Contributions of gaze-centered and object-centered coding in a double-step saccade task

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The position of a saccade target can be encoded in gaze-centered coordinates, that is, relative to the current gaze position, or in object-centered coordinates, that is, relative to an object in the environment. We tested the role of gaze-centered and object-centered coding in a double-step saccade task involving the Brentano version of the Müller-Lyer illusion. The two visual targets were presented either sequentially, requiring gaze-centered coding of the second saccade target, or simultaneously, thereby providing additional object-centered information about the location of the second target relative to the first. We found that the endpoint of the second saccade was affected by the illusion, irrespective of whether the targets were presented sequentially or simultaneously, suggesting that participants used a gaze-centered updating strategy. We found that variability in saccade endpoints was reduced when object-centered information was consistently available but not when its presence varied from trial to trial. Our results suggest that gaze-centered coding is dominant in the planning of sequential saccades, whereas object-centered information plays a relatively small role.

Introduction

Humans make several saccades per second to direct their gaze to interesting objects in the environment. To perform a goal-directed saccade, (at least) two types of visual information can be used. Namely, the position of the saccade target could be encoded relative to the current gaze position, that is, in gaze-centered coordinates, or the position of the target could be encoded relative to the environment, that is, in object-centered (or allocentric) coordinates (Burgess, 2006; Colby, 1998). When performing a sequence of saccades, such as in a double-step saccade task, information about the previously made eye movement (for gaze-centered coding) or the resulting eye position relative to the object (for object-centered coding) is used to plan the next saccade (Bock, Goltz, Bélanger, & Steinbach, 1995; Collins, 2010; Hallett & Lightstone, 1976; Munuera, Morel, Duhamel, & Deneve, 2009).

Several behavioral and neuroimaging studies have shown that visual targets are encoded and continuously updated in gaze-centered coordinates. However, these studies are often performed in sparse visual environments. In more real-world situations, goal-directed movements could also be performed by relying on object-centered visual information. In support of this idea, both immediate and memory-guided saccades to visual targets have been shown to become more accurate and/or precise when object-centered information is available, for example, by adding a visual landmark (Karn, Møller, & Hayhoe, 1997) or a (structured) background (Gerardin, Gaveau, Pélisson, & Prablanc, 2011; Gnadt, Bracewell, & Andersen, 1991).

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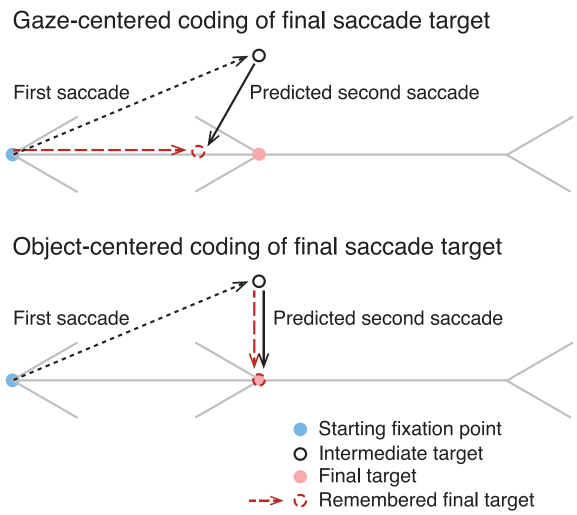

Figure 1. Predictions for gaze-centered and object-centered coding of the final saccade target. (Top) If the final target at the middle vertex of the illusion is coded in gaze-centered coordinates, its distance from the starting fixation point will be biased as a result of the illusion (as for single saccades along the illusion; red dashed arrow and circle). The second saccade will thus be directed to this biased position (black arrow). (Bottom) If the final target position is coded relative to the intermediate target, its position will not be biased because the illusory length is not relevant, and the illusion does not affect directions (as for single saccades; red dashed arrow and circle). The second saccade will thus be directed to the correct position (black arrow). Note that in all conditions, the starting fixation point and the illusion with the final target disappeared before the onset of the first saccade.

In fact, a number of studies suggests that the brain weights egocentric and object-centered information when planning a goal-directed movement (Byrne, Cappadocia, & Crawford, 2010; Byrne & Crawford, 2010; de Grave, Brenner, & Smeets, 2004; Fiehler, Wolf, Klinghammer, & Blohm, 2014; Schütz, Henriques, & Fiehler, 2013; Thompson & Henriques, 2010). This relative weighting depends on various factors, such as the proximity of the landmark to the target (Krigolson, Clark, Heath, & Binsted, 2007), the stability of the landmark or background (Byrne & Crawford, 2010; Fiehler et al., 2014), and the duration of the memory interval preceding the action (Diedrichsen, Werner, Schmidt, & Trommershauser, 2004; but see Schütz, Henriques, & Fiehler, 2015).

The aim of the current study is to determine the role of gaze-centered and object-centered coding in a double-step saccade task by manipulating the relative timing of the presentation of the two targets. When the two targets are presented sequentially, object-centered information about the relative position is not available, so one should rely on a gaze-centered updating strategy to perform the second saccade. However, when the two targets are presented simultaneously, an object-centered strategy may contribute to planning the second saccade. That is, one could use the retinally derived coordinates of the second target relative to the first target.

In normal circumstances, the target positions derived from gaze-centered and object-centered information overlap. To distinguish between the use of gaze-centered and object-centered information in the programming of the second saccade, we presented the target for the second saccade within the Brentano version of the Müller-Lyer illusion. Importantly, this illusion of length affects the endpoint of saccades along its shaft (Binsted & Elliott, 1999; de Grave, Smeets, & Brenner, 2006; Yarbus, 1967) but hardly affects the endpoint of saccades perpendicular to its shaft (de Grave et al., 2006). We presented the illusion such that it was aligned with the starting fixation point and the final saccade target, whereas the line between the intermediate and final target was oriented perpendicular to the illusion. We outlined our predictions in Figure 1. If gaze-centered coding is used to perform the second saccade, we expect systematic errors in the endpoint of the second saccade (de Brouwer, Smeets, Gutteling, Toni, & Medendorp, 2015). The rationale is that after the first saccade directed to the intermediate target above the illusion, updating of the distorted vector representing the distance from the starting fixation point to the final target on the illusion will result in an end position that is biased in the direction of the illusion. In contrast, relative coding of the two targets may not be affected by the illusion. Thus, if the relative position of the two targets is used to plan the second saccade, this may reduce illusion-related errors in the endpoint of the second saccade. Furthermore, the use of object-centered information in addition to gaze-centered information might be reflected in a reduced variability in the endpoint of the second saccade compared with when only gaze-centered information is used (Gnadt et al., 1991; Karn et al., 1997).

Object-centered information may play a larger role when it is consistently available, compared with when it is not consistently available. In support, the use of visual feedback in reaching and grasping depends on implicit knowledge about its availability, resulting in larger differences in kinematic parameters when visual feedback is present in all trials than when trials with and without visual feedback follow in random or alternating order (Elliott & Allard, 1985; Jakobson & Goodale, 1991; Khan, Elliott, Coull, Chua, & Lyons, 2002; Whitwell, Lambert, & Goodale, 2008; Zelaznik, Hawkins, & Kisselburgh, 1983). A second aim of our study was to test whether the contribution of object-centered information is dependent on its availability. We hypothesized that the contribution of object-centered information in planning the second saccade is substantial when trials with simultaneous target presentation are displayed in a blocked manner, whereas the contribution decreases or even completely vanishes when trials with simultaneous target presentation are mixed with sequential target presentation trials.

Methods

Participants

Eleven participants volunteered to take part in the experiment (age 18–33 years, six women). All participants had normal or corrected-to-normal vision. Participants received both verbal and written instructions before providing their written informed consent. The experiment was performed in accordance with the Declaration of Helsinki and was part of a research program that was approved by the ethics committee of the Faculty of Behavioural and Movement Sciences of the Vrije Universiteit Amsterdam.

Setup

Participants were seated in a dimly lit room with their head stabilized by a chin rest positioned ~57 cm from a CRT monitor (40 × 30 cm, 800 × 600 pixels, refresh rate 85 Hz). At this distance, 1 cm on the monitor corresponds to approximately 1° of visual angle. Visual stimuli were controlled using the Psychophysics Toolbox (Brainard, 1997) for Matlab (Mathworks Ltd., Natick, MA). Eye movements of both eyes were recorded with an Eyelink II Eye Tracker (SR Research Ltd., Ottawa, Ontario, Canada), with a temporal resolution of 500 Hz and a spatial accuracy <0.5° of visual angle.

Stimuli

The stimulus consisted of the Brentano version of the Müller-Lyer illusion that was always presented with a white target dot at its middle vertex, which served as the final target in the single- and double-step saccade tasks. The illusion was presented horizontally, with a shaft length of two times 9° of visual angle, in ~0.1° thick black lines. The inward or outward pointing fins, which had a length of 2.7° each (30% of shaft length), were connected to the ends of the two shafts with an angle of 30° or 150°. In one fin configuration, the left part of the horizontal shaft appears shorter than the right part (L-illusion; Figure 1), whereas this effect is reversed in the other configuration (R-illusion). A blue fixation dot was presented at the left or right vertex of the Brentano illusion for single horizontal saccades and double-step saccades. For vertical saccades, the fixation dot was presented 4.5° above the final target. In five of the seven conditions (see the Procedure section), a second white dot was presented 4.5° above the final target: as a landmark for single horizontal saccades and as the intermediate target for double-step saccades. In two thirds of trials, the fixation, landmark, or intermediate target dot presented above the final target was vertically aligned with this target, whereas in the other trials, the dot had an offset of 1.4° to the left or right (these "catch" trials were not analyzed) to ensure that participants did not assume that the two dots were always presented vertically aligned. The diameter of the fixation, landmark, and target dots was 0.4°. The stimuli were presented on a light gray background. In each trial, the set of stimuli was horizontally and vertically displaced with a random offset between −2 and +2° with respect to the center of the screen to ensure that participants were not making a saccade to the same screen position in each trial, especially in the single-saccade conditions.

Procedure

All participants performed four sessions on separate days. The first session consisted of three single saccade conditions, each performed in a separate run: single *horizontal* saccades (i.e., along the illusion), single horizontal saccades with *landmark*, and single *vertical* saccades (i.e., perpendicular to the illusion). The order of conditions within this session was counterbalanced across participants, and short breaks were given in between runs. The illusion effects in these single-saccade conditions were used for comparison with the double-step conditions.

The other three sessions, of which the order was counterbalanced across participants, consisted of double-step saccades. In the *blocked* session, trials in which the targets were presented sequentially and trials in which the targets were presented simultaneously were presented in separate runs, in counterbalanced order (*sequential-blocked* and *simultaneous-blocked* condition, two runs per condition). The *random* session consisted of four runs of sequential and simultaneous trials in random order (*sequential-random* and *simultaneous-random* condition). Because we anticipated differences in behavior between the blocked and random presentation schedule, another session was run with a semi-blocked presentation schedule. As the anticipated differences were absent, we decided not to analyze the results of this session and not present any details here. Figure 2 provides a schematic illustration of the sequence of events in the single- and double-step

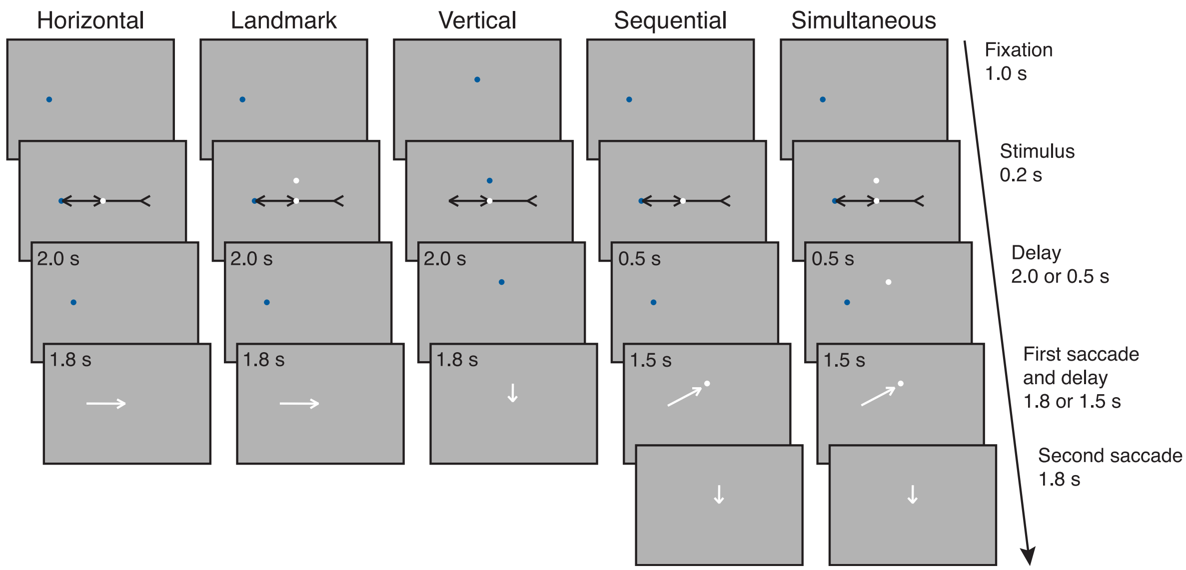

Figure 2. Schematic illustration of the sequence of events in the single saccade and double-step saccade tasks. In all conditions, the stimulus in the second frame could be the L-illusion, as shown, or its mirrored version, the R-illusion. The white arrows in the lower frames represent the saccades to the intermediate and final (remembered) target.

saccade tasks. The procedure is described in detail below.

Single-saccade conditions

In the *horizontal* and horizontal with *landmark* condition, a trial started with the presentation of a fixation dot at the left or right of the screen for 1.0 s. The Brentano illusion, with the target dot at its middle vertex, was presented with its left or right vertex at the fixation dot for 0.2 s. In the *landmark* condition, object-centered information was provided simultaneously with the illusion and target, by presenting a landmark above the target. Participants were instructed to maintain fixation during the presentation of the illusion and remember the position of its target. After a delay of 2.0 s, the fixation dot disappeared as a cue to make a saccade to the remembered target. If the eyes deviated from initial fixation by more than 3° during this delay, a beep sound was played to warn the participant for making an early saccade, and the trial was aborted and repeated at the end of the block. A new trial started 1.8 s after the go cue. The *horizontal* condition consisted of 80 trials, all of which were analyzed: 2 illusion configurations (L-illusion and R-illusion) × 2 starting positions (left and right) × 20 repetitions. The *landmark* condition contained the same 80 trials, and 40 catch trials were added that were not analyzed (2 illusion configurations × 2 starting positions × 2 offset directions × 5 repetitions), resulting in a total of 120 trials.

A trial in the *vertical* condition started with the presentation of a fixation dot at the top of the screen for 1.0 s. The Brentano illusion with the target dot was presented 4.5° below the fixation dot. After 0.2 s, the illusion disappeared while the fixation dot remained on the screen for another 2.0 s. Participants were instructed to maintain fixation during this delay and make a saccade to the remembered position of the target in response to the disappearance of the fixation dot. This run contained 40 trials in which the fixation and target dot were vertically aligned (2 illusion configurations × 20 repetitions), plus 20 catch trials (2 illusion configurations × 2 offset directions × 5 repetitions).

Double-step saccade conditions

All trials started with the presentation of a fixation dot at the left or the right of the screen for 1.0 s. In the two *sequential* conditions, the Brentano illusion was presented for 0.2 s with its left or right vertex at the fixation dot. The fixation dot remained on the screen for another 0.5 s after the disappearance of the illusion. At the same time as the fixation dot disappeared, the intermediate target dot appeared at a position above the previously presented target within the illusion, triggering a visually guided saccade. If the eyes deviated from initial fixation by more than 3° before the appearance of the intermediate target, a beep sound was played, and the trial was aborted and repeated at the end of the block. In correct trials, the intermediate target disappeared after a delay of 1.5 s, cueing the participant to make a saccade to the remembered target that was presented with the illusion. By choosing the 0.5- and 1.5-s delays, we ensured that the total delay between the presentation of the illusion with its target and the saccade to the final target was equal in the single- and double-step conditions. The design of this task was very similar to the design used by de Brouwer and colleagues (2015).

In the two *simultaneous* conditions, object-centered information was provided by presenting the intermediate target simultaneously with the illusion and the final target. When the illusion with its target disappeared, the fixation dot and intermediate target remained on the screen for another 0.5 s. Next, the fixation dot disappeared, triggering a visually guided saccade to the intermediate target. After a delay of 1.5 s, the intermediate target disappeared as a cue to make a saccade to the remembered target that was presented with the illusion. Thus, the only difference between the simultaneous and sequential trial types was that the intermediate target appeared together with the illusion and final target in the simultaneous trials, whereas it appeared 0.5 s after the disappearance of the illusion and final target in the sequential trials.

In both the blocked and the random session, 96 *sequential* target presentation trials and 96 *simultaneous* target presentation trials were performed with the targets vertically aligned (2 illusion configurations $\times$ 2 starting positions $\times$ 24 repetitions), and 48 catch trials were added (2 illusion configurations $\times$ 2 starting positions $\times$ 2 offset directions $\times$ 6 repetitions).

Data analysis

Horizontal and vertical eye velocities were calculated from the eye positions that were given by the eye tracker and averaged across the left and right eye. Eye movements with a resultant velocity above 75°/s for two or more consecutive samples ($\geq$4 ms) were referred to as *saccades*. For these saccades, movement onset was defined as the last of five consecutive samples (10 ms) before eye velocity reached a threshold of 30°/s preceding the velocity peak. Saccade offset was defined as the first of five consecutive samples (10 ms) during which the velocity was below the 30°/s threshold, following the velocity peak. Saccades with an amplitude of 2.0° or more were analyzed.

Drift of the eye tracker within 10° was corrected by assuming correct fixation during the onset of the illusion. These fixations were calculated as the mean eye position during 10 consecutive samples (20 ms) in which eye velocity was below the 30°/s threshold immediately preceding the onset of the illusion, or if eye velocity was above the threshold in these 20 ms, we searched for a period of stable fixation within a window of 200 ms surrounding the onset of the illusion. Trials were discarded if the eyes were moving too fast within this time window or if the correction was larger than 10°. Trials were also discarded if the first saccade onset occurred before the cue (i.e., during the fixation period) and if the second saccade of a double-step trial occurred before the second cue (i.e., during the delay between the first and second saccade). Furthermore, trials were discarded if the saccade did not move the eyes closer to the target, if the (corrected) onset of the first and/or second saccade was farther than 2.0° from the position of the fixation dot, and if the endpoint of the first and/or second saccade was farther than 3° vertically from the target position. Saccade detection and rejection were verified by visual inspection. On average, 88% correct single saccades and 73% correct double-step saccades were included in the analysis.

For the correct trials, we calculated the horizontal endpoint of the saccade directed to the final target. Next, for each participant and each combination of condition, illusion configuration, and starting position, we computed the median horizontal coordinate of the endpoint and the corresponding horizontal interquartile range. The interquartile range, which describes the width of the middle 50% of the distribution of endpoints, was used as a measure of variability in the direction of the illusion. The effect of the illusion on saccade endpoints was calculated by subtracting the median horizontal endpoint positions for the two configurations (L-illusion and R-illusion). The illusion effects were averaged over starting position (left and right), and the interquartile ranges were averaged over both starting position and illusion configuration.

Statistical analyses

The goal of our study is to determine the contributions of gaze-centered and object-centered coding in a double-step saccade task and to determine if the contribution of object-centered information depends on the presentation schedule. To test our hypotheses, we examined the illusion effect and the variability in saccade endpoints. Because the participants' head and body were stationary in our experiments, it is impossible to distinguish between object-, head-, and body-centered reference frames. For simplicity, in this article we refer to these possibilities as *object-centered*.

We first verified that single saccades along the illusion were affected by the illusion, whereas the horizontal component of saccades perpendicular to the orientation of the illusion was not affected (de Grave et al., 2006), by testing the illusion effects in the *horizontal*, *landmark*, and *vertical* condition against zero using a one-sample t test. To make sure that illusion effects on double-step saccades were due to updating and not to a progression of errors on the first saccade, we first tested for an illusion effect on the endpoint of the first saccade in the sequence and the starting point of the second saccade in the sequence.

Our first hypothesis was that sequential target presentation requires encoding of gaze-centered information, whereas with simultaneous target presentation,

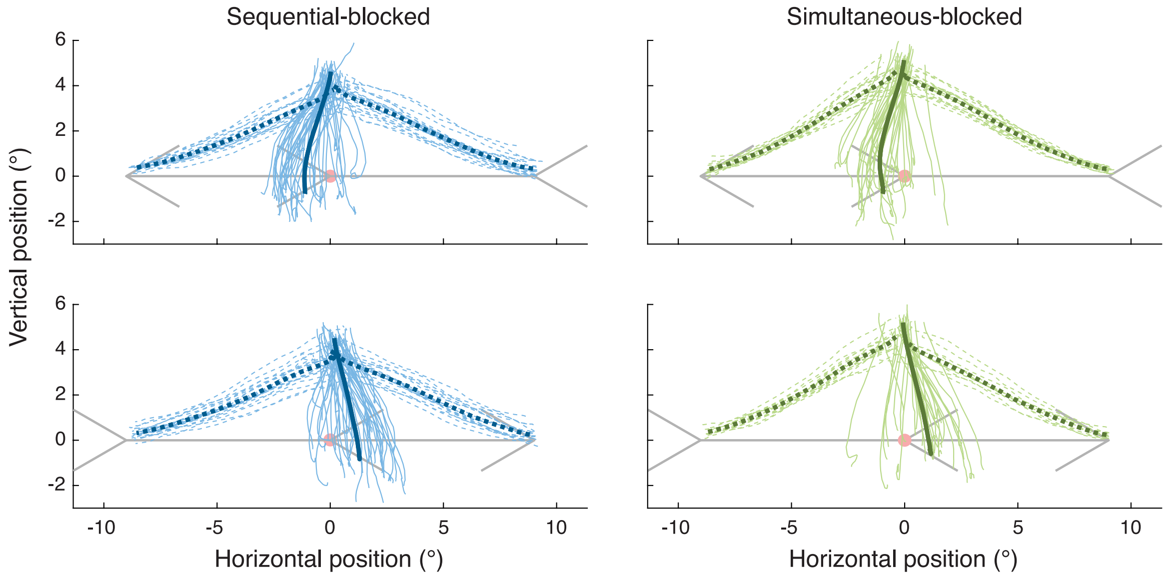

Figure 3. Saccade trajectories for the L-illusion (top row) and the R-illusion (bottom row) of a single example participant in the sequential-blocked (left column; in blue) and simultaneous-blocked condition (right column; in green). Dashed lines depict first saccades, continuous lines depict second saccades, darker and thicker lines depict average trajectories. Note that the end positions of the average trajectories differ slightly from the median end positions used to calculate the illusion effects. The illusion is drawn for illustrative purposes; it was not visible during the execution of the saccades.

object-centered information might contribute as well. To test this, we compared the illusion effect in the *sequential-blocked* and *simultaneous-blocked* condition to the effect in the single *horizontal* condition using paired t tests. Comparable illusion effects in the single and double conditions would suggest that the second saccade of a double-step trial is performed by updating the gaze-centered vector representing the distance between the initial fixation position and the target within the illusion. A smaller effect in the double-step condition would suggest that object-centered information is used in addition to gaze-centered information. To test for a relation between the effects in the single and double conditions, we computed Pearson's correlation coefficient between the illusion effect in the *single* and *sequential-blocked* condition and between the illusion effect in the *single* and the *simultaneous-blocked* condition.

Second, we hypothesized that the combination of gaze-centered and object-centered information is dependent on whether trials with sequential and simultaneous target presentation are displayed in a blocked or random manner. To test this, we compared the illusion effects and variability between the double-step saccade conditions. We performed a 2 (trial type: *sequential* or *simultaneous*) $\times$ 2 (presentation schedule: *blocked* or *random*) repeated-measures analysis of variance (ANOVA) on the illusion effect on the second saccade. An influence of object-centered information would be expressed by a smaller illusion effect in the *simultaneous* trials. Further, a dependency on presentation schedule would be revealed by an interaction effect between trial type and presentation schedule. A similar analysis was performed on the horizontal variability in saccade endpoints. We used a 2 (trial type) $\times$ 2 (presentation schedule) repeated-measures ANOVA with the interquartile ranges as the dependent variable. Again, the effects of interests were a main effect of trial type and an interaction between trial type and presentation schedule. We verified that any differences between the *sequential* and *simultaneous* conditions were due to the use of relative coding in the programming of the second saccade and not simply due to the presence of irrelevant object-centered information. This was done by comparing the illusion effect and variability of single horizontal saccades with and without landmark using paired t tests.

Results

We investigated the contributions of gaze-centered and object-centered information in a double-step saccade task by examining the effect of the Brentano illusion and the variability in saccade endpoints. Latencies of the first and second saccades are given in Supplementary Table S1. The saccade trajectories of the participant with the largest illusion effects in the double-step conditions are shown in Figure 3. Second saccades were clearly influenced by the illusion: On average, the continuous lines in the top graphs end to

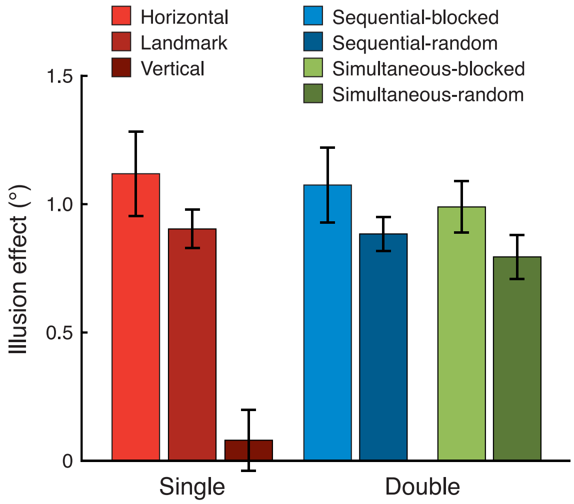

Figure 4. Illusion effects. The illusion effects were calculated as the difference in horizontal saccade endpoint for the two configurations of the illusion. Error bars represent the standard errors within participants.

the left of the target on the L-illusion, whereas the lines in the bottom graphs end to the right of the target on the R-illusion. The horizontal coordinates of the median endpoint of the second saccade in each condition, averaged across subjects, are given in Supplementary Figure S1. Figure 4 shows the average illusion effect, expressed as the difference in the horizontal coordinate of the saccade endpoint for the L-illusion and R-illusion, in each of the conditions. For single saccades, there is a considerable illusion effect in the two horizontal conditions (*horizontal* $t[10] = 7.8$, $p < 0.001$; *landmark* $t[10] = 5.8$, $p < 0.001$), without a difference in illusion effect between these conditions ($t[10] = 1.1$, $p = 0.314$). In line with the findings of de Grave and colleagues (2006), there is no significant effect of the illusion on vertical saccades (i.e., perpendicular to the shaft; $t[10] = 1.3$, $p = 0.214$).

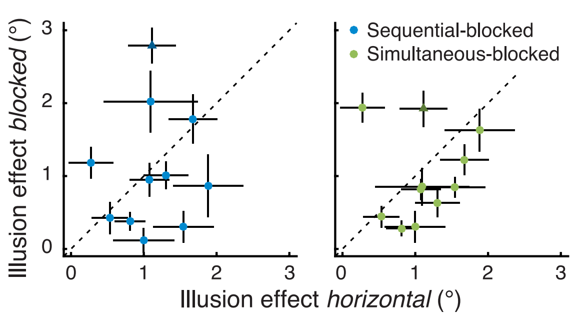

Figure 5. Illusion effect in the *sequential-blocked* condition and *simultaneous-blocked* condition as a function of the illusion effect in the *horizontal* condition for each individual participant. Data points of the example participant in Figure 3 are depicted in slightly darker triangles. The dashed line represents the unity line. Error bars represent the standard error of the mean.

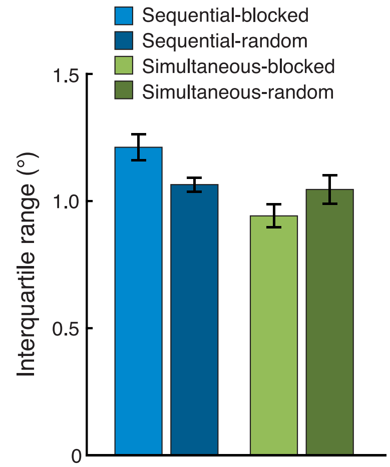

Figure 6. Interquartile range of the horizontal endpoints of the second saccade in the double-step conditions. Error bars represent the standard errors within participants.

For the double-step saccades, we first tested for an illusion effect on the horizontal endpoint of the first saccade in the sequence and the horizontal starting point of the second saccade in the sequence. The mean illusion effect was $0.05° \pm 0.03°$ on the first saccade offset and $0.02° \pm 0.01°$ on the second saccade onset (mean $\pm$ standard error), with none of the conditions differing from zero or from each other. This result is not surprising because the first saccade was visually guided, so even if it were affected by the illusion, this would likely be corrected for by a subsequent corrective saccade. As can be seen in Figures 3 and 4, the endpoint of the second saccade was clearly affected by the illusion. There were no differences between the illusion effect on single *horizontal* saccades and the illusion effect in the *sequential-blocked* condition, $t(10) = 0.2$, $p = 0.875$, or the *simultaneous-blocked* condition, $t(10) = 0.6$, $p = 0.570$. However, across subjects, there was no significant correlation between the illusion effects in the *horizontal* and *sequential-blocked* condition ($r = 0.12$, $p = 0.720$) or between the effects in the *horizontal* and *simultaneous-blocked* condition ($r = 0.11$, $p = 0.747$; Figure 5).

When comparing the double-step conditions, the ANOVA revealed that the illusion effects were larger in the *blocked* presentation schedule than in the *random* presentation schedule, $F(1, 10) = 5.7$, $p = 0.038$. However, the predicted effects were absent: There was no main effect of *sequential* versus *simultaneous* presentation, $F(1, 10) = 0.6$, $p = 0.443$, and no significant interaction, $F(1, 10) < 0.1$, $p = 0.984$. We also investigated whether the horizontal variability in the second saccade endpoints was influenced by object-centered information. Figure 6 shows the average interquartile ranges in each of the double-step conditions. The variability was not affected by presentation schedule, $F(1, 10) = 0.1$, $p = 0.739$. Interestingly, the variability was significantly smaller in the *simultaneous* conditions than in the *sequential* conditions, $F(1, 10) = 9.5$, $p = 0.012$. In addition, there was a significant Presentation Schedule × Trial Type interaction, $F(1, 10) = 6.5$, $p = 0.029$, showing that the reduction of variability for the *simultaneous* condition was more pronounced in the *blocked* presentation schedule. Post hoc paired t tests showed that variability in the *simultaneous-blocked* condition was significantly smaller than in the *sequential-blocked* condition ($p = 0.003$), whereas the other differences were not significant (all $p > 0.3$). We verified that this effect was not simply due to the presence of an irrelevant landmark: There was no difference in variability between the *horizontal* and *landmark* condition (mean ± SEM, 2.0° ± 0.6° and 2.0° ± 0.5°; $t[10] = 0.3$, $p = 0.801$). Note that we computed the horizontal variability in saccade endpoints. Thus, the variability in the *horizontal* and *landmark* condition is in the direction of movement and therefore larger than the variability of the second saccade in the double-step conditions.

In summary, the illusion effect on double-step saccades did not differ from the illusion effect on single saccades along the Brentano illusion, although there was no significant correlation between the illusion effects in the single- and double-step conditions. The illusion effect on double-step saccades was larger in the blocked presentation schedule than in the random presentation schedule, although there was no difference in effect between sequential and simultaneous presentation. Providing object-centered information by presenting the targets simultaneously did result in a smaller horizontal variability in saccade endpoints, particularly when trials were presented in a blocked schedule.

Discussion

We examined the role of gaze-centered and object-centered coding of visual targets in a memory-guided double-step saccade task involving the Brentano illusion. This illusion is known to affect the endpoint of saccades along the illusion but not the endpoint of saccades perpendicular to the illusion. We hypothesized that sequential presentation of the two targets would require a gaze-centered strategy (i.e., visuomotor updating) resulting in large effects of the Brentano illusion on the endpoint of the second saccade (see Figure 1). On the other hand, simultaneous target presentation would facilitate the use of object-centered information (i.e., coding of relative target positions) in addition to gaze-centered information, resulting in smaller illusion effects and a smaller variability in saccade endpoints. A second hypothesis was that the use of object-centered information in the programming of the second saccade is dependent on knowledge about the availability of object-centered information, which was tested using blocked and random presentation schedules. We found that in all double-step conditions, the illusion caused systematic errors in the endpoint of the second saccade that were of a similar magnitude as the errors on single saccades along the illusion. This was true even though the two targets were physically vertically aligned in two thirds of the trials. Although the illusion effect was smaller in the random than in the blocked presentation schedule, the predicted effect was absent: There was no difference in illusion effect when targets were presented sequentially or simultaneously. This suggests that gaze-centered coding of the final target was used in both conditions. However, the horizontal variability in saccade endpoints was smaller in the simultaneous than in the sequential condition, particularly when using a blocked presentation schedule. Thus, although object-centered information did not reduce the illusion effect, it did reduce endpoint variability when the information was consistently available. This shows that object-centered coding does play a role in the planning of sequential saccades when the visual scene is stable.

To obtain a baseline measure of the illusion effect, each participant started with a session of single saccades along (i.e., horizontal) and perpendicular (i.e., vertical) to the Brentano illusion. Consisted with previous research, we found that the endpoints of saccades along the illusion were clearly affected by the illusion, whereas the effect of the illusion on saccades perpendicular to the illusion was close to zero (de Grave et al., 2006). Our results confirm that these effects are independent of whether the saccade is visually guided, as in the experiment of de Grave and colleagues (2006), or memory guided, as in the present study (also see de Brouwer, Brenner, Medendorp, & Smeets, 2014). As argued by de Grave and colleagues (2006), the lack of effect on saccades perpendicular to the illusion provides counterevidence for the idea that effects of this illusion are caused by saccades being directed to the "center of gravity" (Coren & Hoenig, 1972; Findlay, 1982; Herwig, Beisert, & Schneider, 2010) of the vertex of the illusion (Gilster & Kuhtz-Buschbeck, 2010). Based on our results, we would formulate the interpretation of de Grave and colleagues (2006) of the illusion as the arrowheads affecting gaze-centered distance, without affecting gaze-centered direction.

We found that both gaze-centered and object-centered coding play a role in the planning of the second saccade in a double-step sequence (Sharika, Ramakrishnan, & Murthy, 2014), although gaze-centered information played a larger role than object-centered information. Namely, against our hypothesis, we did not find a reduction in the illusion effect on the second saccade of the double-step sequence when object-centered information was provided by presenting the targets simultaneously. This suggests that participants relied more strongly on the egocentric target positions relative to the initial gaze position than on the relative position of the two targets. Surprisingly, this was not reflected by a relation between the illusion effects on single- and double-step saccades. The fact that we did find a correlation in illusion effect between the sequential-blocked and simultaneous-blocked conditions ($r = 0.70$, $p = 0.011$), suggests that people make idiosyncratic errors in the updating process, adding between-subject variations to the illusion effects. Although the relative timing of the targets did not influence the illusion effects, simultaneous presentation of the targets did result in a smaller horizontal variability in saccade endpoints, consistent with previous studies (Gnadt et al., 1991; Karn et al., 1997). The selectivity of this effect seems inconsistent with the idea that egocentric and object-centered information is combined in a statistically optimal manner, as suggested by several researchers (Byrne & Crawford, 2010; Byrne & Henriques, 2013). Namely, if egocentric and object-centered information were optimally combined, we would expect to see a difference in both the illusion effect and the endpoint variability when comparing the sequential-blocked condition with the simultaneous-blocked condition.

Several studies have suggested that the development of a "world-centered" representation for saccades takes time (e.g., about 500 ms; Zimmermann, Morrone, & Burr, 2013; Zimmermann, Morrone, Fink, & Burr, 2013). However, this world-centered coding is fundamentally different from the object-centered coding that we addressed in our paradigm. In studies on world-centered coding, two targets are typically presented at the *same* spatial location, with a certain presentation duration and interval. In contrast, in the simultaneous condition of our paradigm, the illusion with the final target was presented at a *different* location than the intermediate target, allowing immediate relative coding of the two positions. Previous research showed that endpoint errors of saccades were reduced when a visual background was added to a target presented for 300 ms (Gnadt et al., 1991), suggesting that object-centered coding occurs rather quickly. However, the exact time course of object-centered coding for saccades remains to be investigated. In the current study, we used a short presentation time (i.e., 200 ms) because the effect of the Müller-Lyer illusion decreases with longer presentation times (de Brouwer et al., 2014; van Zoest & Hunt, 2011). As such, longer presentation times would make it more difficult to distinguish between gaze-centered and object-centered coding. Despite the presence of a delay following the presentation of the two targets, which has been suggested to facilitate object-centered coding (Hu & Goodale, 2000), our results did not show a strong influence of object-centered information.

Interestingly, the reduction in endpoint variability by adding object-centered information was present only when sequential and simultaneous trial types were presented in a blocked manner. When these trial types were presented in a random schedule, there was no difference in variability. This was not simply due to the presence of an irrelevant landmark, because single horizontal saccades were not affected by the presence of irrelevant object-centered information, either in terms of the illusion effect or in terms of the horizontal variability in saccade endpoints. Thus, object-centered information can improve saccadic performance when it is consistently available and relevant for the task (Fiehler et al., 2014). This suggests that the brain does not switch between using only gaze-centered information and using both gaze-centered and object-centered information on a trial-to-trial basis. Rather, the use of information is dependent on implicit knowledge about the availability of this information. This in is accordance with the finding that the use of visual feedback in reaching and grasping is dependent on the presentation schedule (Elliott & Allard, 1985; Jakobson & Goodale, 1991; Khan et al., 2002; Whitwell et al., 2008; Zelaznik et al., 1983).

Our finding that the endpoints of double-step saccades are less variable when object-centered information is provided differ from the results of the sequential reaching task by Thompson and Henriques (2010). These authors did not find a difference in error or variability of reaching endpoints between blocks of sequential and simultaneous target presentation. The main difference between our task and that of Thompson and Henriques was that they used reaching movements, whereas in the present study, saccadic eye movements were used. This is, however, not a likely explanation for the difference in results, because consistent with studies on saccades, several studies have shown that reaching movements to visual targets are more accurate and/or precise when object-centered information is available (Conti & Beaubaton, 1980; Hay & Redon, 2006; Krigolson & Heath, 2004; Lemay, Bertram, & Stelmach, 2004; Obhi & Goodale, 2005; Schütz et al., 2013).

The results suggest that, in our double-step task, participants employed a gaze-centered updating strategy and did not strongly rely on object-centered information (i.e., relative coordinates) for programming the second saccade. Alternatively, it may be possible that in a memory-guided double-step saccade task, the dimensions of the first saccade are not taken into account when planning the second saccade (i.e., visuomotor updating), but the sequence of saccades is preplanned. Although we do not consider this possibility to be likely, more importantly, it would not change our conclusion. Namely, a sequence of saccades can be preplanned based on gaze-centered information, object-centered information, or on a combination of the two. We found that the contribution of gaze-centered information is dominant over the contribution of object-centered information for saccade planning.

Conclusions

We used a double-step saccade task involving the Brentano illusion to investigate the role of gaze-centered and object-centered coding for saccades. Consistent with previous results, single saccades along the illusion were clearly affected by the illusion, whereas single saccades perpendicular to the illusion were not affected. In the double-step task, we found that the second saccade, which was perpendicular to the illusion, was also affected by the illusion, independent of whether the targets were presented sequentially (i.e., only gaze-centered information) or simultaneously (i.e., both gaze-centered and object-centered information), suggesting that participants use a visuomotor updating strategy. We did find a slightly reduced variability in saccade endpoints when object-centered information was provided. We conclude that gaze-centered information is dominant in planning (multiple) saccades, whereas object-centered information plays a smaller role.

Keywords: eye movements, egocentric, allocentric, memory guided, spatial updating, reference frame

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