Voluntary saccadic eye movements in humans studied with a double-cue paradigm

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Abstract

In the classic double-step paradigm, subjects are required to make a saccade to a visual target that is briefly presented at one location and then shifted to a new location before the subject has responded. The saccades in this situation are “reflexive” in that they are made in response to the appearance of the target itself. In the present experiments we adapted the double-step paradigm to study “voluntary” saccades. For this, several identical targets were always visible and subjects were given a cue to indicate that they should make a saccade to one of them. This cue was then changed to indicate another of the targets before the subject had responded: double-cue (DC) paradigm. The saccadic eye movements in our DC paradigm had many features in common with those in the double-step paradigm and we show that apparent differences can be attributed to the spatio-temporal arrangements of the cues/targets rather than to any intrinsic differences in the programming of these two kinds of eye movements. For example, a feature of our DC paradigm that is not seen in the usual double-step paradigm is that the second cue could cause transient delays of the initial saccade, and these delays still occurred when the second cue was reflexive—provided that it was at the fovea (as in our DC paradigm) and not in the periphery (as in the usual double-step paradigm). Thus, the critical factor for the delay was the retinal (foveal) location of the second cue/target—not whether it was cognitive or reflexive—and we argue that the second cue/target is here acting as a distractor. We conclude that the DC paradigm can be used to study the programming of voluntary saccades in the same way that the double-step paradigm can be used to study reflexive saccades.

Keywords: Saccadic eye movements; Double-step paradigm; Cognitive cues

1. Introduction

Natural visual scenes are generally composed of a myriad variety of stimuli, any of which might require particular scrutiny. Saccadic eye movements are used to orient gaze in this complex environment, facilitating fast and precise foveation of the targets of interest for further detailed analysis. These eye movements have classically been regarded as preprogrammed and ballistic. However, visual scenes can undergo instantaneous changes, as when selective elements move or change their salience, and under these circumstances it might be useful to be able to divert the eyes towards the new images as soon as possible. This requires the programming of a new saccade and, on occasion, the premature suspension or modification of ongoing saccadic programming—to the extent that this is possible. Considerable insight into the brain’s ability to rapidly interrupt or modify ongoing saccadic programming has been gained from the so-called “double-step” paradigm (e.g., Becker & Jürgens, 1979; Carlow, Dell’Osso, Troost, Daroff, & Birkett, 1975; Feinstein & Williams, 1972; Komoda, Festinger, Phillips, Duckman, & Young, 1973; Lisberger, Fuchs, King, & Evinger, 1975; Täumer, 1975; Wheelless, Boynton, & Cohen, 1966). In a typical double-step experiment subjects are required to make a saccade to a visual target that is briefly presented at one location and then shifted to a new one before the subject has responded. The outcome depends critically on the time delay between the target shift and the subject’s response (Becker & Jürgens, 1979): when this response delay is

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short, saccades are directed towards the first stimulus location and, when this delay is long, saccades are directed towards the second stimulus; at intermediate delays, saccades are directed to intermediate locations. Others have repeatedly replicated this amplitude vs. delay dependency using one-dimensional (Baizer & Bender, 1989; Groll & Ross, 1982; van Asten, Gielen, & DeWeinkel, 1988; see, however, Ottes, Van Gisbergen, & Eggermont, 1984) and two-dimensional displays (Aslin & Shea, 1987; Findlay & Harris, 1984; Gellman & Carl, 1991; Hou & Fender, 1979; McPeek, Skavenski, & Nakayama, 2000). These studies indicate that visual information processing continues during the programming of saccades, and can modify a saccade that is already in preparation.

One notable feature of the classic double-step paradigm is that the saccades are always reflexive, i.e., they are made in response to the appearance of the target itself. This feature means there is never more than one target present at any given time. A primary purpose of the present experiments was to adapt the double-step paradigm to study the programming of so-called voluntary saccades. For this, several identical targets were visible throughout the trial and subjects were first given a cue to indicate that they should make a saccade to one of them. On some trials, the cue was then changed to indicate another of the targets before the subject had had time to respond to the first cue: the double-cue (DC) paradigm. Here, the cue was in the form of a pointer at fixation and the programming of the eye movement was interrupted by a change in the cue rather than a shift in the target itself. In Experiment 1 we show that, under these conditions, the first saccade often has the characteristics observed in the classical double-step paradigm although its end-point is less dependent on the exact timing of the second cue, so that even when the first saccade has a long latency it can arrive at either target location, or in between. We also show that some of the first saccades tend to be transiently delayed by the second cue. In that first experiment, subjects were required to make their initial saccade as soon as the first pointer appeared and in Experiment 2 they were required to wait until an acoustic “go” signal was given some time later. This reduced the latency of the first saccades and intensified the transient delay due to the second cue. Furthermore, this transient delay was still very evident even when the subject was instructed to ignore the second cue (Experiment 2a). However, if the second cue was a change in the second target itself (an enlargement) rather than a change in the direction of the pointer at fixation, i.e., a reflexive rather than a cognitive cue, then the delay was appreciable only if the second target was at the fovea and not if that target was in the periphery (Experiment 3). Thus, the transient delay was generally seen only when the second cue/target was foveal. We argue that the second cue causes these delays by acting as a distractor. Finally (Experiment 4), we show that a slight modification of the “classic” double-step paradigm—leaving the first target on when the second target appears—can substantially reduce, or even eliminate, the impact of the second target on the endpoint of the first saccade (cf. our first two experiments). Some preliminary results of this study were presented in abstract form elsewhere (Sheliga, Brown, & Miles, 2000).

2. Experiment 1: the double-cue paradigm

In this experiment we used a visual cognitive cue—a pointer presented at fixation—to inform the subjects about the location of the object that was to be the target for their saccadic eye movement.

2.1. Methods

2.1.1. Subjects

The subjects were the authors (BMS, FAM and VJB) and all had normal or corrected-to-normal vision. Experimental protocols were approved by the Institutional Review Committee concerned with the use of human subjects.

2.1.2. Apparatus and procedure

The presentation of stimuli, together with the acquisition, display, and storage of data, were controlled by a PC using a real-time experimentation software package (REX) developed by Hays, Richmond, and Optican (1982). The horizontal and vertical positions of one eye were recorded with an electromagnetic induction technique using scleral search coils embedded in silastin rings as previously described (Busettini, Miles, Schwarz, & Carl, 1994). The sampling rate was 1 kHz. The subjects sat in front of a computer screen (ViewSonic 21 in. monitor) in a darkened room with their heads secured in place by means of an adjustable head-and-chin rest together with a head band. The distance from the eyes to the screen was 57 cm.

Each experimental session consisted of 648–864 correctly performed trials. Trials in which an error occurred were rerun within the same block. The spatial and temporal events during the individual trials are indicated diagrammatically in Fig. 1. Each trial started with a gray display containing a centered black fixation dot (0.08° × 0.08°), and four white squares (0.4° × 0.4°) located 10° below, above, to the left of, and to the right of the screen center. Subjects were required to fixate the dot for a variable period of time (500–1000 ms) until a pointer in the form of a short white bar (0.16° × 0.08°) appeared, protruding from one side of the fixation dot and pointing in the direction of one of the four squares. Subjects were required to make a saccade to the cued...
square as quickly as possible. At this point, half the trials ended: single-cue (SC) trials. In the remaining trials, a second pointer replaced the first and was aimed at one of the other squares: DC trials. Subjects were told that the square indicated by this new pointer should now take precedence and they should redirect their fixation towards it as soon as possible. The interval between the onsets of the two pointer cues (interstimulus interval, ISI) could be 61, 91 or 122 ms. DC trials in which the cued squares were 90° apart will be referred to as adjacent DC trials, and those in which the cued squares were 180° apart will be referred to as opposite DC trials. The selected squares and ISI varied randomly from one trial to the next.

Each subject participated in 6–7 experimental sessions. In order to encourage the subjects to respond to the first instruction as quickly as possible and to discourage the subjects from guessing about, and/or waiting for, the appearance of the second instruction, subjects were given only a restricted period of time. In order to determine what maximum time period would be reasonable, we first determined the latency of each subject’s response when only SC trials were presented (200 trials). Then, in the main experimental sessions, trials in which the subject failed to make a saccade within 2SDs of the mean latency measured in the pure SC trials—the upper limit on the permissible latency—were aborted and the subject was informed by displaying an error message on the screen. Trials were also aborted, and an error message displayed, if subjects failed to arrive at the cued square in SC trials within 250 ms of this upper limit or at the final cued square in DC trials within 600 ms of this upper limit.

2.1.3. Data analysis
The horizontal and vertical components of eye movements were recorded together with time markers for the major stimulus events occurring during the course of the trials. Velocity traces were derived from raw eye position signals off-line by computing the two-point (20 ms apart) central difference between the symmetric weight moving averages (7 points) of the position signal (Usui & Amidror, 1982). Saccade detection was based on combined velocity and acceleration/deceleration criteria. The saccadic latency was the time that elapsed from the appearance of the first instruction cue to the onset of the first saccadic eye movement. Saccadic latencies were also computed with respect to the appearance of the second instruction cue, which is equivalent to the delay, \( D \), of Becker and Jürgens (1979).

Whenever appropriate, the latencies and amplitudes of the saccades recorded in DC trials were normalized with respect to the mean data obtained in SC trials using the same instruction cue. This permitted the pooling of the data for saccades to all four target locations.

2.2. Results
2.2.1. Double-cue trials: endpoints of first saccades
Saccadic responses in DC trials were subdivided into single responses (SRs) and double responses (DRs). SRs consisted of a single (main) saccade that brought the eye to the vicinity of the square defined by the second cue (Fig. 2D). A small corrective movement usually followed this main saccade. Some SR saccades were strongly curved (e.g., Fig. 2E) but were generally considered to be a single movement because the velocity profile invariably showed a single monotonic profile along one or other principal (horizontal or vertical) axis. DRs consisted of two main saccades, the first of which was directed towards either the square defined by the first cue (e.g., Fig. 2A) or to some intermediate location between the two squares defined by the first and second cues (e.g., Fig. 2B). The second saccade was generally directed towards the square defined by the second cue. An additional small corrective saccade, usually \(<1°\), often followed the first saccade and preceded the second (main) saccade, occurring on average for all subjects in 18% of trials (range: 13–23%); an example is shown in Fig. 2C (labeled “c”). We will refer to DRs that lack...
such correctives as “2-saccade DRs”, and DRs with them as “3-saccade DRs”.

Fig. 3A shows the two-dimensional distributions of the endpoints of the first saccades (i.e. SRs and first saccades in DRs) in adjacent DC trials for each of the three subjects. The ordinate shows the amplitude of the component of the saccades in the direction of the square defined by the first cue ($a_1$), and the abscissa shows the amplitude of the component of the saccades in the direction of the square defined by the second cue ($a_2$). The data have been normalized with respect to the mean amplitudes of the saccades recorded in SC trials. For each subject, the data obtained with all (four) possible opposite-DC-trial combinations have been pooled together. Contrary to the situation with the adjacent DC trials, the distribution of the endpoints in the opposite DC trials shows a gap: small-amplitude responses were not observed in the direction defined by the second cue. (Note that the ordinates in Fig. 3B and C have a logarithmic scale to emphasize the troughs rather than the peaks.)

2.2.2. Double-cue trials: latency of first saccades

The latency distributions of the first saccades with respect to the time of appearance of the first cue in DR trials are shown in Fig. 4A and B in the form of smoothed frequency polygons (bin width: 0.05), in which the centers of the bins have been linked with a cubic spline interpolation. (These smoothed frequency polygons avoid some of the overlap problems of conventional histogram envelopes.) The data have been normalized with respect to the mean latencies of the saccades recorded in SC trials, allowing us to pool the responses directed towards each of the four squares despite the fact that these had somewhat different latencies: average saccadic latencies for all subjects in SC trials were 213, 206, 225 and 206 ms for upward, rightward, downward, and leftward responses, respectively.

Data obtained in adjacent and opposite DC trials were also pooled together since for each of the three subjects there was no significant difference in the latency distributions between these two types of trials ($p > 0.05$; Kolmogorov–Smirnov two-sample test). In Fig. 4A, the data for all three subjects have been pooled together and the latency distribution of the first saccades of DRs (dashed/dotted line) is compared with the latency distribution on SC trials (solid line). It is evident from this figure that the second cue could delay the first saccade: whereas latencies in SC (control) trials are distributed close to normal with only a very slight skew towards longer latencies, the latency distribution in DR trials is broader, has a flattened peak and is shifted towards longer latencies. On average, the latency of the first saccades of DRs was 3% greater than the latency of the (single) saccades in SC trials. Not surprisingly, the effect on latency depended on the time interval between the presentation of the first and the second cues (ISI), and in Fig. 4B the DR data in Fig. 4A have been subdivided...
into three groups based on their ISI. When the ISI was long (122 ms, sparsely dotted line in Fig. 4B), the second cue came too late to influence the earliest saccades so that the initial “build-up” in the distribution of the DR is the same as that for the SC (control) data; however, the DR data peak slightly earlier and then start to decline, with a slight hump in the falling phase. When the ISI was intermediate (91 ms, dotted line in Fig. 4B), the earlier occurrence of the second cue resulted in an earlier deviation from the control and a delayed peak. When the ISI was short (61 ms, dashed line in Fig. 4B) the whole DR distribution was affected, losing the skew towards longer latencies except for a very slight discontinuity in the falling phase of the distribution. The normalized latency data in Fig. 4B are replotted in Fig. 4C in the form of cumulative frequency polygons, which further emphasize that the second cue increases the latency of the first saccade and that, the shorter the ISI, the earlier this effect tends to occur.

In order to determine the time course of the effect of the second cue on the latency of the first saccade, the DR data in Fig. 4 were replotted separately for each
subject with respect to the time of appearance of the second cue (that is, plotted in terms of the delay, $D$, of Becker & Jürgens, 1979): see the smoothed frequency polygons (dashed/dotted line) in Fig. 5. To render the effects of the second cue more salient, Fig. 5 includes the latency distributions for the SC trials (solid line). The latter had to be derived by aligning the SC data with respect to the times that the second cue would have appeared with the three different ISIs and then averaging them together, being careful to maintain the same proportions—with respect to DRs—of the different ISIs. The shaded differences between the two plots indicate that the major effect of the second cue on the latency distribution of the first saccades was to cause a transient dip (gray areas) followed by a small peak (vertical hatching). The first dip occurs 95–155 ms after the appearance of the second cue in subject BMS, 95–120 ms after in subject FAM, and 75–135 ms after in subject VJB. The Kolmogorov-Smirnov two-sample test confirmed that the difference in the $D$-distributions of SC and DC responses was significant in subjects BMS and VJB ($p < 0.001$), but not in subject FAM.

2.2.3. Double-cue trials: dependence of amplitude of first saccade on time of occurrence of second cue (interval, $D$)

A common finding in the classical double-step paradigm is that the spatial characteristics of the first saccade depend on how soon it follows the second cue, i.e., on the time delay, $D$ (Aslin & Shea, 1987; Baizer & Bender, 1989; Becker & Jürgens, 1979; Findlay & Harris, 1984; Groll & Ross, 1982; van Asten et al., 1988). Thus, when $D$ is short, the first saccades are directed exclusively towards the first stimulus location and, when $D$ is long, the first saccades are directed exclusively towards the second stimulus location; at intermediate delays, the first saccades are directed to intermediate locations. In our DC paradigm too, when the first saccades occurred very soon after the second cue ($D$ was small), they were directed exclusively towards the first cued target but, when the first saccades occurred long after the second cue ($D$ was large), they were not always directed at the second cued target: many were still directed at the first cued target and a few to intermediate locations. This is evident from Fig. 6, which shows the dependence of the endpoints of the first saccades (in DC trials) on the delay interval, $D$. Fig. 6A shows the DR data (adjacent and opposite DC trials are pooled together) and so plots the component of the saccade in the direction of the first cued target, whereas Fig. 6B shows the SR data and so plots the component in the direction of the second cued target. For these plots, which show sample data for one subject (BMS), the data were normalized with respect to the mean amplitudes of the saccades to the same cued locations in
the SC trials, thereby allowing the pooling of the data for saccades in all four directions. We then constructed smoothed frequency polygons to delineate the $D$-interval distributions for the DR and SR data. These distributions for subject BMS are shown in Fig. 6C and the distributions for the other two subjects are shown in Fig. 6D and E, the DR data being shown in thin solid lines and the SR data in thick solid lines. It is clear from
these plots that the distributions of the first saccades in DR and SR trials overlapped substantially (see the shaded areas in Fig. 6C–E), in contrast to the situation in the classical double-step paradigm. The percentage of DRs that overlapped SRs was 16%, 16% and 19% for the three subjects (BMS, FAM, VJB) and the corresponding percentage of SRs that overlapped DRs was 71%, 94% and 45%. (For the reader unfamiliar with the usual double-step data, it might be useful to preview Fig. 13A–E, which shows corresponding plots for the classical double-step paradigm. In particular, compare the data for subjects BMS (Figs. 6C and 13D) and FAM (Figs. 6D and 13E).) The horizontal dotted lines in Fig. 6A delineate the ±2 SD limits of the saccadic amplitude distributions in SC trials, and endpoints outside these limits were deemed to be intermediate-amplitude DRs. Using this 2SD criterion, we partitioned the DR data into first saccades that ended near the first target (dotted lines in Fig. 6C–E) and first saccades that ended at intermediate locations (dashed/dotted lines in Fig. 6C–E). It is now evident that intermediate-amplitude saccades were relatively few in number, most saccades ending near one or other target.

2.3. Discussion of Experiment 1

In the DC paradigm, in which several potential saccade targets were continuously visible and subjects were cued by pointers at fixation, most of the first saccades tended to land in the vicinity of the two targets but a few fell in between. In one of our subjects, the saccades that landed at intermediate locations were clearly spread around the line joining the two targets (Fig. 3A), as though resulting from the sum of two weighted vectors directed towards the two target locations (cf. Aslin & Shea, 1987; Becker & Jürgens, 1979; see also Fig. 5 from Schiller & Sandell, 1983). In the other two subjects, however, many of the intermediate saccades fell short of this line. The saccadic endpoints did not show the pattern of dependence on the time elapsed since the second cue (i.e., on the time interval, D) that is so characteristic of the double-step paradigm (Aslin & Shea, 1987; Baizer & Bender, 1989; Becker & Jürgens, 1979; Findlay & Harris, 1984; Groll & Ross, 1982; van Asten et al., 1988); even when D was long—allowing what would have been adequate time for the subject to program saccades exclusively to the second target in the double-step paradigm—subjects continued to make some of their first saccades to the first target (or to intermediate locations) in the DC paradigm.

A second observation in our DC paradigm that was at odds with the findings in the usual double-step paradigm concerned the latency of the first saccades. Thus, compared with SC trials, on DC trials some latencies were under-represented, giving rise to a trough, whereas some subsequent latencies were over-represented, giving rise to a transient peak: see the latency distributions plotted with respect to the delay, D, in Fig. 5. This trough-peak sequence suggests to us that saccades that normally would have occurred during the period 75–155 ms after the second cue are delayed by 25–60 ms. Later experiments will show that this transient delaying effect of the second cue can be much more pronounced.

One other feature of our data—the absence of intermediate-amplitude first saccades towards the second target in the opposite DC trials—appeared to be in accord with observations in the usual double-step paradigm: see Fig. 3C (cf. Aslin & Shea, 1987; Becker & Jürgens, 1979; Findlay & Harris, 1984; Groll & Ross, 1982).

Subsequent experiments will further examine the effect of the second cue on the latency (Experiments 2 and 3) and the end-point (Experiment 4) of the first saccade.

3. Experiment 2: the double-cue paradigm with an acoustic “go” signal

In these experiments the first cue was divided up into two parts: as in Experiment 1, a pointer appeared near the fixation point but this time it appeared only briefly and indicated only where the first saccade should be directed; a subsequent brief tone indicated when that saccade should be executed. On half the trials, another pointer—aimed at the same or another target—subsequently appeared and, as before, immediately took precedence over the first one. Thus, subjects now had time to prepare some aspect(s) of the required response while waiting for the acoustic “go” signal. For example, they could begin to discriminate the first cue and select the target for their saccade before the go signal was presented. We were interested in the extent to which the phenomena seen in Experiment 1 were still evident when the programming of the first saccade was allowed to proceed to a later stage before any change in the required goal could occur. This slight modification of the paradigm eliminated SRs in DC trials and intensified the effects of the second pointer on the latency of the first saccade in DRs. In a separate variant with the acoustic go signal (Experiment 2a), we found that the first saccade was still transiently delayed by the second pointer even when the subjects were instructed to ignore it.

3.1. Methods

Subjects and experimental setup were the same as in Experiment 1, except that in Experiment 2a one subject
(FAM) was replaced by another (JWB) who was naïve as to the purpose of the recordings and had not previously participated in any experiments in this study. The spatial and temporal events during the individual trials are indicated diagrammatically in Fig. 7. Each trial started with a gray display containing only a central black fixation dot with an adjacent white pointer that indicated the future location of the target for a saccade. Subjects were required to fixate the dot for a variable period of time (500–1000 ms), after which the pointer was removed and four peripheral white target squares, like those in Experiment 1, immediately appeared. Subjects were required to continue fixating the dot for a variable period of time (500–2500 ms) until a brief tone (7 ms) was presented, at which time subjects were required to make a saccade to the cued square as quickly as possible. At this point, half the trials ended: SC trials (where “single” here refers to the fact that there was only a single cued target). In the remaining trials, a second pointer, similar to the first, now appeared and could be aimed at any one of the four squares: DC trials (where “double” here refers to the fact that there were two cued targets, and the second pointer will still be referred to as the “second” cue). The interval between the onset of the tone and the onset of the second pointer cue (ISI) could be 39, 59 and 79 ms. In the main experiment, subjects were told that the square indicated by this new pointer should now take precedence and they should redirect their fixation towards it as soon as possible. In an additional experiment, subjects were instructed to ignore the second cue, i.e., they were always required to make a saccade to the first cued target (Experiment 2a).

3.2. Results

3.2.1. Double responses: latency of the first saccades

Using a tone as a go signal, saccadic latencies were shorter than in Experiment 1 (for which the go signal had been the appearance of a pointer at the fixation point). For example, the average saccadic latencies (3 subjects) in SC trials were 159, 158, 167 and 161 ms for upward, rightward, downward, and leftward responses, respectively, which is on average 45–60 ms less than in Experiment 1. The other major consequence of using the tone as a go signal was to intensify the effects of the second cue on the latency of the first saccade to the first cued square. This is evident from the normalized latency distributions of the first saccades in DR trials shown in Figs. 8 and 9, which have a similar layout to Figs. 4 and 5, respectively. Thus, the overall latency distributions for Experiment 2 show a pronounced decrement compared with the control SC data (Fig. 8A), and this is manifest as a clear trough in the data for each ISI (Fig. 8B) that commences at earlier times with the shorter ISI than with the longer ISI—an effect now very clear in the cumulative frequency polygons (Fig. 8C). Further, when these latency data are replotted separately for each
Fig. 8. Experiment 2: normalized latency distributions of first saccades in DRs with respect to the time of appearance of the first cue (pooled data for three subjects). Layout and conventions as in Fig. 4.

Fig. 9. Experiment 2: normalized latency distributions of first saccades in DRs with respect to the time of appearance of the second cue. (A–C) Smoothed frequency polygons comparing the latency distributions of first saccades in DRs (dashed/dotted line) with the saccadic latencies in the SC trials (solid line) for each of the three subjects. Layout and conventions as in Fig. 5. (D) Effect of the second cue on the latency distribution of the first saccades in DRs: differences between the D-distributions of the DC and SC responses (DC–SC) for each of the three subjects. Abscissa, delay, $D$ ms (bin width, 20 ms).
subject with respect to the onset of the second cue (time interval, \(D\)), the troughs are now much more pronounced and followed by a substantial peak so that the distributions are now clearly bimodal: see the smoothed frequency polygons in Fig. 9A–C. The Kolmogorov–Smirnov two-sample test confirmed that the difference in the \(D\)-interval distributions of SC and DC responses were significant in all three subjects (\(p < 0.001\)). The time course of the trough-peak sequence differed slightly in the three subjects and this is apparent from Fig. 9D, which shows the differences between the \(D\)-distributions of the DC and SC responses (DC–SC).

The second cue still transiently delayed the occurrence of the first saccade even when subjects were instructed to ignore that cue (Experiment 2a): see plots of the differences between the \(D\)-distributions of the DC and SC responses (DC–SC) for each of the three subjects in Fig. 10, which are very similar in form (and magnitude) to those in Fig. 9D. The Kolmogorov–Smirnov two-sample test confirmed that the differences in the \(D\)-distributions of DC and SC responses in Fig. 10 were significant in all subjects, one of which (JWB) had had no prior experience or knowledge of the purpose of any of the experiments in this paper. That our subjects complied with the request to ignore the second cue is indicated by the fact that none of them made any saccades to the second cued location.

3.2.2. Other observations in Experiment 2

Within the (ample) response time permitted—two standard deviations longer than the mean latency in the SC experiments—our subjects almost never made saccades directly towards the second cued target. Thus, SRs were virtually absent (0–2 cases per subject) in the DC trials with an acoustic go signal. Further, there were very few saccades directed to intermediate locations between the two cued targets, so that the endpoints of the vast majority of first saccades of DRs were in the vicinity of the square defined by the first cue. We, therefore, restricted our quantitative analysis of first saccades to the latency data. Three-saccade DRs were common in the DC trials (average for the 3 subjects: 38% of trials; range: 25–59%).

3.3. Discussion of Experiments 2 and 2a

In these experiments, subjects had to withhold their responses to the first cue until an acoustic go signal was presented. This resulted in the first saccades having shorter latencies than in Experiment 1 (on average by 51 ms in Experiment 2), which is perhaps not surprising because subjects now had time to prepare some aspect(s) of the required response while waiting for the acoustic go signal. Furthermore, this completion of certain early stages of the programming of the first saccade in DC trials might be responsible for the almost complete absence of SRs in Experiment 2 (in sharp contrast with Experiment 1); programming of the first saccade had reached a point where it could no longer be completely cancelled. Also, in these new experiments, more of the first saccades were delayed by the second cue (compare Figs. 8 and 4), and when the latency of the first saccade was plotted with respect to the onset of the second cue (Fig. 9), there was now a very pronounced trough followed by a peak. The time course of this effect is best seen when the SC responses are subtracted from the DC responses: Fig. 9D. These plots suggest that many saccades that would normally have occurred 80–135 ms after the second cue were delayed on average by 40–50 ms. The finding that the second cue had a greater effect on the latency of the first saccade in Experiment 2 than in Experiment 1 might reflect differences in the salience of the second cues, the abrupt appearance of the second cue perhaps being more obvious when it occurs in isolation (the first cue having disappeared some time earlier in Experiment 2) than when combined with the disappearance of the first cue (as in Experiment 1).

The finding that the second cue still caused a transient delay of the first saccade when subjects were instructed to ignore the second cue (Experiment 2a, Fig. 10) strongly suggested that this delaying effect was not related to the cognitive nature of the second cue and led us to consider the possibility that such an effect might also be observed with a reflexive second cue. In the next study (Experiment 3), we examined this possibility using...
a hybrid paradigm in which the first cue was cognitive
(as in the DC paradigm) and the second cue was re-
flexive (as in the double-step paradigm).

4. Experiments 3a and 3b: a hybrid paradigm in which the first cue is cognitive and the second cue is reflexive

In these experiments, we examined the effect of a re-
flexive second cue on the latency of the first saccade. In
Experiments 1 and 2 the second cue was a cognitive one—a small pointer that appeared adjacent to the fix-
ation point—and caused a transient delay of the first
saccade. In the present experiments, the second cue was
the target itself—either its sudden appearance or dou-
bling in size—indicating directly to the subject that this
was now the new target, i.e., we used a reflexive second
cue/target rather than a cognitive cue. We again used
the acoustic go signal—because it gave the most pro-
nounced delaying effect—and instructed the subjects to
ignore the second cue/target, exactly as in Experiment
2a—because this had little effect on the outcome and
subjects found it much easier to do (allowing us to ac-
quire the data in fewer sessions). We report that a re-
flexive second cue/target could also delay the first
saccade but this effect was pronounced only when the
cue/target was presented at the fovea (Experiment 3b)
and not when presented in the periphery (Experiment
3a).

4.1. Methods

Three subjects participated in these experiments
(BMS, FAM, JWB). Subject JWB was naïve as to the
purpose of the experiment. The experimental setup and
instructions to the subjects were the same as in Experi-
ment 2a, i.e., subjects were asked to ignore the second
cue/target and to always make a saccade to the first cued
target. In Experiment 3a the second cue/target was a
sudden enlargement of one of the peripheral white
squares (from $0.4^\circ \times 0.4^\circ$ to $0.8^\circ \times 0.8^\circ$), and in Exper-
iment 3b it was the sudden appearance of a white square
($0.8^\circ \times 0.8^\circ$) at fixation: see the cartoons in Fig. 7.

4.2. Results

In Experiment 3b, when the reflexive second cue/
target was presented at fixation, the first saccade was
transiently delayed so that the normalized $D$-distribu-
tions were again bimodal and the differences of the differ-
ences between the $D$-distributions of the DC and SC responses (DC–SC) again showed a trough followed by a peak: Fig. 11A–C, solid traces. The Kolmogorov–Smirnov
two-sample test confirmed that the differences in the $D$-
distributions of the DC and SC responses were signifi-
cant in all three subjects in Experiment 3b ($p < 0.001$).
Thus, Experiment 3b essentially replicated the data ob-
tained in Experiments 2a (Fig. 10) using a second cue
that was reflexive in place of one that had been cognitive
in the previous experiment. However, in Experiment 3a,
when the reflexive second cue/target was presented in the
periphery rather than at fixation, the $D$-distributions
were essentially unimodal and plots of the differences
between the DC and SC responses at best showed only
small troughs and peaks: Fig. 11A–C, dotted traces.

Indeed, the Kolmogorov–Smirnov two-sample test in-
dicated that the differences in the $D$-distributions of the

![Fig. 11. Experiments 3a and 3b: effect of a reflexive second cue on the latency of the first saccade and its dependence on the retinal eccentricity of the second cue. Cartoon shows the time sequence of events along with a schematic drawing of the associated eye movements. Plots show differences between the DC and SC responses (DC–SC) for each of the three subjects when the second cue was peripheral (Experiment 3a, dotted line) and at/near the fovea (Experiment 3b, solid line). Abscissa, delay, $D$ (bin width, 20 ms).]
DC and SC responses in Experiment 3a were significant only in one subject (JWB), and even for this subject the trough in the $D$-distribution was appreciably smaller in Experiment 3a than in Experiment 3b (Fig. 11C). That none of the subjects made any saccades to the second cued location in Experiments 3a and 3b indicates that, again, they complied with the request to ignore the second cue.

4.3. Discussion of Experiments 3a and 3b

Despite the fact that the subjects were instructed to ignore the second reflexive cue/target entirely and to make only one saccade to the first cued target—which they did—the second cue/target consistently delayed the first saccade when presented at the fovea (Experiment 3b), though not when presented in the periphery (Experiment 3a). In fact, the effects in Experiment 3b were almost as strong as in Experiment 2a. Thus, in order for the second cue to delay the first saccade it was much more important that it be located near the fovea than that it be cognitive or reflexive.

5. Experiments 4a and 4b: effect of leaving the first target on in the classical double-step paradigm

In their double-step experiments using reflexive cues/targets, Becker and Jürgens (1979) showed that when the first saccades occurred soon after the second target appeared they were directed exclusively at the location of the first stimulus and when the first saccades occurred long after the second target appeared they were directed exclusively at the location of the second target; at transitional times, the first saccades were directed at intermediate locations. This led to the idea that the sole determining factor for the endpoint of the first saccade was the latency of that saccade with respect to the appearance of the second target (the delay interval, $D$). In our DC paradigm (Experiment 1), we did not see such a sharp division: subjects continued to make some of their first saccades to the first cued location even as $D$ increased and as other first saccades were directed at the second cued location. One clear difference between the two kinds of experiments—in addition to the cognitive vs. reflexive nature of the cues—was that in the usual double-step paradigm there was only ever one target visible at any given time whereas in our DC paradigm all of the potential targets for a saccade remained visible throughout. We now report that a slight modification of the standard double-step paradigm—leaving the first target on—was sufficient to cause subjects to continue to make some of their first saccades to the first target even as the time elapsed since the appearance of the second target increased and subjects began to make some of their first saccades to the second target.

5.1. Methods

Three subjects (AI, BMS and FAM) participated in the experiments using a setup that was the same as in Experiment 1. Subject AI was naïve as to the purpose of the experiment and had not participated in Experiments 1–3.

All trials started with a gray display containing a central black dot (Fig. 12) that subjects were required to fixate for a variable period of time (500–1000 ms) until a white square ($0.08 \times 0.08^\circ$) appeared in the periphery at one of four locations $10^\circ$ below, above, to the left of, or to the right of, the fixation dot. Subjects were instructed to make a saccade to the square as soon as possible. At this point, half the trials ended: single-step trials. In the remaining (double-step) trials, after a variable ISI (38, 60 or 76 ms), a new square appeared at one of the three remaining peripheral locations. In Experiment 4a, the first square disappeared as soon as the second one appeared, as in the usual double-step experiment, whereas in Experiment 4b the first square remained present throughout the remainder of the trial. Subjects were told that the second target should take precedence over the first one and they should now redirect their gaze to this second target as soon as possible.

In a preliminary attempt to run Experiment 4a, subjects were required to respond within two standard deviations of their mean latencies in a control experiment that had only single steps but we found that this could not be achieved with the shortest ISI. Because of this, we raised the permissible maximum latency by 50 ms.

5.2. Results

In Experiment 4a—the classical double-step paradigm—the first saccades tended to arrive in the vicinity of the first target for small values of $D$, in the vicinity of the second target for large values of $D$, and at intermediate locations for intermediate values of $D$. This tendency is clearly evident from the $D$-distributions in Fig. 13A–E, which has the same layout as Fig. 6. Thus, Fig. 13A and B shows the raw endpoint data for the naïve subject (AI), with the DRs (in which the first saccades landed near the first target or at an intermediate location) in A, and the SRs (in which the first saccades landed in the vicinity of the second target) in B. Fig. 13C–E shows the frequency polygons for each of the three subjects for SRs (thick solid lines) and DRs (thin solid lines), as well as the breakdown of the latter into those saccades that ended near the first target (dotted lines) and those that ended at an intermediate location (dashed/dotted lines). The major point of
interest here is that the \( D \)-distributions for the DRs and SRs generally show only modest overlap (see shaded areas). The percentage of DRs that overlapped SRs was 5\%, 3\% and 25\% for the three subjects (AI, BMS, FAM) and the corresponding percentage of SRs that overlapped DRs was 17\%, 2\% and 23\%.

The data for Experiment 4b—the modified double-step paradigm in which the first target stayed on—are shown in Fig. 13F–J (same layout as for Experiment 4a in Fig. 13A–E), and it is immediately obvious that there is now much more overlap between DRs and SRs than in Experiment 4a because some first saccades to the first target (and to intermediate locations) are more delayed. The percentage of DRs that overlapped SRs was 21\%, 19\% and 34\% for the three subjects (AI, BMS, FAM) and the corresponding percentage of SRs that overlapped DRs was 69\%, 22\% and 60\%. Most of these values are appreciably higher than in Experiment 4a.

To assess the statistical significance of the differences in the \( D \)-distributions in Experiments 4a and 4b, the individual \( D \)-values of the DRs obtained in each experiment were normalized with respect to the mean \( D \)-value of all SRs in the same experiment (\( D_{sr} \) measures). When normalized in this way, the distributions of the first saccades in DRs in Experiment 4b clearly lagged those in Experiment 4a: see Fig. 14, which shows the average data pooled from all three subjects, with the data from Experiment 4a in dotted line and the data from Experiment 4b in thick solid line. The Kolmogorov–Smirnov two-sample test indicated that the differences in the \( D_{sr} \)-distributions in Experiments 4a and 4b were significant for each of our three subjects (\( p < 0.001 \)). Thus, the “classical” dependence of the endpoint of the first saccades on the time elapsed since the appearance of the second target was significantly disrupted when the first target was left on.

In most experiments, our subjects generally ended up acquiring the correct target, and in Experiment 4a, for example, none of the subjects \textit{ever} ended up at the wrong target (though they did sometimes fail to arrive within the allotted time). In Experiment 4b, however, subjects made errors, on average ending up at the wrong target.
5.3. Discussion of Experiment 4

One of the interesting aspects of the classical double-step experiments was that the endpoint of the first saccade was largely determined by the time when it occurred with respect to the second cue, i.e., by the delay interval, $D$. We confirmed the classical finding: when $D$ was small the first saccades were directed exclusively to the second target and when $D$ was large the first saccades were directed exclusively to the first target; for intermediate values of $D$ there was a gradual transition in which many saccades ended at intermediate locations.

target in 14.4% of trials (20%, 8.8%, 14.4% for the three subjects).

Fig. 13. Experiment 4: dependence of the endpoint of the first saccade in double-step trials on the time of appearance of the second target and the effect of leaving the first target on. (A–E) Experiment 4a in which the first target is turned off when the second appears, as in the usual double-step paradigm. (F–J) Experiment 4b in which the first target stays on. Layout and conventions as for Fig. 6, except that $D$ was normalized with respect to the average latency of the saccades in the corresponding single-step trials (see text). (A, B, F, G) data of subject AI.
This dependence on $D$ tended to break down if the first target stayed on: subjects continued to make DRs in which the first saccades ended near the first target even as the $D$-interval increased and as subjects began to make SRs directly to the second target.

However, leaving the first target on rendered the task more difficult, especially when the ISI was short, so that subjects now made errors, i.e., ended up at the wrong target, presumably because they could not always discern the true sequence of target presentation. This raises the possibility that some (or all?) of the changes in the $D$-distributions of the DRs caused by leaving the first target on simply resulted from false-positive errors. If we had used an ISI of zero (synchronous onset), for example, we might have expected that our subjects would have performed at chance levels, ending up at the wrong target in half the trials. In this worst-case scenario, the probability of making a correct response by chance (a false positive) is the same as the probability of making an error. We can therefore use the DR errors in Experiment 4b as a worst-case estimate of the number of correct DR that occurred by chance in that experiment. Accordingly, for each subject, we determined the $D_{sr}$-distribution of the DRs on error trials and then subtracted this from the $D_{sr}$-distribution of the DRs on correct trials, effectively excluding the maximum amount of data likely to have resulted solely from chance (false positive errors). The resulting $D_{sr}$-distribution of correct DRs in Experiment 4b then had to be rescaled so that the sum was still 100%. Even after this subtraction of the estimated (maximum number of) false-positive errors and rescaling, the Kolmogorov–Smirnov two-sample test indicated that the differences in the $D_{sr}$-distributions of the DRs in Experiments 4a and 4b were still significant for each of our three subjects ($p < 0.01$). The thin solid line in Fig. 14 plots the average $D_{sr}$-distributions of the DRs for the three subjects after subtracting the estimated (maximum) false-positive errors and rescaling, indicating that the data from Experiment 4b still clearly lagged those from Experiment 4a. We conclude, therefore, that although likely to contribute, false-positive errors cannot fully account for the observed differences in the $D$-distributions of the first saccades in Experiments 4a and 4b.

6. General discussion

6.1. General characteristics of the double-cue paradigm

The saccadic eye movements in our DC paradigm, in which cognitive cues signaled the targets (Experiments 1 and 2), had three major features in common with the saccadic eye movements in the classical double-step paradigm, in which the targets themselves provide this information (Experiment 4a). First, there were two types of responses: DRs (IARs of Becker & Jürgens, 1979; type I of Carlow et al., 1975; type a of Robinson, 1973) and SRs (FARs of Becker & Jürgens, 1979; type II of Carlow et al., 1975; type b of Robinson, 1973). Second, the endpoints of the first saccades were spatially distributed between the two targets when those targets were located within a single visual quadrant, as in the adjacent DC trials (Aslin & Shea, 1987; Becker & Jürgens, 1979; Findlay & Harris, 1984; Groll & Ross, 1982). Third, there were no intermediate-amplitude saccades in the direction of the second target if the two targets were on opposite sides of the initial fixation point, as in the opposite DC trials (Aslin & Shea, 1987; Becker & Jürgens, 1979; Findlay & Harris, 1984; Groll & Ross, 1982). On the other hand, there were other respects in which the first saccades in the two paradigms differed. Thus, in the DC paradigm, the endpoints of the first saccades showed much weaker dependence on the time elapsed since the second cue ($D$) than is usual in the double-step paradigm. Further, many of these first saccades were delayed by the second cue in our DC paradigm but there was little evidence of such delays in the wake of the second target in the double-step paradigm. These differences in the saccadic eye movements in the two paradigms seem to be unrelated to the cognitive and reflexive nature of the second cue and will be the major focus of the remainder of the discussion.
6.2. Endpoint of the first saccade: dependence on the delay, D

In the usual double-step paradigm (Experiment 4a), the first target is turned off when the second appears and first saccades that occur soon afterwards tend to go to the first target whereas first saccades that occur later tend to go straight to the second target. If the first target is left on throughout the trial (Experiment 4b) then subjects persist in making some of their first saccades to that first target even long after the appearance of the second target, and we have provided evidence that this is not simply due to confusion about the target sequence (false positive errors). Thus, when there is no explicit invalidation of the initial goal by turning off the first target, that target continues to be a candidate for a saccade, i.e., the physical removal of the first target is critical for the dependence on D to emerge. The lack of dependence on D in our DC paradigm is consistent with this insofar as the first cued target remains present after the second cue appears. Thus, turning off the first cue when the second cue appears in our DC paradigm does not have the impact of turning off the first target in the double-step paradigm, consistent with the idea that it is the continued presence of the previously cued target per se that is the important factor. The relative paucity of saccades of intermediate amplitude in our DC paradigm—most saccades ended in the vicinity of one of the two targets—implies a winner-take-all situation that others have modeled with mutual inhibition: for recent review see Findlay and Walker (1999).

6.3. Latency of the first saccades

When the second cue/target appeared at the fovea it caused a transient increase in the latency of the first saccade, regardless of whether it was reflexive (as in Experiment 3b) or cognitive (as in Experiments 1 and 2), so that saccades that ordinarily would have been expected to appear \( \sim 80-135 \) ms after the onset of the second cue/target were delayed \( \sim 40-50 \) ms (Figs. 5 and 9), often resulting in a bimodal latency distribution. Others have reported phenomena that we think might be related to this delaying effect of a second cue/target at the fovea and we will now briefly review these findings.

In the experiments of Becker and Jürgens (1979) there was an experimental condition (SP: symmetrical pulse) in which the target briefly stepped to the periphery and then stepped back to the original fixation point. For one of their subjects the frequency distribution of saccadic amplitudes plotted against D shows a clear gap for delays around 100 ms (see their Fig. 5; third row; right column). Becker and Jürgens did not comment on this result, perhaps because their data sample was small and hence the gap was not always apparent. Hanes and Schall (1995) utilized a countermanding paradigm to investigate saccade initiation. Monkeys were trained to generate a saccade to a peripheral target but, on a fraction of trials, the fixation point reappeared after 25–250 ms, indicating to the animals that they should try to withhold their responses. Note that this paradigm is similar to the “SP” condition in the double-step experiments of Becker and Jürgens (1979), except that in Hanes and Schall’s (1995) experiments the peripheral target was left on when the fixation point reappeared. With longer delays, monkeys increasingly failed to withhold the response and the authors hypothesized that there was a race between go and stop processes, estimating the average covert latency to a stop signal to be 80 ms. Although Hanes and Schall (1995) do not present latency distributions of nonwithheld responses, data from their Fig. 7 indicate that the reappearance of the fixation point delayed those saccadic responses that it failed to abort. In a follow-up study on humans, these authors estimated the stop-signal reaction time to be 125–145 ms (Hanes & Carpenter, 1999), which compares well with the timing of the “trough” in the D-distributions in our experiments. Others have estimated the average stop-signal reaction time to be 113 ms (Cabel, Armstrong, Reingold, & Munoz, 2000).

Walker, Deubel, Schneider, and Findlay (1997) presented two stimuli simultaneously, one a target for a saccade and the other a distractor, and showed that the distractor produced a robust increase in the latency of the saccades to the target. This occurred with distractors at any location in the visual field except for a narrow sector of \( \sim 40^\circ \) width centered on the target axis. The increase in latency was maximal when the distractor appeared at the central fixation point, and decreased monotonically as the distractor was positioned more peripherally. Using monkeys, Chou, Sommer, and Schiller (1999) also showed that the selection of one stimulus as a target and the avoidance of another as a distractor led to an increase in saccadic latency. These authors compared the latencies of saccades to a single visual stimulus to those when a pair of identical visual stimuli was presented isoecentrically with a variety of angular separations. Even though in the latter condition neither of the two stimuli was explicitly defined as a distractor or a target (so that the animals were free to make a saccade to either), the “pair” condition resulted in elevated latencies. The effect was minimal when the angular separation between the two stimuli was 30\(^\circ\), but it was robust and consistent when the angular separation was 60\(^\circ\) or 90\(^\circ\). However, many of the responses that Chou et al. recorded in the pair condition were averaging saccades, and those were more frequently observed when the angular separation between the two
stimuli was minimal. At the same time the authors reported a significant negative correlation between the frequency of averaging saccades and the latency. This means that the elevated latencies in the pair condition at 60° and 90° separations occurred when the selection of one of the stimuli was complete and the influence of the second stimulus was effectively wiped out. This short review of the literature suggests that when a second stimulus appears at the fovea it acts as a powerful distractor and we suggest that this is a useful way to view the second cue in our study. Although the “distractor” paradigms are clearly different in many respects from the double-step and DC paradigms, the similarity of the results in all three types of experiments (in regard to delays, and foveal vs. peripheral effects) implies common brain mechanisms that might underlie all of them.

Others have observed a distinct “gap” in the latency distributions of first saccades when the second stimulus was peripheral. Sommer and Tehovnik (1999) trained monkeys to perform a double-step task in which the target was initially presented for 110 ms at one peripheral location and then positioned at another peripheral location for 20 ms, before being extinguished. Monkeys were required to make sequential saccades to the two locations in the same order that the target traversed them. Sommer and Tehovnik observed a ~20-ms gap in the latency distribution of the first saccades ~190 ms after the target appeared at the first location, i.e., ~80 ms after the shift to the second location, which is close to the latency of the delay in our experiments (on humans). In our experiments, the second stimulus generally delayed the onset of the first saccade only when presented at the fovea, which seemingly conflicts with the results of Sommer and Tehovnik. However, in our DC paradigm subjects were free to direct their initial response towards either of the two successively presented stimuli, that is, both DRs and SRs were allowed. In the experiments of Sommer and Tehovnik, on the other hand, the subjects had to remember and follow the order of stimulus presentation. We would argue that, in the latter situation, the second stimulus was much more of a distractor because the monkeys were required not only to remember its location but also to avoid responding to it until they had executed the saccade towards the first stimulus.

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References


