

Judging relative positions across saccades

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Abstract

When components of a shape are presented asynchronously during smooth pursuit, the retinal image determines the perceived shape, as if the parts belong to the moving object that the eyes are pursuing. Saccades normally shift our gaze between structures of interest, so there is no reason to expect anything to have moved with the eyes. We therefore decided to examine how people judge the separation between a target flashed before and another flashed after a saccade. Subjects tracked a jumping dot with their eyes. Targets were flashed at predetermined retinal positions, with a 67–242 ms interval between the flashes. After each trial subjects indicated where they had seen the targets. We selected the trials on which subjects made a complete saccade between the presentations of the two targets. For short inter-target intervals, subjects' judgements depended almost exclusively on the retinal separation, even when there were conspicuous visual references nearby. Even for the longest intervals, only part of the change in eye orientation was taken into consideration. These findings cannot simply be accounted for on the basis of the mislocalisation of individual targets or a compression of space near saccades. We conclude that the retinal separation determines the perceived separation between targets presented with a short interval between them, irrespective of any intervening eye movements.

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Localising objects is an important function of the visual system. To do so it is not enough to know the retinal positions of the objects' images. In order to reach out and pick up objects, the brain must relate retinal positions to postures of the arm. For this the orientation of the eyes must be considered. And indeed, there is compelling evidence, both from single cell recordings (e.g. Duhamel, Colby, & Goldberg, 1992; Kusunoki & Goldberg, 2003; Walker, Fitzgibbon, & Goldberg, 1995) and from studies of the errors that occur if targets are flashed during smooth pursuit or near the time of saccades (e.g. Brenner, Smeets, & van den Berg, 2001; Honda, 1993; Mateeff, 1978; Matin, Matin, & Pola, 1970; Rotman, Brenner, & Smeets, 2004; Schlag & Sch-

lag-Rey, 1995, 2002), that objects are localised by combining retinal positions with information about the orientation of the eyes.

For other functions of the visual system, such as determining the colour or texture of objects' surfaces, there is less to be gained from knowing the orientation of the eyes, so presumably such surface properties are determined on the basis of the retinal images alone. For judgments of objects' shapes it is not evident whether the eye orientation is relevant. Shape judgments could be built up from locations that are determined by considering the orientation of the eyes. This would have the advantage of allowing our brain to build up judgements of shape as we look around, possibly even combining different parts of an object as they come into view as a consequence of our own movements or the movements of other, nearby, occluding objects. Alternatively, shape judgments could be derived directly

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from the retinal images, without considering eye movements. If so it would be undesirable to combine positions across eye movements. The latter method clearly has its limitations, but it is simpler, and therefore probably also faster, which is advantageous if such information is to guide our actions (Brenner & Smeets, 2001).

One way to determine whether eye movements are taken into consideration when judging objects' shapes is by presenting separate parts of the objects asynchronously while the eyes are moving. If this is done during smooth pursuit eye-movements the retinal image alone determines the shape that we perceive (Brenner & Cornelissen, 2000; Li, Brenner, Cornelissen, & Kim, 2002). This could mean that we generally do not consider the orientation of the eyes when judging shape. However smooth pursuit may not be the best kind of eye movements to test this hypothesis. A possible explanation for the lack of consideration of eye movements during smooth pursuit is that we cannot tell whether the components are parts of the object that we are pursuing with our eyes, or parts of another static object, because they are visible for too short a time interval. Since we usually direct our eyes at the object that interests us, the former interpretation may be the most reasonable. Moreover, the lack of retinal smear, due to the short presentation, may be taken to indicate that the object is moving with the eyes, because normally that is the condition in which an image will not shift across a moving retina. The intermittent presentation could (automatically) be attributed to occlusion by nearby objects. Thus the fact that the eye has moved may "intentionally" be ignored when targets are flashed during pursuit, rather than this reflecting the inability to consider eye movements.

If this explanation is correct then we do not expect the same to happen if saccades rather than smooth pursuit moves the eyes, because saccades shift our gaze between structures of interest, so there is no reason to expect anything to have moved with the eyes. To find out whether a change in eye orientation that is due to saccades is also ignored, one can examine how people perceive the relative positions of a target presented before and another presented after a saccadic eye movement (Hayhoe, Lachter, & Feldman, 1991; Irwin, 1991; Irwin, Brown, & Sun, 1988; O'Regan & Lévy-Schoen, 1983; Sogo & Osaka, 2002). Sogo and Osaka (2002) conducted the most similar experiment to the one that we have in mind, and found that changes in eye orientation that are caused by saccades are ignored if the interval between the presentations is short. However they flashed the two targets in complete darkness, so their subjects had to rely on extra-retinal signals to determine the presence and moment of the saccade. In the present study we examine whether the same happens under more natural conditions, in which both retinal and extra-retinal information is available about the saccade. There is some evidence that it does not (see points

for the trials in which the first bar was presented about 100 ms before the onset of the saccade in Fig. 3 of Ross, Morrone, & Burr, 1997), although in that case space appeared to be compressed just before the saccade rather than the displacement of the eye being accounted for.

As in our previous study with targets flashed during smooth pursuit (Brenner & Cornelissen, 2000), we flashed two targets sequentially, both near the fovea, in the presence of a clearly visible background. We examined whether people consider the fact that the eye has moved when they determine the relative positions of the two targets. In order to ease the comparison with our previous data for smooth pursuit we kept as many parameters the same as possible. Subjects were asked to track a jumping dot with their eyes. While they did so we flashed two targets, with a short interval between them, at predetermined retinal positions. After each trial subjects indicated the two targets' positions. We selected trials on which subjects made a complete saccade in between the presentation of the two targets, and examined the extent to which the saccadic eye movement was considered when determining the targets' relative positions.

1. Methods

The stimuli were presented on a computer screen. Images were presented at 120 Hz, with a resolution of 640×480 pixels for an image size of 38.0×28.5 cm. Subjects sat with their head in a chin-rest at 38 cm from the screen, so that 1° of visual angle corresponds with about 10.7 pixels. The right eye's orientation was measured at 250 Hz with an Eyelink Gazetracker (SR Research Ltd., Mississauga, Ontario, Canada). The room in which the experiments were conducted was dimly illuminated by the light coming from the 25 cd/m^2 grey background on the screen. The stimulus presentation and eye movement recordings were controlled from Matlab using the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Pelli, 1997; see <http://psychtoolbox.org/>).

1.1. Subjects

Six subjects took part in the experiment. One was an author (S6). The other five had no idea about the purpose of the experiment. This study is part of an ongoing research program that has been approved by the local ethics committee. There were several different kinds of sessions within the experiment. Not all subjects took part in all the different kinds of sessions, but all six were tested in the main, basic condition (see below). The number of sessions in which each subject took part is given in Table 1, together with the total number of trials (excluding practice trials) and the kinds of sessions involved.

Table 1
Which sessions individual subjects performed in and the total number of trials

	Subjects					
	S1	S2	S3	S4	S5	S6
Total number of sessions	4	46	40	44	32	44
Including ones with various intervals	No	Yes	Yes	Yes	Yes	Yes
Including ones with conspicuous references	No	Yes	Yes	Yes	Yes	Yes
Including ones with retinal offset in first Target	No	Yes	Yes	Yes	No	Yes
Total number of trials	656	4789	3812	4646	3140	4482

1.2. Eye movements

Each session started with a standard, nine-point calibration of the eye movement recordings. Once this was completed subjects were subjected to a series of trials. In order to start a new trial the subject had to be fixating a small (0.25° diameter; 69 cd/m^2) yellow dot on the left side of the screen (25° from the midline). Subjects indicated that they were ready for the trial by pressing the space bar of the computer's keyboard. At that moment, errors in fixation that were smaller than 2.0° were attributed to drift, and the calibration was adjusted accordingly. If the errors in fixation were larger than 2.0° we assumed that the subject was not fixating adequately and an auditory signal was presented indicating that the subject had to try again. If several successive attempts failed then a new standard calibration was carried out.

If fixation of the yellow dot's initial position was deemed adequate, the dot started jumping horizontally across the screen. The dot jumped once every 500 ms in steps of 58 pixels (3.4 cm, or about 5°) from the left to the right side of the screen. There could be up to nine steps. The dot continued to jump until 1500 ms after the second target was presented, or until it reached the final position. Subjects followed the dot with their eyes. Since the step size had a fixed amplitude in pixels, it varied between 4.4° and 5.2° . We will therefore present all our data in pixels. Note that a distance of 10 pixels is about 1° of visual angle.

For the analysis, saccades were identified on the basis of a velocity threshold of at least five times the median eye velocity during the first 5 s of each trial. For an eye movement to be considered to be a saccade the velocity threshold had to be exceeded for at least four consecutive samples (16 ms) and the total amplitude of the change in eye orientation had to be at least 10 pixels (about 1°). The sample at the beginning of the first interval above this velocity threshold was defined as the saccade onset.

1.3. Targets

The targets were a 1° diameter white circle and a 3° long white vertical line (both 0.3° wide and 75 cd/m^2).

The two targets were presented at different times at fixed retinal locations, always 6° below the dot's path. Either target could be presented first. On most trials the first target was aligned horizontally with the fovea, and the second target could be centred at the same retinal position, or it could be 15 pixels (1.34°) to the left or right of this position. However, on some trials of some sessions the first target's position was 15 pixels to the left or right of the fovea, and the second target was at the same retinal position or 15 pixels to the left or right of that position. Due to the inevitable delays in the system, targets were not always presented at exactly the correct positions. If the error was larger than 5 pixels then that trial was discarded. Similarly, if either of the targets was presented during a saccade the trial was discarded.

The targets appeared between the third and the seventh step of the yellow dot (Fig. 1a–c shows an example with two targets appearing just after the fourth step). Subjects knew in advance that they would have to indicate where they had seen these targets. Before we started testing each subject, he or she took part in a practice session of about 60 trials. This got the subject accustomed to the procedure, as well as providing the experimenters with an estimate of the subject's saccadic latency. The practice trials were not included in the data analysis, but the estimated saccadic latency was used to plan the timing of the target presentations. Since we were interested in trials in which one target appeared just before and the other just after a saccade, we used the estimated saccadic latency to plan the first target to appear just before the estimated time of the saccade.

On most trials two targets were presented with a 67 ms interval between the presentations. However, in all sessions there were also trials with only one target (about 17% of the trials). Moreover, in some sessions there were also trials in which the interval was 125 or 242 ms. Finally, in some sessions there were trials with intervals of 67 or 242 ms, or with single targets, in which there were 10 additional conspicuous references on the screen. These references were spread regularly to form a 43.1° wide horizontal row of shapes, 2.7° below the jumping dot's path. The shapes were white 0.9° , 1.7° and 2.1° wide circles and squares, so that they formed a row of clearly recognisable references near the top of the flashed targets.

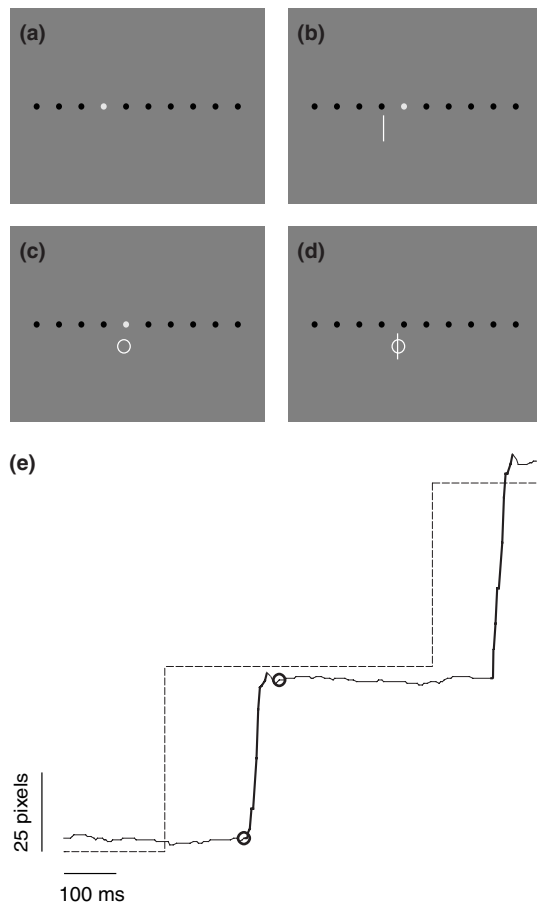


Fig. 1. A successful trial. Panels (a)–(d) illustrate four moments during the experiment. The black dots show the positions between which the bright dot jumped (they were not visible). Shortly after the bright dot jumped from the fourth (a) to the fifth position, a line was flashed directly below the subject's direction of gaze (b). The subject had not yet made a saccade to the fifth position, so the line was approximately below the fourth position. Just after the line was flashed the subject made a saccade to the fifth position, so that when a circle was flashed directly below the subject's direction of gaze 67 ms later, it was approximately below the fifth position (c). Later the subject reproduced what he had briefly seen, and where it had been, by moving a circle and a line to the appropriate positions (d). Panel (e) shows the horizontal eye movement (upwards in the figure is an eye movement to the right) in response to two of the dot's steps (indicated by the dashed lines). The thick parts show what were considered to be two saccades. The circles show the positions and the moments of presentation of the two targets. 10 pixels is about 1° of visual angle.

1.4. The task

After following the dot with their eyes until it stopped jumping across the screen, subjects had to indicate where they had seen the flashed targets. They did so by moving a continuously visible circle and line to the appropriate positions on the screen. They always first placed the circle at the position at which they had seen the flashed circle. Once they had indicated that the circle was in place (by pressing a mouse button) the line ap-

peared. The circle remained visible until the subject indicated that the line was also in place (by pressing the button again; Fig. 1d) after which both targets disappeared and the next trial could start. The circle and line that were used to indicate where the targets had been could be moved horizontally by moving the computer mouse. Their vertical positions were fixed to the correct value (6° below the jumping dot's path). They appeared at random horizontal positions on each trial. The subjects could also indicate that they had missed the target or that a setting was incorrect (because they accidentally pressed the button too soon), in which case the trial was discarded.

1.5. Analysis

The detection of saccades and the definition of saccade onset are described above (see *Eye Movements*). The saccadic latency is the time between the moment that the dot jumped and the moment that a saccade started. The real separation between two targets is the distance between the flashed targets' centres as presented on the screen. The set separation is the distance between the centre of the circle and that of the line as set by the subjects. The retinal separation is the separation on the retina, as calculated by combining the screen positions with the eye orientations at the time of presentation. In all cases a positive separation is one in which the target that was flashed last was further to the right. The individual errors for each of the targets is the difference between the real position of the flashed target on the screen and the position set by the subject for that target. A positive error is one in which the subject sets the target too far to the right.

2. Results

Fig. 1 shows an example of a successful trial. The dashed line in Fig. 1e shows the horizontal position of the dot that the subject was following with his eyes, as a function of time. The continuous line shows the horizontal eye orientation. The thick sections are the parts that were identified as saccades. The circles show the times and positions at which the two targets were flashed. In this case both were flashed directly below the direction of gaze, so they have the same horizontal orientation as the eyes themselves. It is evident from this example that the timing of the saccade is very critical, because we need trials in which the saccade starts just after the first target is flashed. We estimated when the saccade would occur on the basis of the individual subject's saccadic latencies during the practice trials, and used this estimate to time the target presentations (see *Targets* section of the *Methods*). We later selected the trials in which the timing was successful.

2.1. The saccades

Fig. 2 shows the distribution of saccadic latencies for each of the six subjects (excluding the latencies for the first, unpredictable step). All the subjects had a large peak in their response latency distribution slightly more than 100 ms after the dot stepped to its next position. In most subjects' data we can also see a second peak with a wider distribution slightly earlier in time, presumably

representing anticipatory saccades (rather than stimulus driven saccades). This is most evident for subjects S1 and S4. There is also some indication of a third kind of response, even later than the main peak. This is most evident for subject S4, and could be caused by the subject sometimes not automatically responding to the dot's steps, but intentionally making saccades after localising the new position.

Our main interest is in the trials in which we succeeded in presenting the two targets exactly before and after a saccade, with a 67 ms interval between them, as in the example in Fig. 1e. Table 2 shows the number of trials for which this was the case. It also provides information about the amplitude of the saccades in these trials. Note that the successful trials obviously always involved saccades with latencies of slightly more than 100 ms, because we presented the targets in anticipation of such latencies.

2.2. The perceived separation

More important than the number of successful trials, is how subjects judged the separation between the two targets in such trials. This is shown by the solid symbols in Fig. 3. Fig. 3 shows average values for each subject. There are three points because we divided the trials on the basis of the retinal offset that we introduced in the second target. The points' horizontal positions show the average retinal separation, which is mainly determined by the imposed retinal offset (remember that we excluded trials in which the retinal offset was incorrect due to delays in our equipment). The points' vertical positions show the average separation set by the subject. The thick solid line shows the real separation on the same trials (which depends on the saccade amplitudes). The dotted line is the unity line. If subjects had taken the change in eye orientation during the saccade into consideration, the solid points would have fallen on the thick lines. If they had ignored the eye movement altogether the points would lie on the dotted line. In most cases the points are close to the dotted line, but they tend to lie above that line, indicating that the eye movement is not ignored altogether.

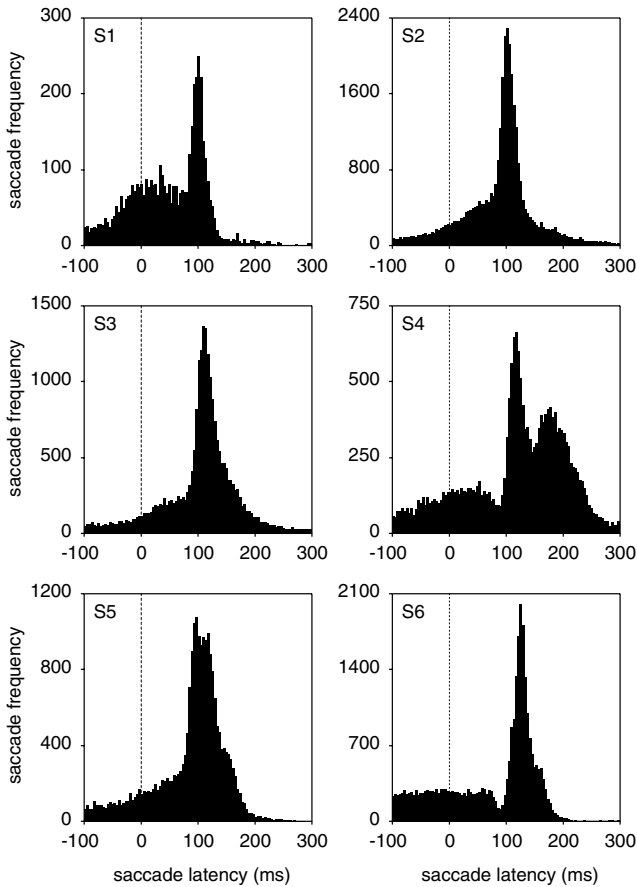


Fig. 2. Distribution of saccadic latencies in response to all steps except the very first of each trial. Each panel shows the data of one subject. The vertical scales differ a lot between the subjects because some subjects participated in many more sessions than others (see Table 1).

Table 2
Information about various parameters for the successful 67 ms-interval trials with (*italic*) and without (**bold**) conspicuous references

	Subject					
	S1	S2	S3	S4	S5	S6
Number of successful trials	48	87	167	273	126	626
	–	<i>27</i>	<i>76</i>	<i>51</i>	<i>72</i>	<i>153</i>
Mean saccade amplitude in pixels (dot jumps in steps of 58 pixels)	26.8	44.0	46.7	41.2	46.5	46.6
	–	<i>46.7</i>	<i>49.3</i>	<i>46.2</i>	<i>51.8</i>	<i>31.9</i>
Standard deviation in saccade amplitude (in pixels)	8.6	10.9	12.7	13.3	12.3	14.0
	–	<i>13.4</i>	<i>15.7</i>	<i>18.3</i>	<i>10.3</i>	<i>11.7</i>
Correlation between the errors for the two targets	0.84	0.84	0.92	0.84	0.41	0.62
	–	<i>0.20</i>	<i>0.48</i>	<i>0.55</i>	<i>0.34</i>	<i>0.46</i>

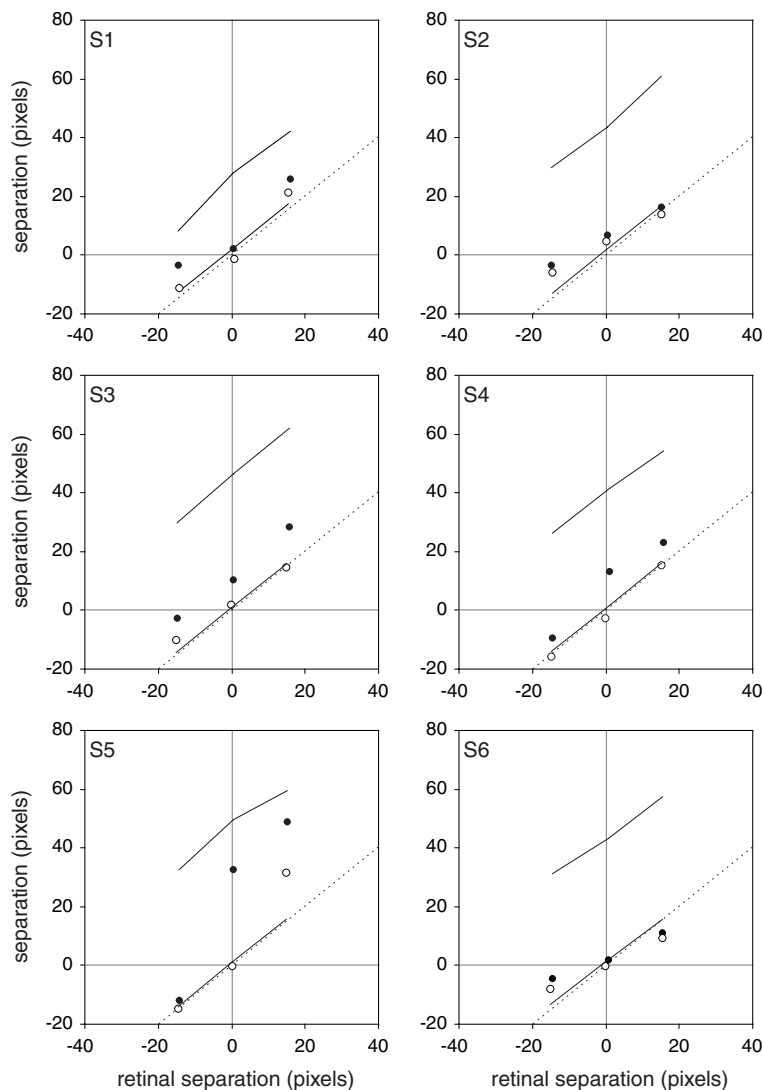


Fig. 3. The mean set separation on trials in which we did (solid symbols) or did not (open symbols) succeed in presenting one target before and the other after a saccade. The two targets were either both presented directly below the direction of gaze (data at a *retinal separation* of zero), or else the second target was presented 15 pixels further to the left or to the right (the other two values of *retinal separation*). The lines indicate the average screen separation on the trials in which we were (thick lines) or were not (thin lines) successful in timing the targets with respect to the saccade. Each panel shows the data of one subject. There was an interval of 67 ms between the targets and the targets were flashed on an empty grey screen (except for the jumping dot). 10 pixels is about 1° of visual angle.

In order to determine whether the systematic deviations from purely retinal matching are really caused by the eye movement being considered, rather than being the result of some other bias, we also analysed the set separation for trials in which the eyes did not move between the two target presentations. These are trials in which the saccade latency was so different from our estimate that both targets were shown either before or after the saccade. The thin lines in Fig. 3 show the average real separation for such trials. The retinal and set separations are shown by the open symbols. It is evident that some of the deviations from purely retinal matching for the trials with a saccade between presentations are caused by biases that are not related to the eye movements (as in O'Regan, 1984). This is particularly evident

in the data of subjects S2 and S6, where most of the solid points' deviations from the dotted line are also present in the corresponding open symbols. However it is equally evident that not all eye movements are ignored altogether, because all the solid symbols lie higher than the corresponding open symbols.

Five of the six subjects also took part in sessions in which the interval between the two target presentations was twice or four times as long. Of course, timing the saccades was much easier for the longer intervals. Whereas we only succeeded in placing one target before and the other after a saccade in about one in four trials when the interval was 67 ms, we were successful in doing so in about two out of every three trials when the interval was longer. Fig. 4 shows the five subjects' mean set

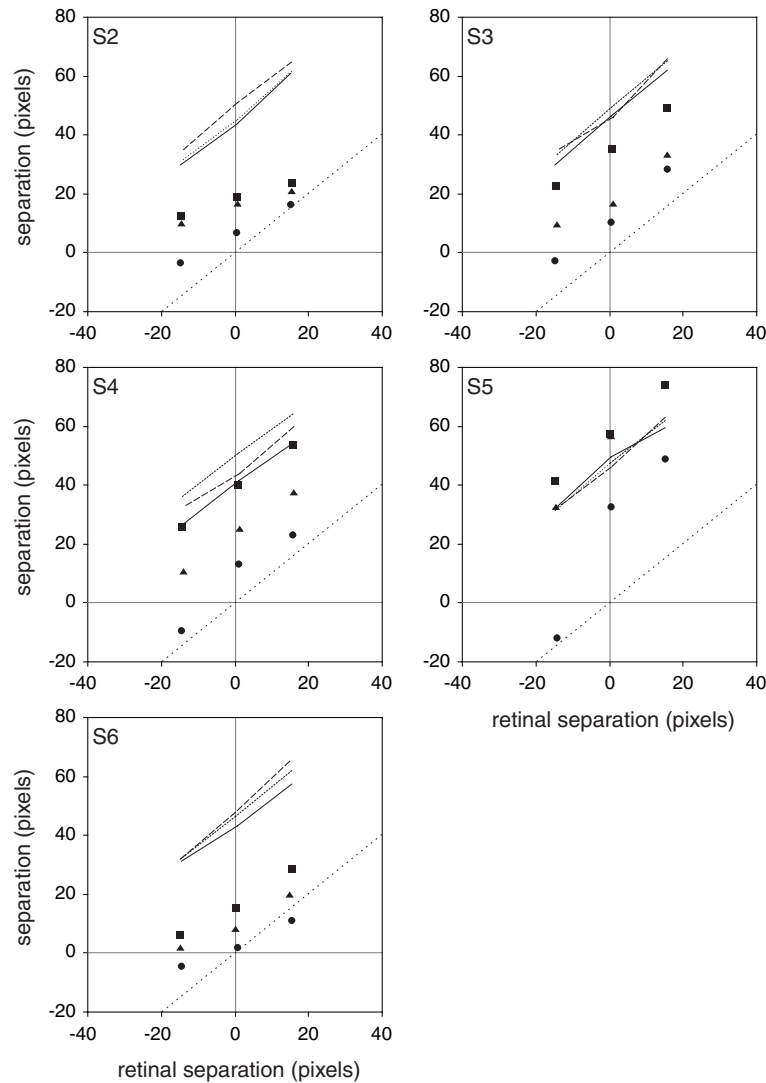


Fig. 4. The mean set separation on trials in which we succeeded in presenting one target before and the other after a saccade. Data are shown for an interval between the targets of 67 ms (circles; solid lines), 125 ms (triangles; dashed lines) and 242 ms (squares; dotted lines). Other details as in Fig. 3.

separations for trials with a saccade between the target presentations when the interval was 125 ms (triangles and dashed lines) and 242 ms (squares and dotted lines). The mean set separations for the successful 67 ms trials are also shown for comparison (circles and solid lines; same data as in Fig. 3).

All subjects set a separation that was closer to the real separation (and less close to the retinal separation) when the interval was longer. Subjects S2 and S6 still underestimated the separation considerably when the targets were 242 ms apart. Subjects S3 and S4 only underestimated the separation modestly for the longest interval, while subject S5 overestimated the separation. Comparing the latter subject's data in Fig. 3 with that of the other subjects in that figure suggests that she has an overall tendency to exaggerate the separation whenever the second target appears to be further to the right than the first. Whereas the other subjects reproduced the ret-

inal separations that we imposed rather well, this subject appeared to have a discontinuity in her settings as the set separation changed sign. This was not only the case when there was a saccade between the two target presentations, but also when there was no saccade between the two target presentations (rightmost open symbol for subject S5 in Fig. 3). It is therefore unlikely to have anything to do with the instantaneous eye movement signals.

2.3. Visual references

In the trials reported about in Figs. 3 and 4 the only structures that appeared on the grey screen were the jumping dot and the flashed targets. Of course, subjects could see the edges of the screen, and the light from the screen illuminated objects surrounding the screen, but all these structures were quite far from the targets. Five

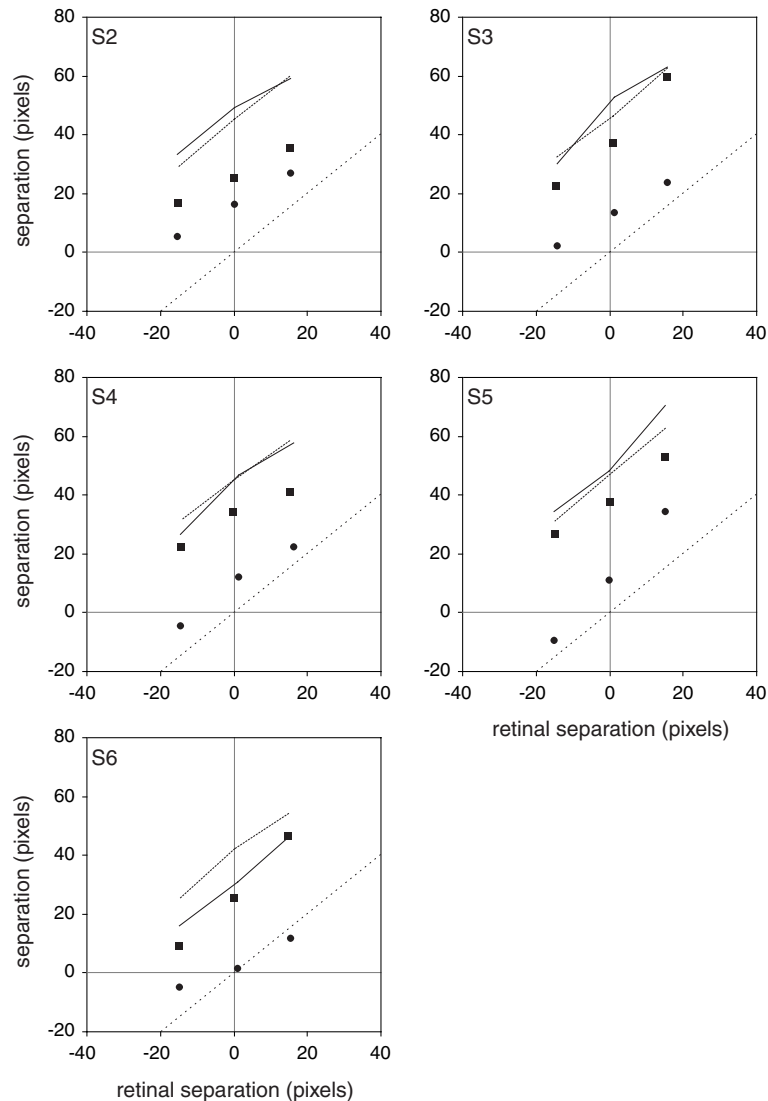


Fig. 5. The mean set separation on trials in which we succeeded in presenting one target before and the other after a saccade in the presence of conspicuous references. Data are shown for an interval between the targets of 67 ms (circles; solid lines) and 242 ms (squares; dotted lines). Other details as in Fig. 3.

subjects also took part in sessions in which there were conspicuous static references near the positions at which the targets were flashed on the screen. The targets were presented with an interval of either 67 ms or 242 ms. Fig. 5 shows the set separation for these trials, in the same format as in Fig. 4. In general the results are almost the same. For the 67 ms interval (circles), subject S2 appears to consider slightly more of the change in eye orientation (than in Fig. 4). For the 242 ms interval (squares), subject S6 considers slightly more of the change in eye orientation. The clearest difference, however, is for subject S5, who appears to consider slightly *less* of the change in eye orientation in the presence of conspicuous references. Our impression is that this is because she no longer overestimates the separation in the presence of such references.

2.4. Accounting for less of the eye movement or doing so less frequently

In order to determine whether subjects fully accounted for the eye movement on some trials, and failed to do so altogether on other trials, or whether they did so partially on all trials, we must analyse the individual trials. Rather than averaging the set separations and real separations separately (as shown in Figs. 3–5), we determined the proportion of the eye movement that was accounted for separately for each trial (by dividing the set separation on that trial by the real separation). In order not to have to consider the retinal separation we only used the trials with retinal separations that were close to zero (the data in the central points in Figs. 3–5). Fig. 6 shows the distribution of the proportions of the

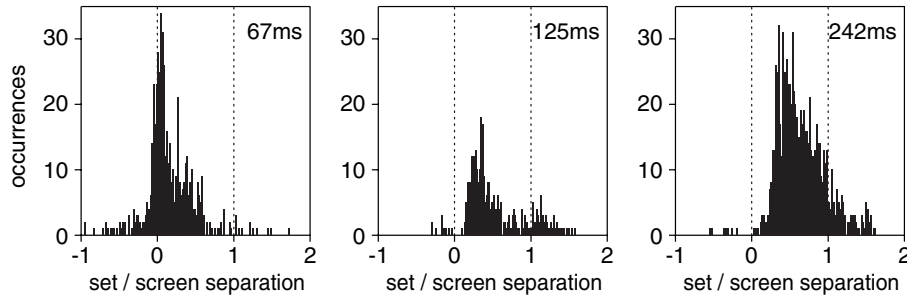


Fig. 6. The extent to which the fact that the eye orientation had changed was considered when judging the separation between the two targets: ratio of set separation to screen separation for all trials with a saccade between the target presentations and no additional retinal offsets. Note that for these trials the screen separation is practically identical to the change in eye orientation. The intervals are indicated within the panels. No distinction is made between trials with and without visual references.

eye movements that were accounted for. Each panel shows the distribution for one interval, irrespective of the presence of conspicuous references. The low overall number of trials for the 125 ms interval is a result of this interval having been presented much less often. The high overall number of trials for the 242 ms interval is a result of it being much easier to present one target before and the other after a saccade when the interval between the targets is large, so that fewer trials were excluded. If subjects had sometimes completely accounted for their eye movement and sometimes not at all, we would have seen two peaks in the data, at the values of zero and one (vertical dotted lines). This is clearly not the case: subjects partially account for the eye movement on all trials. Subjects must have even accounted for their eye movements more consistently across trials than is suggested by the widths of the distributions in Fig. 7, because a

substantial part of the variability is due to differences between subjects (as we saw in Figs. 3–5).

We can also conclude from Fig. 6 that subjects usually account for even less of their eye movements than the mean values shown in Figs. 3–5 suggest, because the distributions are clearly skewed. To get a better overall estimate of the proportion of the eye movement that was accounted for in the presence and absence of conspicuous references, we therefore determined the median value and the intra-quartile range for each interval between the targets (Fig. 7). This figure confirms our impression that the references hardly help in accounting for the eye movement, and that people altogether rely almost exclusively on the retinal image when there is an interval of 67 ms between the target presentations (less than 10% of the eye movement is accounted for). Even when the interval was 242 ms only part of the change in eye orientation was accounted for.

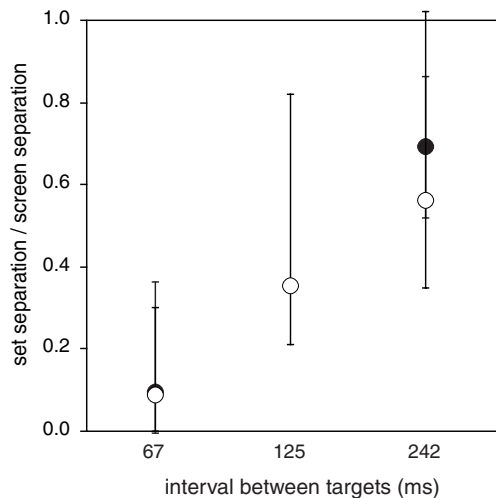


Fig. 7. Median extent to which the fact that the eye orientation had changed was considered when judging the separation between two targets presented at the same retinal position with a saccade between the presentations (no additional retinal offsets). Solid symbols are for trials with additional conspicuous static visual references near the targets and open symbols are for ones without such references. The error bars show the inter-quartile range.

2.5. The actual errors

In our instructions to the subjects we had not emphasised relative positions. We had asked our subjects to indicate where they had seen each of the targets. Nevertheless, in the preceding figures we only show the relative positions of the two targets. The reason for doing so is that we were mainly interested in the relative perceived positions of targets presented across saccades. However, it may be informative to also look at the settings in terms of the errors made for individual targets. The left column of Fig. 8 shows the errors in localising individual targets as a function of the time that they were presented (relative to saccade onset). Each point represents one target. The data are for successful trials without conspicuous references (all intervals). Thus the targets before the saccade were always “first targets” while those after the saccade were always “second targets”. The thick curve is a weighted average of these points, after removing all points that deviated by more than 3 standard deviations from the mean value within a 40 ms-wide moving window. The weight for the averaging depended

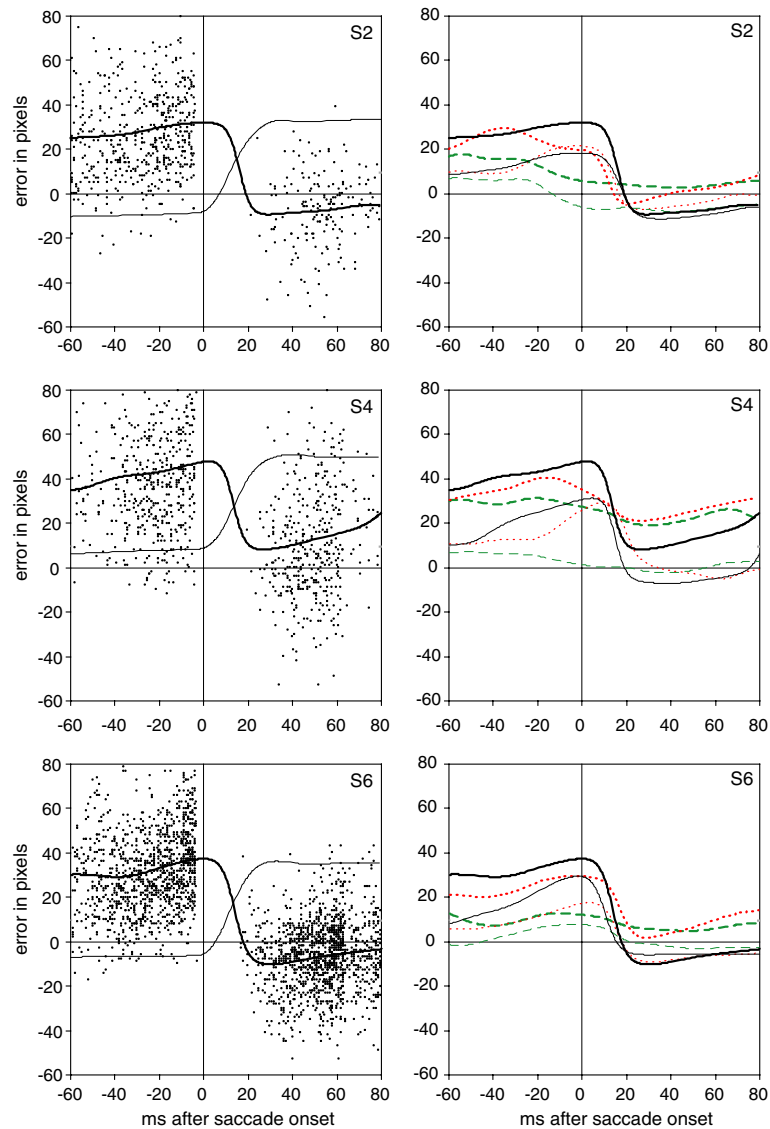


Fig. 8. Three subjects' (mean) errors in identifying the individual targets' positions on the screen, as a function of when the target was presented relative to the saccade. The left panels show individual errors on trials in which we succeeded in presenting one target before and the other after the saccade (dots; no additional references; all three time intervals). The thick curve is a weighted average of these dots (for details see methods). The thin curve shows the average saccade (its vertical position within the panel is arbitrary, but the scale corresponds with that of the errors). The right panels show weighted averages for six conditions. The continuous curves are for trials in which one target was before and the other after the saccade (as in the left panels). The dotted curves are for trials in which only one target was presented. The dashed curves are for trials in which both targets were either presented before or after the saccade (i.e. both during a single fixation). The thin curves are for trials in which there were conspicuous visual references on the screen. The thick curves are for trials in which there were no such additional references. Ten pixels is about 1° of visual angle.

on the distance in time from the moment of interest according to a Gaussian curve with a standard deviation of 10 ms. The thin line shows the average eye orientation during the relevant period of the same trials, thus representing the average saccade (at the same scale but with an arbitrary vertical position).

The fact that the mean error patterns are inverted versions of the saccades is not surprising, because this must be so if the eye orientation is ignored when determining the relative positions. However, these panels also reveal that the mean error is largest before the saccade, and that there is a lot of variability in the actual errors.

These two observations may help us to interpret the data.

2.6. Pre-saccadic mislocalisation

The fact that the errors are largest before the saccade raises the possibility that our findings are due to a well-established phenomenon known as pre-saccadic mislocalisation (Matin et al., 1970). Pre-saccadic mislocalisation is believed to be related to the way in which retinal and extra-retinal signals are combined (reviewed in Schlag & Schlag-Rey, 2002), and has even been shown

to give rise to perceived horizontal separations when there are none on the retina (Cai, Pouget, Schlag, & Schlag-Rey, 1997; Jordan & Hershberger, 1994; Matin et al., 1970; Schlag & Schlag-Rey, 1995). So could pre-saccadic mislocalisation account for the set separations in our study?

In order to find out we compared the errors in our successful trials (left panels of Fig. 8) with those on other trials. A set of trials that we had specifically included in order to be able to make this comparison is the set of trials in which only one target was presented. If the errors were caused by independent saccade-related mislocalisation of the two targets then we would expect a similar pattern of errors for single targets. The right panels in Fig. 8 show the weighted averages from the left panels (thick black curves), together with similar curves for various other conditions. The thick (red¹) dotted curves are for trials with a single target and no conspicuous references. For these targets we do find clear differences between the errors found before and after the saccade (i.e. we find the pre-saccadic mislocalisation), but these differences are smaller than when two targets were presented successfully. Clearer evidence that the perceived separation cannot (completely) be accounted for by independent saccade-related mislocalisation of the two targets can be found in trials with two targets in which either the second target was presented just before the saccade, or the first target was presented just after the saccade. The thick (green) dashed curves in the right panels of Fig. 8 show that the errors in these cases are practically independent of the timing with respect to the saccade (in contrast to when the first target remains visible until the second one flashes; Cai et al., 1997).

Another way of showing that the errors in localising the two targets of a single trial are not independent is by looking at the relationship between the errors for the two targets across trials. This is shown in Fig. 9 for the successful 67 ms interval trials without conspicuous references. The correlation between the errors is evident: the points cluster around a diagonal line. This line lies to the right of the unity line, because the error is larger (more positive) for the first target, as we saw in Fig. 8 and as it must be if the separation is always underestimated. The fact that most of the variability is along this line means that subjects were more reproducible in their relative judgements than in their absolute judgements of position. It is evident from the points in the left panels of Fig. 8 that the variability in the absolute judgements of position is large. The variability in the relative judgements is even smaller than that suggested by the width of the distribution in Fig. 9, because variability in sac-

cade amplitude (see Table 2) also contributes to the uncorrelated variability in the errors. The relatively low correlation for subject S5 is consistent with her relying least consistently on the retinal separation when making her settings for the two targets (see Fig. 3). The variability in the errors in the absolute judgement of position seems to be larger in our study than in studies with single saccades (e.g. Morrone, Ross, & Burr, 1997). This could be because our subjects could not use the target of the saccade as a visual reference, or because of the longer time between stimulus and response, or because of the additional saccades that our subjects made.

Could it be that for short intervals subjects judge the separation on the basis of the relative retinal position, independently of the perceived position, while for longer intervals subjects judge the separation on the basis of independent estimates of the targets' positions? Although many of our findings indicate that this may be so, it is not that simple, because we find equally high correlations between the errors for the two targets for the long intervals (Table 3). The fact that there is consistently more variability in the error for individual targets than for the separation between the targets shows that the relative positions of the flashed targets and their positions on the screen are treated independently at some stage for all intervals that we tested. This is also evident from the influence of visual references. Although the references hardly reduced the saccade-related errors in set separation (Fig. 7), they did reduce the saccade-related errors in localisation (Fig. 8). The thin lines in the right panels of Fig. 8 show the data for the same conditions as the thick lines, but for trials with conspicuous visual references. The references reduced both the bias in the direction of the saccade (the thin curves are closer to zero) and the variability in the errors (a decrease of about 40% irrespective of the interval; not shown). Thus whereas the references are irrelevant for the perceived separation between the two targets, they do influence their apparent positions on the screen (as shown in Brenner et al., 2001; Deubel, Schneider, & Bridgeman, 2002).

2.7. Compression of space near saccades

Could a compression of perceived space near the time of saccades (as reported by Lappe, Awater, & Krekelberg, 2000; Matsumiya & Uchikawa, 2003; Morrone et al., 1997; Ross et al., 1997) account for our findings? A strong compression towards the target of the saccade could explain why the first target is perceived too far to the right as well as why the separation is underestimated. However, we found no indication of such compression: our subjects accurately reproduced the additional retinal separations that we introduced. Nevertheless, since the compression is believed to be most

¹ The dotted curves are only red and the dashed ones green in the web version of this article.

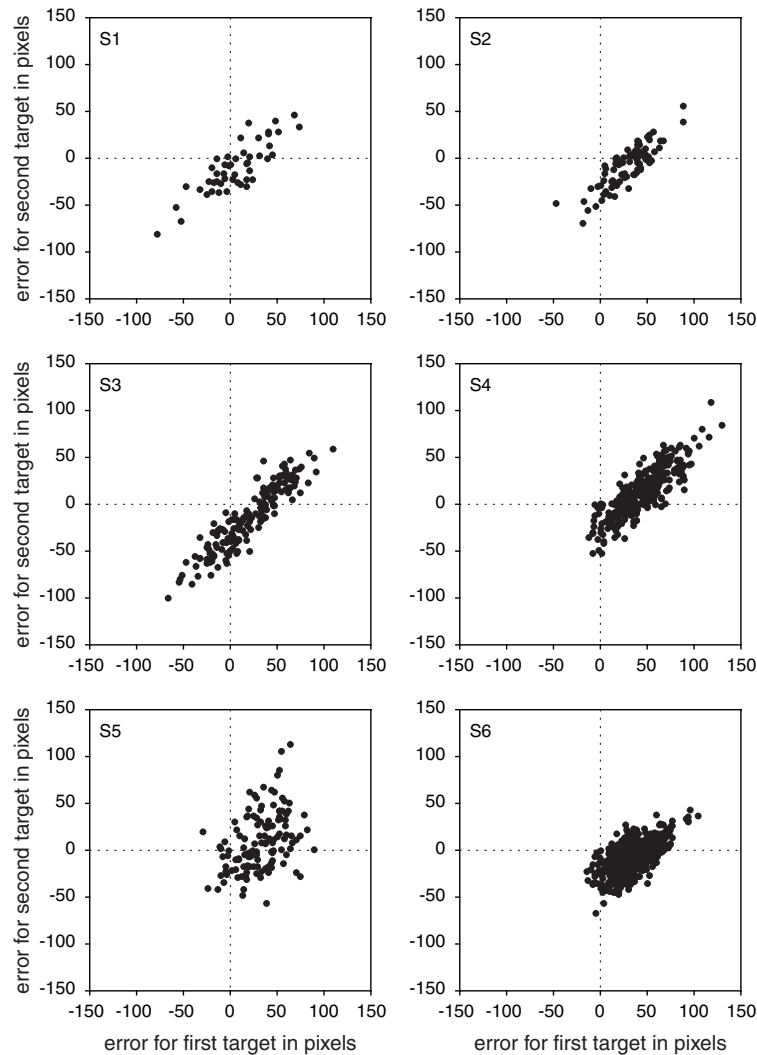


Fig. 9. Relationship between the errors for the first and second target. Each point represents a setting on a trial in which we succeeded in presenting one target before and the other after the saccade (no additional references; 67 ms interval). The correlation between the two errors is given in the last row of Table 2. Ten pixels is about 1° of visual angle.

Table 3

Correlation between the errors for the two targets on successful 242 ms-interval trials (with the number of trials within brackets)

	Subject				
	S2	S3	S4	S5	S6
Without conspicuous references	0.85 (483)	0.72 (346)	0.79 (149)	0.46 (635)	0.81 (471)
<i>With conspicuous references</i>	<i>0.25 (205)</i>	<i>-0.03 (119)</i>	<i>-0.14 (53)</i>	<i>0.20 (255)</i>	<i>0.17 (208)</i>

prominent before the saccade, whereas the retinal separations that are shown in Figs. 3–5 were always introduced by changing the position of the target that was presented *after* the saccade, we also examined data for four of our subjects in trials in which the first target was displaced horizontally relative to the eye orientation. The second target could have one of the same three offsets as before (relative to the first target's position).

Fig. 10 shows the set separation for the three different offsets of the first target. The black symbols and lines are

the data that were already shown in Fig. 3 (first target presented directly below gaze). The light grey points and lines show the corresponding data when the first target was presented 15 pixels to the left of the direction of gaze. The dark grey points and lines show the corresponding data when the first target was presented 15 pixels to the right of the direction of gaze. It is evident from this figure that it makes very little difference whether the retinal offset is introduced just before or just after the saccade. This is particularly evident for subjects

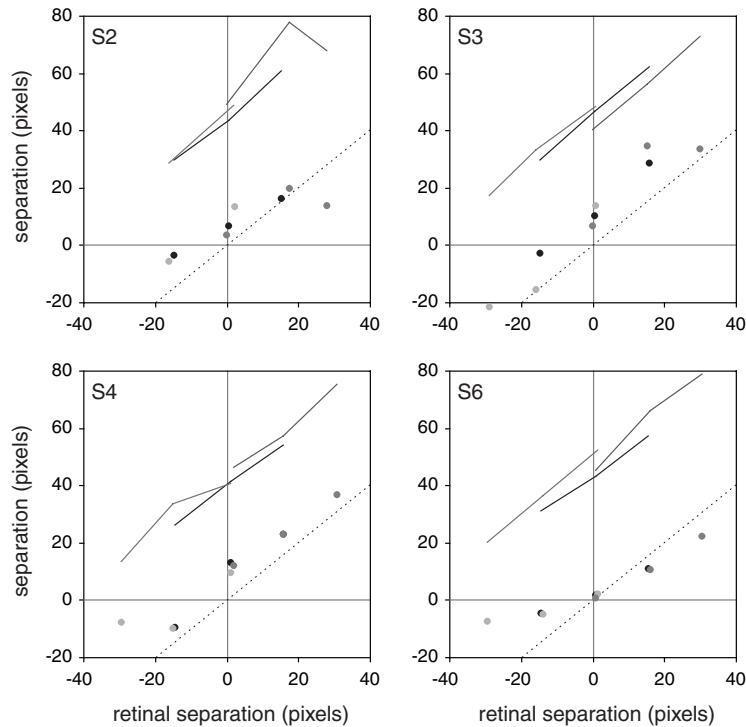


Fig. 10. Mean set separation on trials in which we succeeded in presenting one target before and the other after a saccade (no additional references; 67 ms interval). The first target was either directly below the direction of gaze (black circles and lines; same data as in Fig. 3), or it was 15 pixels to the left (light grey circles and lines) or to the right (dark grey circles and lines). The second target was either aimed at the same retinal position, or 15 pixels to the left or right of the first. Other details as in Fig. 3.

S4 and S6, where the three kinds of points for each retinal separation coincide almost perfectly. It is also clear from this figure that subjects reproduce the retinal separation almost perfectly (except for subject S6 who always tends to underestimate the separation).

3. Discussion

For short intervals between two flashed targets, subjects' judgements of the targets' relative positions are almost exclusively determined by the retinal separation, even if the eye orientation has changed substantially in the meantime. This had already been shown to be the case when targets are flashed in complete darkness (Sogo & Osaka, 2002). Here we show that it is even the case when ample visible structures are available. In the present study the outline of the image on the screen and various structures around the screen were always clearly visible. On some trials there were additional conspicuous shapes right near the targets. All these structures could have been used as references for localising the targets.

Alternatively, the motion of these structures' retinal images across the retina could have been used to judge the time and amplitude of the saccade. However we found no evidence that the presence of such stable visi-

ble structures influences the perceived separation between the two flashed targets. As long as the interval between the presentations is short, the human brain ignores saccadic eye movements when determining relative positions, just as it ignores pursuit eye movements.

Hayhoe et al. (1991) concluded that subjects do consider the changed eye orientation when judging the relative positions of images presented across saccades. When there were visual references, their subjects' judgements were almost as reliable as during steady fixation. When there were no visual references their subjects did worse, but most of them still accounted for a large part of the change in eye orientation. Hayhoe, Lachter and Feldman presented their targets for 100 ms, with an inter-stimulus interval of at least 200 ms. We also found that a substantial part of the eye movement is accounted for when the interval between the targets is long (Figs. 4–6). O'Regan and Lévy-Schoen (1983) performed a related experiment with an interval of only 50 ms. They flashed parts of letters before and the remaining parts after a saccade. Subjects had to recognise the word that they formed. O'Regan and Lévy-Schoen flashed the parts at the same *real* position. Their subjects could not recognise the words, showing that the eye movement is not completely accounted for (see Irwin, 1991 for a similar study involving same–different judgements rather than word recognition). Our present results

suggest that if they had flashed the parts at the same retinal position, and thus at different real positions, their subjects may have been able to read the words.

Our findings are less easy to reconcile with those of the alignment task presented in Ross et al. (1997). The strong pre-saccadic compression that was evident in their alignment task and has also been found in many other studies is characterised by a tendency to localise everything presented just before a saccade near the saccade target, irrespective of where it really was. Thus, the fact that we did not find such compression does not undermine our conclusions, because a compression does not indicate that changes in eye orientation are accounted for when judging the relative positions of asynchronously presented targets. However, it is not clear why we did not find this kind of compression. Perhaps because we only used high contrast targets that were presented near the direction of gaze, whereas the compression is largest when the contrast is low (Michels & Lappe, 2004) and the retinal eccentricity is large (the clearest compression is usually seen beyond the saccade target). Another possibility is that the difference is due to our use of a continuous following task, in which subjects made relatively small saccades (about 5°) to follow a dot as it jumped repeatedly and predictably across the screen. In most previous studies subjects were required to make a single large saccade (about 20°). Irrespective of the reason, we are glad to have found little or no saccadic compression, because a strong compression would have made it much more difficult to draw any conclusions about accounting for the change in eye orientation.

Perceived target positions must be judged by combining information about the part of the retina that is stimulated by the flash with either extra-retinal information about the orientation of the eyes, or retinal information about the positions of other visible structures, or both. We already discussed that the errors that we found cannot simply be explained by subjects misjudging the timing of the saccades or by deformations of space near the time of saccades, because the errors depend on the presence and timing of other targets (Fig. 8), and because additional retinal separations were perceived more or less correctly (Fig. 10). The correlations and the different influences of the conspicuous references also make it clear that the perceived separation and the perceived position on the screen cannot rely on the same information to the same extent. So how can we reconcile all these findings?

3.1. Our interpretation

The gradual increase in the extent to which the eye movement is accounted for in judgements of the perceived separation suggests that the signals involved in the relative localisation do not even nearly have the tem-

poral resolution that would be required to faithfully follow the saccade. The accuracy with which the relevant signals can be synchronised within the brain is probably limited by the fact that the signals each have their own neuronal delay that is influenced by a specific combination of external factors. Moreover, the precision is probably limited by the fact that signals originating at different and extended periods of time are combined due to the persistence of neuronal activity. Such persistence is inevitable because of factors such as retinal persistence, but also because much of the processing within the brain relies on a frequency coding of signals and therefore necessarily on activity across an extended period of time. Thus the neuronal representation of eye movements appears to be “damped” (Dassonville, Schlag, & Schlag-Rey, 1992) because the retinal stimulation by the flash is combined with extra-retinal information about the eye orientation during an extended period of time (due to the temporal overlap between the signals). Similarly, the spatial separation between retinal stimulation at different moments contributes to the localisation of flashed targets, even if the eye orientation has changed between those moments, because the neuronal activities that the signals induce overlap in time.

Combining information across extended periods of time can account for the fact that people make substantial localisation errors when transient events (such as flashes) occur near the time of saccades, because the information changes abruptly at that moment so that relationships before and after the saccade are confused (e.g. relating pre-saccadic retinal stimulation to an eye orientation after the saccade; for an example of a possible neuronal substrate see Kusunoki & Goldberg, 2003). However, it does not automatically explain why we found a strong correlation between the errors for the two targets. Neither does it explain why the apparent position of a target that was presented at a certain time relative to a saccade depended on whether a second target was presented, and if so where the eyes were looking when the other target was presented. In order to explain these findings we have to presume that the *relative* positions of the two flashed targets is determined independently of their positions in space.

For judging the relative positions of overlapping parts of an object it is usually enough to know which parts of the retina were stimulated. There is little to be gained by also considering the orientation of the eyes or the relationships with other objects. Doing so would normally only introduce additional variability, so little weight is given to such information. If the parts are presented sequentially, there is less temporal overlap between the neuronal responses to the retinal stimulation by the two targets, so judgements of relative retinal separation are less reliable, and will therefore be given less weight. In that case the orientation of the eyes and the relationships with other objects will also influence the

judgements. As a result the change in eye orientation will no longer be ignored. The similarity between our results and ones obtained in the dark (Sogo & Osaka, 2002), and the very modest influence that our conspicuous references had on the perceived separation, suggest that increasing the interval between the presentation of the targets mainly increased the extent to which the change in eye orientation was accounted for by making people consider extra-retinal information. However people may also have considered the flashed targets' positions relative to the target of the saccade, which is a very important visible structure at that moment (and is therefore unlikely to be ignored; Gersch, Kowler, & Doshier, 2004).

It is obviously impossible to judge positions in space without considering the orientation of the eyes or the positions of structures that remain visible until the response is made. Therefore it is not at all surprising that we found that conspicuous visual references had much more influence on the judged position on the screen than on the judged separation between the two targets. Presumably extra-retinal information and other visible references (such as the outline of the screen) also contribute more strongly to localising the targets on the screen. If so, then targets that are presented further in time from the saccade should be localised more accurately. Obviously, the average interval between the target presentation and the saccade will be larger when the interval is larger. So why does the variability in the localisation errors (and therefore also the correlation between the errors for the two targets) not decrease dramatically when the interval is increased? Perhaps this is because the timing of the targets with respect to the saccade is more variable when the interval is long, resulting in more variability in the weights given to the many relationships, and thereby in additional variability in the settings (especially when one considers that the two targets are not localised independently).

3.2. Objects and parts

Although we were mainly interested in the perceived separation between the two flashes, the task that we used was to judge the two targets' positions on the screen. Thus the fact that the results are best interpreted in terms of separate judgements of relative position (or shape) and egocentric position (or position on the screen) does not follow directly from our experimental design. However, since our goal was to study how information about shape is combined across saccades, we did intentionally stimulate the notion that the two flashes were parts of a single shape by making sure that the two targets always overlapped on the retina. We previously used a line moving behind an invisible occluding object of which the shape was to be judged, to show that the changing eye orientation is ignored when judging

shape during smooth pursuit (Li et al., 2002). We found very similar results when a single shape was drawn gradually in this manner, as when it was built up of two discrete parts (Brenner & Cornelissen, 2000). In the present experiment, we could not draw our shape gradually in this manner, because of the abrupt nature of the eye movement. However, as we already pointed out, there is ample evidence in our data that the subjects did not simply determine two target positions.

So, how representative are these findings for vision in everyday life. Obviously, the problem that our subjects' visual systems had to deal with (targets presented very briefly in close temporal proximity to a fast eye movement) is very unlikely to occur in daily life. Normally parts of objects are visible simultaneously for prolonged intervals, and a new retinal image will mask the previous one after each saccade, so basing judgements on retinal separations across saccades will seldom give rise to the errors that we see here. The present experiment was not designed to mimic natural conditions, but specifically to determine whether the change in eye orientation during saccadic eye movements is automatically considered when judging relative positions of objects that are not visible simultaneously. Our results suggest that they are not.

We conclude that the simplest explanation for our findings is that subjects make two independent judgements: one of the target's *shape* (relative positions) and one of this shape's *position* on the screen (Brenner & Cornelissen, 2000). This is consistent with evidence that shape perception involves very different pathways in the brain than judgements of position (Milner & Goodale, 1993; Rossetti, 1998; Mishkin, Ungerleider, & Macko, 1983). For both judgements, retinal stimulation by each target is related to retinal stimulation by other structures and to extra-retinal information about the orientation of the eyes. Moreover, in both cases not only the retinal images and eye orientation at exactly the same time as the target flashes are considered. Due to the limited temporal resolution of the signals involved and to systematic differences in latency between these signals, signals that originate at slightly different moments are combined. Normally this hardly matters, but near saccades it can introduce substantial errors. The extent of such errors depends on the information that is used. Our data suggest that judgements of shape are primarily based on the relative retinal positions of the components. Thus when combining a component that is flashed before a saccade with one flashed after the saccade we make large errors because the eye movement should have been considered. In contrast to the judged shape, the judged position of the combined shape is always based on a combination of extra-retinal signals and the components' positions relative to other visual references, so the orientation of the eyes is always considered, though not always correctly.

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