: When the fixation circle turned blue, the participants were to move the joystick to the left as quickly as they could, and when the fixation circle turned green, the participants were to move the joystick to the right as quickly as they could. The moment a joystick motion was made that surpassed a certain threshold (the equivalent of 100 pixels on the *x*-axis), the trial terminated. If the participants failed to move the joystick after 1,000 msec or if they moved the joystick in the incorrect direction on the *x*-axis, a short error tone was presented. The next trial began 500 msec after each response.

Posttraining block. The posttraining block was identical to the pretraining block, with the color of the fixation cue again being independent of the task. The participants were instructed to fixate the center fixation point until target onset and to then move their eyes to the target location as quickly and as accurately as possible.

Design

The pretraining and the posttraining blocks each consisted of 240 trials. Short breaks were offered every 30 trials. The training block consisted of 800 trials, with short breaks being offered after every 200 trials.

Data Analysis

Saccade latency was defined as the interval between target onset and the initiation of a saccadic eye movement. If saccade latency was lower than 80 msec, higher than 600 msec, or further than two and a half standard deviations away from the mean latency, the trial was removed from the analysis. Moreover, trials were excluded from analysis in which no saccade or a too small first saccade (<3°) was made. Furthermore, the initial saccade starting position had to be within 1° from the center fixation point. If the endpoint of the first saccade had an angular deviation of less than 22.5° from the center of the target, the saccade was classified as having landed on the target. In other situations, the saccade was classified as an error and was not analyzed.

Saccade trajectories to the target location were examined by calculating the mean angle of the actual saccade path, relative to the mean angle of a straight line between the starting point of the saccade and the saccadic target. The angle of the actual saccade was calculated for each 2-msec sample point by examining the angle of the straight line between the starting point of the saccade and the current sample point. Angles were averaged across the whole saccade and were subtracted from the angle of the straight line between fixation and the target location (for a more detailed overview of saccade trajectory computation, see Van der Stigchel, Meeter, & Theeuwes, 2006). To compute the influence of the color of the fixation circle on saccade trajectories, we subtracted the mean deviation value of

the blue and the green fixation circle trials. If there was no effect of the color of the fixation circle, this difference should be zero. Deviations were signed so that a positive value indicated deviation toward the direction associated with the color (i.e., during the training session) and a negative value indicated deviation away from the direction associated with the color. This way, we also accounted for the natural directional biases that exist in saccade trajectories (Van der Stigchel et al., 2006), because these directional biases should be present for both color trials. Trials on which the saccade deviation was two and a half standard deviations away from the mean outcome were removed from the analysis.

Results and Discussion

Excluded Trials

On the basis of the above-mentioned requirements, 13.8% of the trials were excluded pretraining and 12.8% of the trials were excluded posttraining.

Training Block

The mean reaction time in the training block was 604 msec, with an error rate of 1.2%.

Saccade Latency

An ANOVA with session (pretraining, posttraining) and SOA (100, 500, 800 msec) as factors revealed a main effect of session [F(1,13) = 4.94, p < .05]. Saccade latencies were significantly longer pretraining (M =195 msec, SD = 23) than posttraining (M = 184 msec, SD = 18). This is unsurprising, since saccade latencies decrease over time as a function of practice. There was also a main effect of SOA [F(2,26) = 16.97, p <.0001]. All three SOAs differed significantly from each other (ps < .02), with the 100-msec SOA having the longest latency (M = 203 msec, SD = 26), followed by the 500-msec SOA (M = 189 msec, SD = 20). Saccade latencies were the shortest for the 800-msec SOA (M =176 msec, SD = 17), reflecting a standard foreperiod effect. The interaction between session and SOA was not significant (F < 1).

Saccade Trajectory Deviation

An ANOVA with session (pretraining, posttraining) and SOA (100, 500, 800 msec) as factors revealed no main effect of session (F < 1) or SOA (F < 1). The interaction between session and SOA was marginally significant [F(2,26) = 2.80, p = .08; see Figure 2].

For each SOA, t tests were conducted to determine whether the deviation was significantly different from zero. Pretraining, there was no SOA for which the deviation was significantly different from zero (ps > .20). Post-training, the deviation was significant for the 500-msec SOA [t(13) = 2.53, p < .03]; saccade trajectories deviated toward the trained direction (e.g., when the fixation circle was blue, the eye tended to deviate to the left, whereas when the fixation circle was green, the eye deviated to the right). Deviations in the other SOAs posttraining were not significant (ps > .30). Comparing pre- and posttraining, the 500-msec SOA was the only SOA in which the deviation was significantly different posttraining than pretraining [t(13) = 2.26, p < .05; other ps > .10].

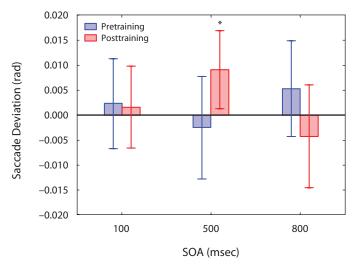


Figure 2. Experiment 1: Saccade deviations pre- and posttraining for all three tested stimulus onset asynchronies (SOAs). Error bars indicate 95% confidence intervals.

After a training session in which the participants were trained to associate a color cue with a horizontal manual movement, eye movement trajectories deviated toward the trained direction in a subsequent saccade task (i.e., when the fixation circle was blue, the eye tended to deviate to the left, whereas when the fixation circle was green, the eye deviated to the right). This was consistently observed for one of three intervals between cue presentation and target onset.

The finding that a significant deviation was observed for only one interval (500 msec) may seem inconsistent with the findings of Dodd and Wilson (2009), who showed training effects for all three tested intervals (100, 500, and 800 msec). It is worth noting, however, that the cuing effects normally observed with other central nonpredictive cues (e.g., arrows, numbers) are usually most apparent at SOAs of about 500 msec and are not typically observed at earlier SOAs (e.g., Fischer et al., 2003). Moreover, it is important to note that the responses of the participants were very different between the present study and that of Dodd and Wilson. In the present study, the participants had to make vertical eye movements in the posttraining block, whereas Dodd and Wilson had participants perform a target detection task. Because target detection had to be performed for a target presented on the horizontal plane, it is perhaps not surprising that the effects of attention shifts are more robust for tasks performed on the horizontal plane. To test this hypothesis, we performed an additional experiment in which the task in the pre- and posttraining blocks was performed in the horizontal direction. The participants executed an eye movement to a target that was presented on the horizontal meridian.

Furthermore, in the previous experiment, we did not monitor eye movements during training, given that participants are generally good at following instructions to maintain fixation. It is possible, however, that if the participants made eye movements in the direction of the motor movement, our results might be explained by a motor association, rather than by covert shifts of attention. In the present experiment, gaze was monitored with a closed circuit camera system to ensure that eye movements were not being made.

EXPERIMENT 2

Method

Participants

Ten undergraduate students at the University of Nebraska, Lincoln, volunteered in exchange for course credit. All the participants had normal or corrected-to-normal vision and were naive as to the purpose of the experiment. All the persons gave their informed consent prior to their inclusion in the study.

Apparatus, Procedure, Design, and Data Analysis

The only difference between the present experiment and Experiment 1 was the location of the target for the eye movement in the pretraining and posttraining blocks. The target was presented on the horizontal meridian instead of the vertical meridian, as in Experiment 1. The distance from the central fixation point was the same as that in the previous experiment (6.5°).

We controlled for eye movements during the training block, using a closed circuit video. This method of eye movement monitoring does not allow for the removal of any data but does provide the experimenter the opportunity to remind the participants not to make eye movements if any are detected. Eye movements were rare or nonexistent for all the participants.

As opposed to saccade trajectory, which was the critical measure in Experiment 1, our focus in the present experiment was saccade latency. The same requirements were used as in Experiment 1, except the requirement that excludes outliers in terms of saccade trajectory deviations (note that we did not measure trajectory deviations in this experiment).

For both the pretraining and posttraining blocks, an ANOVA was run with SOA (100, 500, 800 msec) and cue congruency (congruent, incongruent) as factors. Cue congruency refers to the relation between the cue and the target location as defined by the training block. For example, if the color of the cue was blue and the target was presented to the left, the trial was congruent. If the color of the cue was blue and the target was presented to the right, the trial was incongruent.

Results and Discussion

Excluded Trials

On the basis of the requirements, 9.0% of the trials were excluded pretraining and 8.4% of the trials were excluded posttraining.

Training Block

The mean reaction time in the training block was 598 msec, with an error rate of 1.6%.

Saccade Latency

Pretraining block. An ANOVA with SOA (100, 500, 800 msec) and cue congruency (congruent, incongruent) as factors revealed no main effect of SOA [F(2,18) = 2.88, p = .08] or cue congruency (F < 1). The interaction between SOA and cue congruency was not significant (F < 1).

Posttraining block. A main effect of SOA was revealed [F(2,18) = 3.92, p < .05], reflecting a standard foreperiod effect, as in Experiment 1. Again, the longest SOA had the shortest latency. The effect of cue congruency was not significant [F(1,9) = 3.17, p = .11].

Importantly, there was a significant interaction between SOA and cue congruency [F(2,18) = 6.43, p < .01]. Post hoc t tests revealed a significant difference between congruent and incongruent trials for the 500-msec [t(9) = 2.32, p < .05] and the 800-msec [t(9) = 2.50, p < .04] SOAs. For both SOAs, the congruent trials had shorter latencies than did the incongruent trials (see Figure 3). There

was no significant difference between congruent and incongruent trials for the 100-msec condition [t(9) = 1.72, p = .11], which is not surprising, given that in many studies with central cues, effects have failed to emerge until later SOAs (e.g., Dodd et al., 2008; Fischer et al., 2003).

The results of Experiment 2 show that saccade latencies were shorter in the direction of the learned cue than in the direction away from the learned cue. This was observed for two of the three tested SOAs. Because the effect on saccade trajectory deviations in Experiment 1 was observed only in one interval, the present results therefore indicate that the effects of attentional shifts evoked by trained stimuli are more robust for tasks performed in the same plane as the one with which the trained stimuli are associated.

Large eye movements during the training block cannot account for the effects observed posttraining. The experimenter who observed all the participants noted very few eye movements (with most participants not making any), and once warned, no participant made an eye movement again. It cannot be ruled out, however, that smaller eye movements during the training session influenced our results. This will be discussed further in the General Discussion section.

GENERAL DISCUSSION

The present study used a prediction of the premotor theory of attention to test whether the shifts of atten-

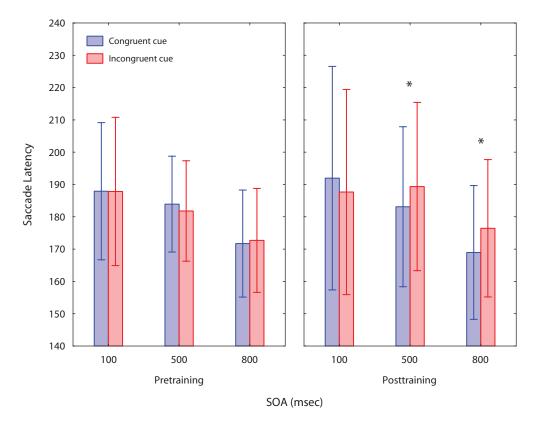


Figure 3. Experiment 2: Saccade latencies for congruent and incongruent cues in both pre- and post-training blocks. Error bars indicate 95% confidence intervals. SOA, stimulus onset asynchrony.

tion evoked by trained spatial cues are truly obligatory. Participants were trained to associate a color cue with a horizontal manual movement. Experiment 1 showed that, posttraining, trajectories of vertical eye movements to a target deviated in the direction of the trained response, despite the fact that the color cue was irrelevant. Experiment 2 showed that saccade latencies of horizontal eye movements were shorter when an eye movement had to be made in the direction of the trained response. In both experiments, three intervals between cue presentation and target presentation were tested. The finding that the effect of the cue was significant for one interval in Experiment 1 (500 msec) and for two intervals in Experiment 2 (500 and 900 msec) reveals that the effects of attention shifts are more robust for tasks performed in the same plane as that in which the response was trained.

The present study shows that shifts of covert attention evoked by trained central cues are truly obligatory. Given that different response modalities were used in the training and posttraining blocks (unlike in Dodd & Wilson, 2009), the effects of covert attentional shifts in response to trained cues were tested in an indirect way in which carryover effects were unlikely. This indicates that the training effects are not restricted to the response modality with which the training was performed. This provides strong evidence for a compulsory link between attentional shifts and trained central cues, although it is not necessarily the case that attention shifted in the presence of the cue on every trial (like exogenous cues, which also will not evoke a shift of attention on all trials). We argue that the shift of attention evoked by a trained stimulus is not the result of voluntary processes but is imposed by the association between the color of the cue and the trained direction.

The premotor theory gives a clear explanation of the present results. In the training block, the horizontal manual movements were accompanied by a horizontal shift of attention, because attentional shifts were involved in preparing and executing a response, irrespective of the response modality (Craighero et al., 1999; Deubel et al., 1998; Schiegg et al., 2003). During this training, the participants learned an association between colors and motor movements, as well as an association between colors and the shift of attention that accompanies motor movements. Although the cue was nonpredictive, the presence of the cue in the posttraining block evoked an obligatory shift of attention as dictated by the training session. Because of the close link between attention and eye movements, a horizontal shift of attention resulted in deviation of the trajectory of vertical eye movements in Experiment 1 and shorter saccade latencies for horizontal movements in Experiment 2.

The vector theory of Tipper and colleagues (Tipper, Howard, & Jackson, 1997) explains the deviation observed in Experiment 1 in terms of the competition between two movement vectors. Because attention and eye movements are so closely linked, a shift of spatial attention to a horizontal location evokes a horizontal movement vector in the oculomotor system. When, at the same time, an eye movement has to be executed in the vertical direction, there is competition between the horizontal vector evoked by the cue and the vertical vector evoked by the task in-

struction. The competition between these two vectors is resolved by the stronger activity of the vertical movement. This eye movement is directed to the sum of both vectors, however, resulting in an initial vector that deviates toward the cued location.

One might wonder why the direction of the deviation was toward the cued location instead of away, as is generally observed in studies with voluntary shifts of attention (Sheliga et al., 1994). Moreover, eye movement trajectories have been found to deviate away from the direction of gaze cues, which are also hypothesized to evoke an automatic shift of spatial attention (Nummenmaa & Hietanen, 2006). Because deviations away have been associated with top-down inhibition (which causes the initial vector to deviate away from the inhibited location), this suggests that the obligatory shift of attention, as present in our study, is more reflexive than those evoked by gaze cues, resulting in a lack of top-down inhibition. Indeed, it is known that a lack of top-down inhibition results in a saccade deviation toward the cued location (Van der Stigchel et al., 2006). The absence of top-down inhibition in the present study might have been caused by the fact that social stimuli have to be interpreted in order to reveal their meaning, in contrast to the color cues used in our study. This lack of interpretation might result in an obligatory shift of attention that is not controlled by top-down inhibition.

Besides the shift of attention in the presence of a trained cue, there is an alternative explanation for the present findings. It could be that small eye movements during the training session influenced the results. If there were eye movements in the direction of the trained association, our results might be explained by a motor association, rather than by covert shifts of attention. In Experiment 2, we monitored eye movements and concluded that very few eye movements larger than 0.75° occurred. It cannot be ruled out, however, that smaller eye movements during the training session influenced our results (although note that the target was positioned 6.5° away from central fixation). It is unknown what could be the underlying mechanism for such a generalization. In line with our conclusions, we propose that one possible mechanism for such a generalization could be the deployment of attention associated with the execution of a motor movement.

The results of the present study demonstrate that the shifts of attention evoked by trained spatial stimuli are obligatory, in addition to providing further support of the premotor theory and the connection between the attentional, motor, and oculomotor systems.

AUTHOR NOTE

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NOTES

- 1. We thank an anonymous reviewer for this suggestion.
- 2. We tested the spatial resolution of this method of eyetracking by having the experimenter who ran all the participants in Experiment 2 perform a forced choice task in which eye movements of different amplitudes had to be detected. The setup of this task was similar to the training block with respect to number of trials and trial duration. The participant made eye movements on half of the trials, as dictated by the color of the fixation cross. The target was presented to the left or to the right of fixation with a distance of 0.25°, 0.50°, 0.75°, 1.00°, 1.25°, 1.50°, 1.75°, or 2.00°. Results showed that for eye movements larger than 0.75°, accuracy in detecting an eye movement was higher than 85% and the false alarm rate was less than 10%. Even for eye movements as small as 0.25°, eye movements were correctly detected over 73% of the time, with few false alarms. This indicates that the spatial resolution of this method is high enough to detect eye movements larger than 0.75°.

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