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Orientation Dependent Misalignments in a Visual Alignment Task

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Subjects performed a three-dot alignment in the frontoparallel plane. We found systematic deviations in alignment, especially for diagonally oriented stimuli. The biases did not depend on the angular size of the stimuli which was varied between 0.8 and 20 deg. We put forward a tentative explanation based on saccade trajectories. Extending the task to judgements of the straightness of virtual lines consisting of a varying number of dots showed that the biases decrease gradually when the number of dots increases. This suggests that there are two different and competing mechanisms to judge the straightness of virtual lines.

Perceptual straightness Direction estimation Scale invariance Perceptuo-motor interaction Human

INTRODUCTION

One purpose of visual perception is to gather information about the position of objects around us. This enables us to judge situations and successfully plan goal-directed actions such as reaching out towards desirable objects or avoiding dangers and obstacles. Relative position can be specified by direction and distance. We here focus on the perception of relative direction, i.e. the direction in which an object is positioned relative to a second one. Relative direction seems to be a primary control variable for fast goal-directed arm movements, since these movements typically begin in what is roughly the correct direction, even when they start as early as 150 msec after the presentation of the visual target (Van Sonderen & Denier van der Gon, 1991; Wadman, Denier van der Gon & Derksen, 1980). This implies that the involved muscles are activated at the appropriate relative levels, suggesting that the central nervous system (CNS) has immediate access to the information about the direction in which the goal of a movement sits relative to the position of the limb before any movement is performed. The direction in which a movement is going to be performed does seem to be represented in the neuronal activities of premotor and primary motor cortex (e.g. Caminiti, Johnson, Galli, Ferraina & Burnod, 1991; Kalaska & Crammond, 1992). This suggests that direction information is available not only at the movement execution stage but also at the movement planning stage. We can only approximately learn

what direction information is available to the CNS from the performance of fast movements, since such movements are typically curved due to mechanical forces acting on the arm (Hollerbach & Flash, 1982; Wadman *et al.*, 1980). More accurate knowledge about the subject's directional information at the start of a movement has to be obtained from the trajectories of very slow goal-directed limb movements.

The perception of the direction in which an object is positioned relative to a second one on the same horizontal surface has been shown to be biased (De Graaf, Sittig & Denier van der Gon, 1991b). This was demonstrated by having subjects direct a pointer towards visual targets positioned at some 30 cm from the pointer pivot in various directions. The subjects consistently misdirected the pointer such that the tip of the pointer was closer to their body than it should have been. Visually-guided slow arm movements from the pivot position to the same targets proved to start in similarly biased directions even if the movements reached the goal eventually. It appears that the same biased information about the relative direction is used to direct a pointer and to control arm movements, and that the biases arise from the visual perception of spatial relations.

We now investigate the phenomenon of biased perception of relative positions further. We first ask if the demonstrated biases in pointing are related to differences in depth: the biases were demonstrated in a setup where the observers were seated at a stimulus table with, obviously, their eyes above, and also behind, the pivot position. The distances from which they viewed the pivot and the target, therefore, differed considerably. In a setup where the pivot and the target would be at approximately the same distance from the observers' eyes any effects arising from differences in depth should be greatly diminished. Therefore, we now had subjects

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perform a three-dot alignment task in the frontoparallel plane and analysed the systematic deviations. This task can be considered a pointer-setting task but has the advantage of circumventing problems related to the limited resolution of the stimulus monitor, such as the ragged appearance of an obliquely oriented pointer. Initially, the dimensions of the stimuli were chosen to match those in the directing tasks on the horizontal table (De Graaf *et al.*, 1991b). In that study the stimuli subtended about 15–25 deg visual angle from pivot to target. Note that the observers will need to shift their gaze direction to perform the alignment. Secondly, we varied the size of the stimuli to investigate the effect of eccentricity of the stimulus dots. The results show consistent biases in three-dot alignment, which do not depend on the size of the stimuli but do depend on the orientation of the stimulus relative to the longitudinal head axis. Lastly, we investigated whether these biases persisted in a comparable task with an increasing number of dots. Preliminary results have been published in abstract form (Sittig, 1991).

METHODS

Subjects

Eight subjects aged 26–45 participated in the experiments. All but two were naive as to the purpose of the experiments. The results of the informed subjects could not be distinguished from the results of the others. All subjects had normal or corrected to normal vision.

Apparatus and stimuli

We used a PC to control the experiment and record the data. Visual stimuli consisting of clearly visible bright dots on a dark background were presented on a high resolution (1268 × 1012 pixels) monitor. The edges of the monitor were concealed from sight by a black paper annulus. Subjects viewed the stimuli in an otherwise dark room. The subjects were seated facing the monitor with, in most cases, their head supported by a chin rest. When they fixated the centre of the screen, the screen was perpendicular to their line of sight. The stimuli consisted of three dots which had to be aligned [Fig. 1(A)]. We can think of this task as setting a pointer: one of the dots functioned as the *pivot* of the virtual pointer, another one as the *target*. These two dots remained stationary during a trial. The third one (the *tip* of the virtual pointer) could rotate on a circle around the pivot with a radius of one-third of the distance from pivot to target. In the basic experiment, the pivot was positioned in the centre of the screen, and the target in the periphery at various orientations. The subject adjusted the position of the pointer tip, and thus the direction of the pointer, by pressing the right, or left, arrow key on a keyboard to effect clockwise, or anti-clockwise, rotation, respectively. The subjects could make the pointer tip move by a step of a single pixel by a brief keypress. A continued keypress caused the pointer tip to rotate at approx. 3 deg/sec. The initial

orientation of the virtual pointer was chosen randomly for each trial anew within a 10 deg angle around the straight line between pivot and target. A stimulus subtended 2.5, 8 or 20 deg visual angle. The 20 deg stimuli were viewed from 40 cm and the smaller stimuli from 1 m. The size of the individual dots was 0.006 times the size of the entire stimulus. The dimensions of the 20 deg stimuli were chosen to roughly match the visual angles that the distance from pivot to target and the length of the pointer subtended in the pointer setting experiments on a horizontal table (De Graaf *et al.*, 1991b).

Procedure

The subjects were instructed to adjust the position of the middle dot (the pointer tip) such that it would lie on the imaginary straight line between the two fixed dots. The subjects were never allowed to move their head during the trials. Whether or not the head was restrained by the chin rest did not influence the results. Eye movements were allowed. The subjects could take as long as they wanted to perform the adjustment. All three dots remained visible during this time. When the subject was satisfied with the adjustment, the positions of the dots were stored, the screen was cleared, and the next stimulus to be adjusted was presented. The subjects typically used one or two continued keypresses and up to five brief keypresses to position the pointer dot. Each adjustment took approx. 5–15 sec. In a typical session 192 stimuli were presented in quasi-random order [32 stimulus orientations × 3 repetitions × 2 pivot positions (pivot in the centre or in the periphery of the screen) for the 20 deg stimuli; or 32 stimulus orientations (with the pivot in the centre) × 3 repetitions × 2 stimulus sizes (2.5 and 8 deg)]. A session lasted about 30 min.

In additional sessions two subjects were asked to tilt their head maximally towards their left shoulder and to maintain this posture during all trials. To limit the duration of these sessions, and thereby the subjects'

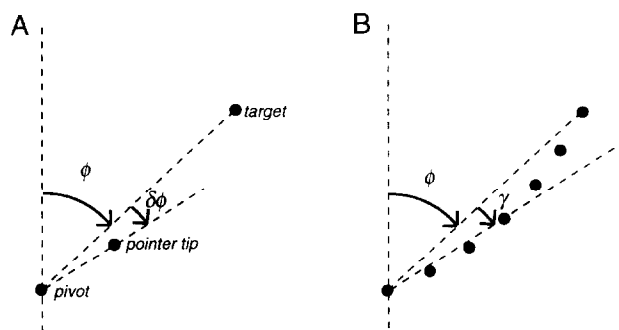


FIGURE 1. Illustration of the analysis. The relative size of the dots is exaggerated for the sake of clarity. Clockwise rotations are defined as positive. (A) The three-dot alignment task. The subject positioned the pointer tip dot to lie on the straight line between pivot and target dots. We determined the resulting deviation $\delta\phi$ in pointer direction as a function of the orientation ϕ of the stimulus. (B) A seven-dot stimulus from the two-alternative forced-choice task. The curvature γ is defined as the angle between the line through the extreme dots and the line through the "pivot" and the middle of the circle arc on which the dots are positioned. We determined the curvature γ that gave subjectively straight lines as a function of the orientation ϕ of the stimulus.

discomfort, the stimuli were presented only once (with subject KS) or twice (with subject EZ) for each orientation in this condition.

Three subjects participated in an additional experiment in which stimuli consisting of a varying number of dots that were evenly spaced on a circle arc (subtending 0.8 or 6 deg visual angle) were presented for 1 sec. The curvature [as defined in Fig. 1(B)] ranged from -6 to 6 deg in 10 equidistant steps. This range of curvatures was chosen to include the range of deviations found in the adjustment task. Sixteen equidistant orientations between -90 and 6 deg, or nine equidistant orientations between -90 and 90 deg, were tested. The subject had to make a two-alternative forced-choice by pressing one of the arrow keys to indicate that the virtual line presented by the multi-dot stimulus was curved either upwards (and to the left) or downwards (and to the right). The curvature of the circle arc for the next presentation with the same orientation was changed by a single step in the direction opposite to the subject's response. Using this staircase procedure we determined the curvatures that gave subjectively straight lines for the tested orientations. Single presentations of stimuli with various orientations, but with a fixed number of dots, were quasi-randomly intermingled. Three subjects viewed the 0.8 deg stimuli with 3 and 7 dots, and one of them also viewed the 6 deg stimuli with 3, 4, 5, 7, 15, and 50 dots.

Analysis

We determined the systematic deviations in alignment as a function of stimulus orientation [see Fig. 1(A)]. We define the orientation of the stimulus as the angle between the line from the dot that serves as the pivot of the virtual pointer to the target dot, and the vertical. Clockwise rotation is defined as positive. The stimulus orientations ranged from -180 to 180 deg. The deviation is defined as the angle target position–pivot position–position of the adjusted dot. Again, a positive deviation denotes a clockwise rotation of the virtual pointer from the correct orientation. The accuracy with which the deviations could be measured was determined by the size of the single pixels of the monitor and amounted to 0.4 deg for the 8 and the 20 deg stimuli and 1.2 deg for the 2.5 deg stimuli. For the multi-dot stimulus, we defined the curvature in a corresponding way now using the middle of the circle arc instead of the pointer tip dot [Fig. 1(B)].

RESULTS

Eight subjects performed the three-dot alignment task for 20 deg stimuli with the pivot dot in the centre of the screen. Their deviations in pointer direction are shown as a function of stimulus orientation in Fig. 2. Figure 8 illustrates the results by schematically showing the positions of pivot, target, and corresponding pointer tip dots on the screen. We can see positive deviations for orientations from 0 to 90 deg (target dot in the upper right quadrant) and negative deviations for orientations

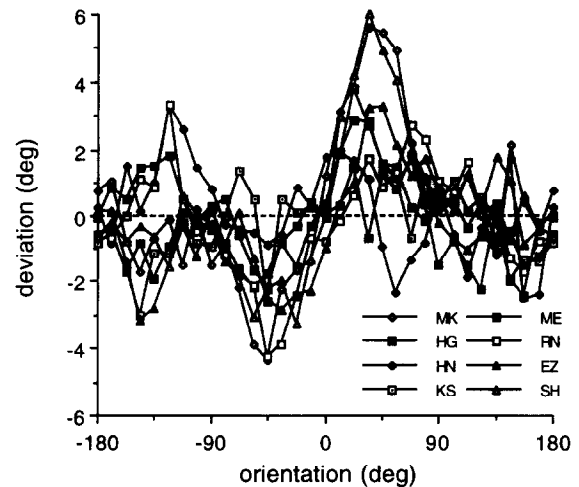


FIGURE 2. The deviations in pointer direction as a function of stimulus orientation for eight subjects. Each point is the mean of 3–5 adjustments. Note the peak around 45 deg and the trough around -45 deg. The stimuli subtended 20 deg visual angle. The pivot was always positioned in the centre of the screen.

from -90 to 0 deg (targets in the upper left quadrant). We compared these biases to those found in the directing task on a horizontal surface (De Graaf *et al.*, 1991b). In that study only target positions from -90 to 90 deg were tested. (The position of the target was defined as the angle between the line from pivot to target and the straight ahead through the pivot on the table.) The deviations showed the same general pattern. No systematic deviations were found for 0 and ± 90 deg targets. These targets correspond to vertical and horizontal lines from pivot to target on the retinae, and therefore to target orientations of 0 and ± 90 deg in the present experiment. For those target orientations we now again find no significant deviations: -0.5 ± 0.9 deg (mean and SD for the -90 deg target orientation), -0.0 ± 1.0 deg (0 deg target orientation), 0.5 ± 0.6 deg (90 deg target orientation), and -0.2 ± 0.8 deg (180 deg target orientation). The directing task on a horizontal surface (De Graaf *et al.*, 1991b) showed maximal positive (and negative) deviations for target positions around 30 (and -30) deg. Under fixation of the pivot lines from the pivot to these target positions would intersect with the vertical on the retina under ± 45 deg. Therefore, we averaged the deviations for stimulus orientations from 34 to 56 deg (and for orientations from -56 to -34 deg) over all subjects to compare our results to these previous ones. The mean deviations (\pm SDs) were 2.5 ± 2.2 deg, and -2.2 ± 1.7 deg, respectively, as compared to 2.8 ± 1.3 and -1.5 ± 1.0 deg in the horizontal pointer setting task (De Graaf *et al.*, 1991b).

If the orientation of the line through the stimulus were the important parameter, we would expect to find similar positive and negative deviations for orientations around 135 and -135 deg, respectively. These orientations, however, do not show comparable consistent deviations (0.3 ± 1.7 deg for the stimulus orientations from 124 to 146 deg and -0.4 ± 1.9 deg for stimulus orientations from -146 to -124 deg).

The discrepancy that we do find consistent biases for stimuli in the upper half of the screen, but not for stimuli in the lower half, is not necessarily related to the position of the stimulus on the screen (and therefore to the position of the eyes in the orbits): it might also be due to a direction asymmetry. This would imply that the biases are determined by the angle between the line from pivot to target and the vertical *through the pivot* and not the vertical through the centre of the screen, or, in other words, that obliquely upwards directed virtual pointers consistently lead to significant directing biases and obliquely downwards directed pointers do not. In order to discriminate between these two possible causes, we repeated the experiment with the target always in the centre of the screen, and the pivot in various positions on a circle around the target. A stimulus orientation of, say, 135 deg according to our definition would now lie in the upper left-hand quadrant of the screen. If the discrepancy between the deviations in the lower and upper quadrants would be a pure position effect, i.e. determined by the position of the eyes in the orbits when the more eccentric dot is being fixated, there should now be well defined deviations for ± 135 deg. If, however, upwards directed pointers would lead to deviations more consistently than do downward oriented ones, the maxima should again be at ± 45 deg. We present the results of one subject as a function of stimulus orientation in Fig. 3. Also shown in this figure are the results from the first experiment for this subject. We can see that the two curves practically coincide, which indicates that orientation and not position on the screen is the relevant parameter. Statistical analysis of the data from all seven subjects who participated in the two experiments supports this idea. For each subject, we twice compared the

TABLE 1. Correlation coefficients of the systematic deviations in the condition with the pivot dot in the centre and in the condition with the target dot in the centre

Subject	Position	Orientation
SH	0.39	0.51
KS	0.16	0.53
ME	0.00	0.05
EZ	0.43	0.65
EZ*	0.46	0.80
HN	0.02	0.28
HG	0.40	0.46
RN	0.15	0.19

Position: the data were compared according to the positions of the stimuli on the screen. Orientation: the data were compared according to the angle between the oriented line from pivot to target and the vertical through the pivot.

*This subject repeated the two tasks with 8 deg stimuli instead of 20 deg stimuli.

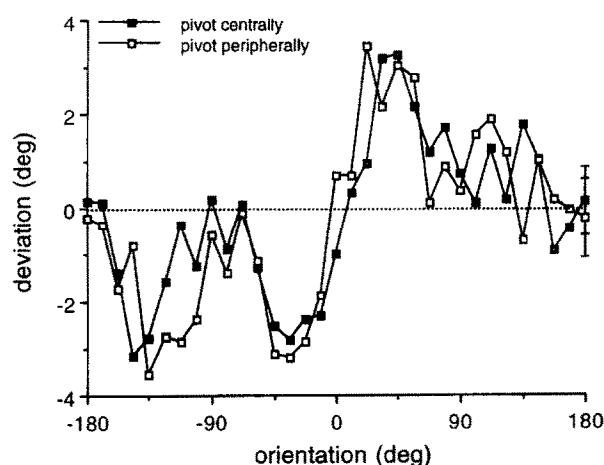


FIGURE 3. The deviations in pointer direction as a function of stimulus orientation relative to the vertical through the pivot. Solid squares, the pivot was positioned in the centre of the screen; open squares, the target was positioned in the centre of the screen. In the latter condition stimuli with orientations between -90 and 90 deg lie in the two lower quadrants on the screen. Each point is the mean of four adjustments. The standard deviations did not depend on the orientation of the stimulus and were averaged over all stimulus orientations. Whiskers at 180 deg indicate the mean standard deviations for the two conditions. The size of the stimuli was 20 deg visual angle. Subject EZ.

deviations found with the pivot in the periphery vs the deviations from the experiment with the pivot in the centre, once by matching the orientations in the two conditions, and once by matching the positions on the screen. We determined the correlation coefficients for the two cases. They are given in Table 1. Although the correlation coefficients are small due to the noisiness of the data (see Fig. 3), the correlation coefficient was larger when we matched orientations than when we matched positions for all subjects. This implies a significant difference in favour of orientation-dependence rather than position-dependence ($P < 0.02$).

With the 20 deg stimuli the subjects made substantial eye movements between the pivot and the target dot during the adjustment phase. To investigate if the biases were related to the eccentric positions of the eyes in the orbits, we had four subjects repeat the experiment with two smaller stimulus sizes: 2.5 and 8 deg. The pivot was always in the centre of the screen with these smaller stimuli. The deviations showed a similar pattern and were of comparable amplitude for all stimulus sizes. A typical example is shown in Fig. 4. Mean deviations for the stimulus orientations that were expected to show the largest deviations are given in Table 2 for the four subjects.

To investigate whether the orientation of the stimulus, which appears to be the relevant parameter for the biases we find, is the orientation relative to the vertical (or the subject's main body axis), or relative to the subject's longitudinal head axis, two subjects cooperated in the same three dot alignment experiment with their head tilted by approx. 60 deg. Figure 5 shows the cross-correlation of the deviations for the head-tilted and the head-vertical conditions for the two subjects tested in this way. We can see a peak for shifts of around 60 deg and a trough at around 230 deg. A shift of 60 deg corresponds to the alignment of the data from the head-vertical and the head-tilted conditions according to

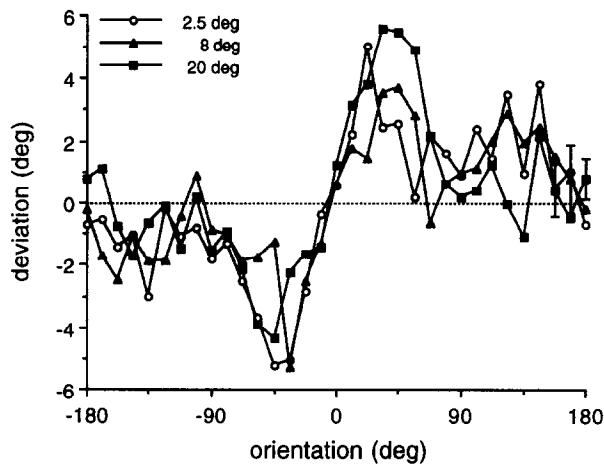


FIGURE 4. The deviations in pointer direction as a function of stimulus orientation for three different stimulus sizes. Circles, 2.5 deg; triangles, 8 deg; squares, 20 deg. Each point is the mean of three adjustments. Whiskers indicate the mean standard deviations for the three stimulus sizes. The pivot was positioned in the centre of the screen. Subject MK.

the direction of the head axis. With a 240 deg shift, the peak in the head-tilted condition coincides with the trough at -135 deg in the head vertical condition. Clearly, the deviations vary with orientation of the stimulus relative to the head axis and not relative to the actual vertical. This is illustrated by Fig. 6 which shows the deviations as a function of the orientation relative to the longitudinal head axis for the head-vertical and the head-tilted conditions for one subject. This result is corroborated by the recent analogous finding for slow goal-directed movements (De Graaf, 1994). Three subjects moved their index finger slowly over a vertical surface to targets in various directions, once with their head upright and once with their head tilted. The initial movement direction showed the same pattern of biases as the pointer orientation in the present adjustment task. When the subjects had their heads tilted, this pattern of biases was shifted by the amount of head tilt.

We would like to emphasize that the specific pattern of deviations as a function of stimulus orientation proved to be consistent, reproducible, and independent of stimulus size and position on the screen, for each

TABLE 2. Averaged maximal deviations for three stimulus sizes: 2.5, 8, 20 deg

Subject	2.5 deg	8 deg	20 deg
MK	-4.7 ± 1.2 1.7 ± 1.6	-2.8 ± 2.3 3.3 ± 0.9	-3.5 ± 2.1 5.3 ± 1.2
RN	-1.5 ± 1.2 0.3 ± 2.0	-3.6 ± 1.7 1.0 ± 1.2	-3.4 ± 1.9 1.3 ± 1.2
HG	-1.3 ± 1.5 1.5 ± 0.8	-1.9 ± 1.1 2.6 ± 0.9	-1.6 ± 0.8 2.0 ± 0.9
EZ	-1.4 ± 1.2 1.9 ± 1.1	-1.0 ± 1.1 3.3 ± 0.8	-2.2 ± 0.9 2.9 ± 1.3

Means (\pm SD) of the settings for the -56 , -45 , and -34 deg stimulus orientations (top row for each subject) and for the 34 , 45 , and 56 deg stimulus orientations (bottom row for each subject). Three settings for each stimulus orientation in each condition.

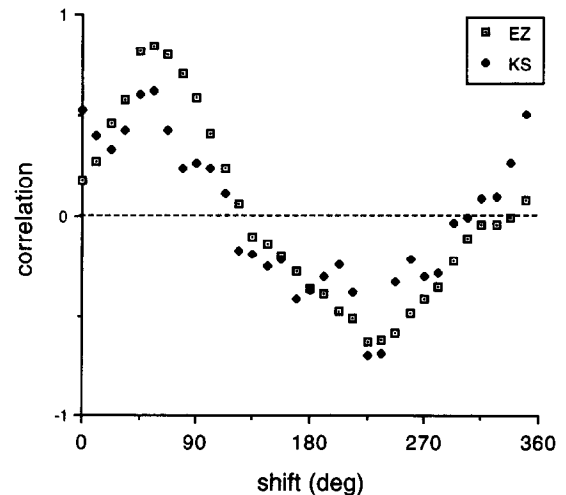


FIGURE 5. The cross-correlation of the deviations in the head-vertical condition and the head-tilted condition for two subjects. The subjects had their head tilted by approx. 60 deg in the counterclockwise direction. A positive shift represents a clockwise shift for the head-tilted data. Subject EZ performed two adjustments per orientation, subject KS only one with the head tilted and two with the head vertically. The stimuli were 8 deg visual angle. The pivot was positioned in the centre of the screen.

subject individually. This is exemplified by the comparison of the patterns in Figs 2 (solid triangles), 3 and 6, which all represent data from the same subject.

Aligning three dots seems to be identical to judging whether the line defined by the three dots is a straight line. Introspectively, we think that we can perceive quite accurately if a line is curved or straight. In the present experiment, however, we show that for a line represented by three dots consistent judgement errors are made if the line is oriented obliquely. To test if judging the straightness of such a sparsely represented line differs from judging the straightness of an actual line, we performed a final experiment. Now, the subject had to judge the

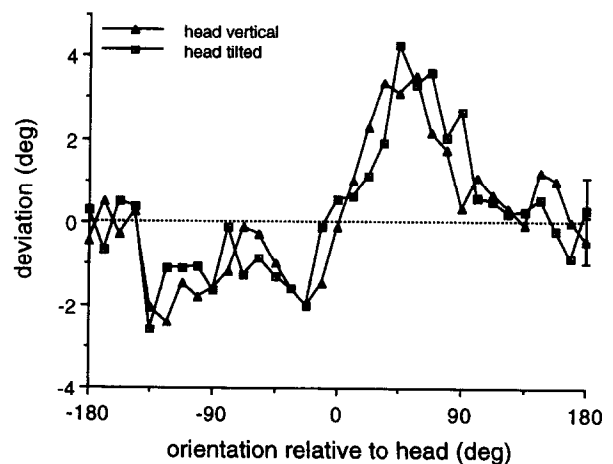


FIGURE 6. The deviations in pointer direction vs the stimulus orientation relative to the longitudinal head axis. Triangles, the head was in the vertical position; squares, the subject held the head tilted by approx. 60 deg. The size of the stimuli was 8 deg visual angle. Each point is the mean of two adjustments. Whiskers indicate mean standard deviations. The pivot was positioned in the centre of the screen. Subject EZ.

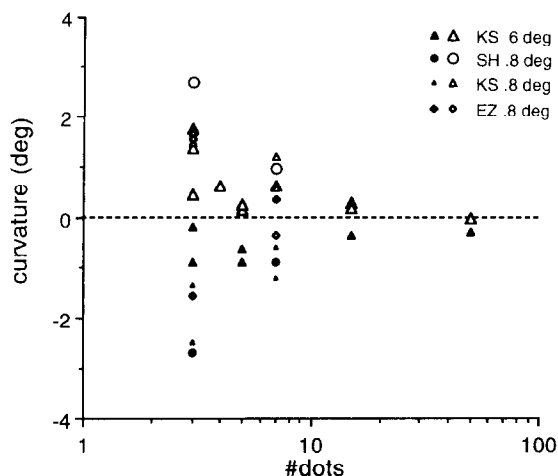


FIGURE 7. The curvatures that gave subjectively straight virtual lines as a function of the number of dots in the stimulus. Averages for stimulus orientations from 34 to 56 deg (open symbols) and for stimulus orientations from -56 to -34 deg (solid symbols), per subject, session, and stimulus size. Mean standard deviations: for three dots, 0.7 deg; for four dots, 0.5 deg; for five dots, 0.4 deg; for seven dots, 0.4 deg; for 15 dots, 0.3 deg; and for 50 dots, 0.15 deg.

direction of the curvature of a virtual line consisting of a varying number of dots lying on a circle arc. Using a staircase procedure we determined the curvatures that produced subjectively straight lines as a function of stimulus orientation. The results are presented in Fig. 7. For lines consisting of three dots we found consistent biases as we did in the adjustment task, both for 0.8 and 6 deg stimuli. (Our present definition of curvature enables direct comparison with the deviations in the adjustment task. As can be seen from Fig. 1, equal curvatures are represented by $\delta\phi$ or γ with $\delta\phi$ slightly larger than γ for small angles.) Increasing the number of dots decreased the effect and eventually no biases persisted.

DISCUSSION

We investigated how subjects performed a three-dot alignment task in the frontoparallel plane. The subjects were asked to adjust the position of a dot (indicating the tip of a virtual pointer) such that it would lie on the straight line from pivot dot to target dot. We were especially interested in any systematic biases that would occur in the pointer setting. In this, our study differs from the vast literature on three dot alignment performance where perceptual thresholds are analysed (e.g. Klein & Levi, 1987; Westheimer & McKee, 1977). Some studies do analyse absolute errors in perceptual comparison (e.g. Werkhoven & Koenderink, 1993). However, in those studies the observers were not allowed to make eye movements but had to fixate a particular point on the screen. In the present study there were no such restrictions. Indeed, the task could not be performed without making eye movements because of the considerable size of the stimuli. Any effects we find should therefore be discussed not primarily in terms of eccentricity or position on the retina, but rather in terms of gaze direction

or (since the head was stationary) the position of the eyes in the orbits.

We found systematic biases in the adjustment of pointer tip position as illustrated by Fig. 8. The adjusted pointer orientation did not deviate systematically from the stimulus orientation for horizontal or vertical orientations. In oblique directions, however, we found that the subjects positioned the pointer tip consistently below the line from pivot to target for stimulus orientations from -90 to 90 deg (the upper two quadrants in Fig. 8). The maximal absolute deviations were about 3 deg, irrespective of the size of the stimulus. The here demonstrated biases match the earlier found misdirections in a horizontal plane (De Graaf *et al.*, 1991b), both in direction and in size. Therefore, we conclude that those misdirections were not related to a difference in viewing distance for the pivot and the target. Similar deviations have been demonstrated in slow goal-directed arm movements (De Graaf *et al.*, 1991b). The occurrence of corresponding misalignments in various types of tasks could either reflect a general property of spatial representations that is not confined to one specific modality or stem from sensory perception, be it vision or proprioception. Mutual calibration of visual and proprioceptive spatial representations would then transfer any distortion from the proprioceptive map to the visual one, or vice versa.

For the three-dot alignments in the lower quadrants the results were less clear cut, although each subject individually showed a consistent behaviour. Some subjects consistently put the pointer below, and others above, the actually straight line for stimulus orientations in one of the lower quadrants. Using this asymmetry we showed (by translating the stimuli to other positions on the screen) that the angle between the oriented line from pivot to target and the vertical through the pivot, and not the actual position of the stimulus on the screen, is the variable that determines the misalignment. This implies that it is essential to the perception of orientation

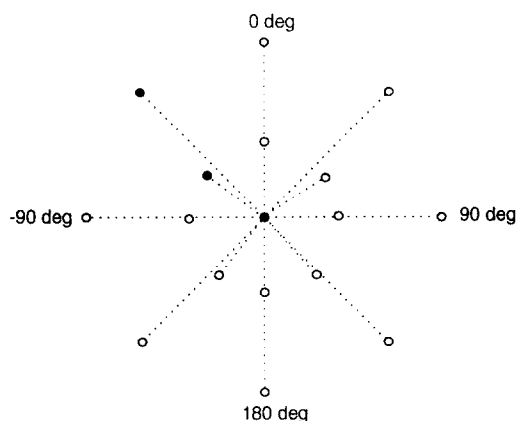


FIGURE 8. Schematic summary of the results of the three-dot alignments. The solid circles show a typical setting for a -45 deg stimulus. The open circles show other target positions with the associated pointer tip positions. The size of the deviations and the dot diameters are exaggerated for the sake of clarity. In this illustration the pivot is positioned in the centre of the screen.

of the virtual line elements in the present task which of the stationary dots is the pivot and which the target. Possible strategies for performing this task could be any kind of comparison of the orientation of the virtual lines from pivot (P) to target (T) and from P to pointer tip (PT), or, alternatively, a comparison of the orientation of the virtual lines from P to PT and from PT to T. In the two-alternative forced-choice experiment we determined the subjectively straight virtual line where the line consisted of three dots with the middle dot midway between the two extreme dots. We found deviations that were very similar to the misalignments in the adjustment task. This indicates that the strategy for judging the alignment of three dots is a comparison of the orientations of the lines P to PT and P to T, and not of the lines P to PT and PT to T, since these two line elements now had equal length and translation over the screen was shown not to effect the orientation judgements.

Mislocalizations have been demonstrated before when subjects performed reaching movements towards visually presented targets (e.g. Roll, Bard & Paillard, 1986; Soechting & Flanders, 1989). For conditions where the head was restrained mismatches of final hand position and peripheral target position have been thought to be associated with the extreme position of the eyes in their orbits (Roll *et al.*, 1986; Biguer, Prablanc & Jeannerod, 1984). However, we here find systematic biases even with very small stimuli that do not involve such extreme eye positions. Soechting and Flanders (1989) suggested that mislocalizations may result from the transformation of the position of the target from the visual frame of reference (used in the perceptual part of the task) to the motor frame of reference (which is used to control the arm movement). In our setup, however, arm movements, and therefore this motor frame of reference, do not play a role. Our results cannot be explained by a transformation from visual to arm motor space, nor by biases caused by extreme eye positions.

How then can we understand the presently demonstrated biases? One possible hypothesis is that the perceived orientation of a point relative to a certain reference position is defined by the direction of the initial part of the saccade from the reference to this point. Saccade trajectories have been shown to be curved, especially for oblique saccades (see e.g. Viviani, Berthoz & Tracey, 1977; Smit & Van Gisbergen, 1990). This is understood to result from a difference in temporal properties of the motor systems that move the eye horizontally and vertically, respectively (Viviani *et al.*, 1977). There are considerable differences between subjects but each subject individually shows a characteristic pattern of saccade trajectories (Smit & Van Gisbergen, 1990). Generally, upwards oblique saccades start in a direction that is more horizontal than the straight line from starting to final position. Matching the direction from pivot to pointer tip to the direction from pivot to target in our experiment would according to our tentative hypothesis imply choosing a pointer tip position such that the initial part of the trajectory of the saccade

to this position would coincide with that of a saccade towards the target. This would indeed result in the deviations we found.

For downward oblique saccades the trajectories seem to be less systematically curved (e.g. Fig. 1 in Viviani *et al.*, 1977), which can be thought to correspond to our finding that the three dot alignments oriented downwards do not show a uniform effect. Strictly horizontal and vertical saccades, on the other hand, have relatively straight trajectories (Viviani *et al.*, 1977; Smit & Van Gisbergen, 1990), which might correspond to the lack of deviations in our horizontal and vertical three-dot alignments. The way the saccades are curved does not depend on the initial gaze direction: translating both starting and final position by 15 deg visual angle in any of the four main directions did not greatly influence the curvatures (Gnadt, Bracewell & Andersen, 1991). Our hypothesis would then predict that the biases we find would not depend on the position of the stimulus on the screen, but would depend on its orientation only. This is indeed what we found (Fig. 3 and Table 1).

Note that the horizontal and vertical directions which do not show curved saccades are defined relative to the subject's head: the pattern of the curvatures arises from the anatomy and physiology of the systems that move the eye in the orbit (Viviani *et al.*, 1977), and these are hardly influenced by gravity or other external factors. Our finding that the orientation of the stimulus relative to the longitudinal head axis, and not relative to the real world vertical, is the variable with which we have to describe the shown biases, is therefore in agreement with the explanation we suggest.

Can we understand that the demonstrated biases are insensitive to decreasing the size of the stimulus from 20 to 0.8 deg visual angle? Such invariance would follow directly from the similarity of saccade trajectories to near and distant targets with identical orientation. Such similarity has indeed been demonstrated (Smit & Van Gisbergen, 1990). They showed that the direction-dependent curvatures remained virtually unchanged when the amplitude of the saccades was decreased from 25 to 5 deg. It remains to be seen, however, if this finding can be extended to saccades as small as 1 deg.

The mechanism we suggest does not imply that the tip of the pointer is seen to be lying on the trajectory towards the target during the performance of the saccade. Such an explanation would not make sense, since the perception is suppressed during the performance of saccades (e.g. Matin, 1974). Rather, we think that the CNS does remember (or predict) the proportion of the activities of the eye muscles that are required to perform saccades from the pivot to the pointer tip and from the pivot to the target. Strictly speaking, the actual execution of the saccades during the performance of the alignment task would not be necessary if the predicted proportions are used. In that case the outcome of the experiment would not be affected by the subjects' continuous fixation of the pivot. Although we could not check this with our apparatus, it is indeed probable that

with our smallest stimuli (2.5 deg visual angle in the adjustment task and 0.8 deg in the two-alternative forced-choice task) the subjects did not move their eyes or moved them less frequently.

We want to mention recent results (De Graaf, Denier van der Gon & Sittig, 1991a) obtained with congenitally blind subjects who were asked to move their index finger slowly over a horizontal surface towards tactile targets they felt with the other hand. They showed consistent biases in initial movement direction that qualitatively resembled the deviations found in sighted subjects directing their finger towards visual targets, even if the size of the deviations was much more variable in the blind subjects. If the misdirections in blind and sighted subjects would reflect the same phenomenon, the origin can obviously not lie in visual experience. However, it has been suggested that blind subjects may use goal-directed eye movements to facilitate localizing auditorily presented targets (Jones, 1975). The control of eye movement might therefore contribute to the perception of spatial relations, even in blind subjects.

Performing the present three dot alignment is equivalent to judging if the line through the three points is a straight line. To judge the straightness of a real line or edge, a different mechanism that relies on local processes (Wilson & Richards, 1989) might be used. Our last experiment suggests that there are indeed two different mechanisms to determine the straightness of a virtual line, one that determines the relative direction between individual points and one that judges the overall straightness using a large number of local detectors. We showed that the perceptual straightness of a virtual line is critically influenced by the number of dots that make up the line. With only three dots a downwards curved oblique virtual line is perceived to be straight. The curvature of the perceptually straight line decreases with the introduction of additional dots, and eventually disappears completely. The gradual decrease of the curvature of the perceptually straight line indicates that the two ways of judging straightness compete: with only three dots the direction-mechanism prevails but with the introduction of additional dots it loses ground to the overall-straightness mechanism. Note that it is the number of dots that make up a line that determines the curvature of the perceptually straight line, and not the distance between the dots. With three dots in a 0.8 deg stimulus the distance between two neighbouring dots is 0.4 deg, as it is with 15 dots in a 6 deg stimulus. Nevertheless, the perceptually straight lines proved consistently curved in the first case and virtually straight in the second case. The effect seems to be scale invariant.

In the present study we found consistent orientation dependent misalignments in a three dot alignment task. These findings are in agreement with the suggestion that the misalignments are related to the trajectories of saccades: first, it is the direction of the oriented line from pivot to target dot that determines the biases, with the most pronounced deviations for obliquely upward ori-

ented lines and with horizontal and vertical directions showing relatively small biases. Second, this orientation must be considered relative to the observer's longitudinal head axis. Thirdly, neither translating nor scaling the stimulus has a considerable effect. Finally, both the curvatures of the saccades and the three dot misalignments show consistent, but individually different, patterns. This also provides a means for investigating the proposed explanation by recording saccade trajectories and the performance in a three dot alignment task for the same subjects.

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