Effects of surrounding frame on visual search for vertical or tilted bars

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It is easier to find a tilted bar among vertical bars than vice-versa, but this asymmetry can be abolished or reversed by surrounding the bars with a tilted frame. The frame effect is important because it challenges bottom-up models of saliency. We conducted two experiments to investigate the causes of this effect. In Experiment 1, we removed different components of a square frame, and concluded that the frame effect was caused by a combination of (1) high-level configural cues that provided a frame of reference, and (2) bottom-up iso-orientation competition from the sides of the frame parallel to the bars. The iso-orientation competition could have arisen from (1) diversion of attention to the parts of the frame parallel to the target, or (2) iso-orientation suppression between nearby units selective for the same orientation. Experiment 2 investigated the nature of the iso-orientation competition process. In this experiment, we used a single line (the “axis”) embedded in a circular field of bar elements, rather than a square frame surrounding them. The effect of the axis declined rapidly to zero with increasing target-axis distance, suggesting that the iso-orientation competition was caused entirely by iso-orientation suppression between nearby units tuned to the same orientation.

Keywords: visual search, orientation, top-down, bottom-up, iso-orientation suppression


Introduction

It is generally easier to find a tilted target among vertical distractors than a vertical target among tilted distractors (Carrasco, McLean, Katz, & Frieder, 1998; Cavanagh, Arguin, & Treisman, 1990; Doherty & Foster, 2001; Foster & Ward, 1991a; Marendaz, 1998; Marendaz, Stivalet, Barraclough, & Walkowiac, 1993; Treisman, 1985; Treisman & Gormican, 1988; Wolfe, Friedman-Hill, Stewart, & O’Connell, 1992). A similar asymmetry applies to orientations at or tilted relative to horizontal (Doherty & Foster, 2001; Foster & Ward, 1991a; Marendaz, 1998; Marendaz et al., 1993). These findings (which we will collectively term the orientation asymmetry) are examples of some of the many asymmetries found in visual search, whereby exchanging the characteristics of the target and distractors changes the difficulty of the search (Treisman & Gormican, 1988; Treisman & Souther, 1985). Some apparent search asymmetries may have resulted from asymmetrical experimental designs (Rosenholtz, 2001), but the orientation asymmetry appears to reflect a genuine asymmetry in the mechanisms of visual search: It involves a simple swapping of target and distractor within orientation space, and still occurs when the stimuli are viewed through a circular window, ensuring that there is no asymmetry in the visual display (Doherty & Foster, 2001; Marendaz, 1998; Marendaz et al., 1993; Treisman & Gormican, 1988).

The orientation asymmetry has been of great interest to researchers working on visual attention, who have used it to infer various properties of orientation coding in the processes mediating visual search. Treisman (1985) and Treisman and Gormican (1988) interpreted the orientation asymmetry in terms of the feature-integration theory (Treisman & Gelade, 1980). In this theory, a “feature” is a value along a stimulus dimension, such as orientation or color. The theory proposes that early, preattentive, visual processes decompose the visual stimulus into separate feature maps representing different orientations, colors, etc. In the theory, integration of these different feature maps requires spatially localized attention, which can only be applied to one location at a time, so the spatially parallel processing required for efficient visual search can only operate within individual feature maps, before integration. If there is a feature map which is activated by the target but not the distractors, then the target “pops out” and is easy to detect; if no feature map responds exclusively to the target, then detection of the target requires a serial search.

The feature-integration theory readily explains the finding that feature presence is easier to detect than feature absence: Only in the former case can a feature map respond exclusively to the target (Treisman & Souther, 1985). To explain the orientation asymmetry, Treisman and Gormican (1988) proposed that a tilted line is encoded as a vertical line with an extra feature representing the tilt. A tilted target among vertical distractors is
Frames of reference

It seems, then, that the horizontal and vertical orientations are processed differently from other orientations in preattentive vision. But what cues does the visual system use to set this frame of reference? Marendaz and colleagues have investigated the effects of postural-gravitational cues (for a review, see Marendaz, 1998). They found that the orientation asymmetry was abolished when the subjects lay on their backs, viewing a screen that was orthogonal to the gravitational axis (Marendaz et al., 1993). Furthermore, when the subjective vertical and horizontal were tilted by applying a transverse centrifugal force to subjects placed in a centrifuge, it was targets aligned with the subjective horizontal (and therefore tilted relative to the gravitational horizontal) that were the hardest to detect (Stivalet, Marendaz, Barraclough, & Mourareau, 1995). It seems that gravitational and gravito-inertial cues can play a part in defining the frame of reference for preattentive orientation coding, although Doherty and Foster (2001) were unable to replicate Marendaz et al.’s (1993) effect of supine posture: They found that the orientation asymmetry remained when subjects were lying on their backs, suggesting that in some experimental conditions the frame of reference can be based entirely on retinal coordinates.

Accounting for the frame effect

The frame effect is important because it provides a potential challenge to bottom-up models of saliency (e.g., Itti, Koch, & Niebur, 1998; Koch & Ullman, 1985; Li, 1999a, 1999b, 2000, 2002). There are several possible bottom-up and top-down processes, any or all of which might contribute to the effect, and the purpose of the current study was to tease apart some of these potential explanations.

Let us first consider bottom-up accounts of the frame effect. When the sides of the frame are parallel to the target, they could compete with it for attention. There are at least two means by which this competition might be
mediated. Firstly, the sides of the frame parallel to the
target could provide a false target, diverting attention
away from the real target; for example, in Treisman’s
feature integration theory (Treisman & Gelade, 1980), the
sides parallel to the target would occupy the same
orientation feature map as the target, so the target would
no longer be unique within the feature map, and it would
not pop out so readily. Secondly, competition might be
mediated by iso-orientation suppression. Most models of
visual attentional selection include mutual inhibition
between units selective for the same feature (e.g., Cave & Wolfe, 1990; Itti et al., 1998; Koch & Ullman, 1985; Li, 1999a, 1999b, 2000, 2002; Wolfe, 1994, 2007; Wolfe & Gancarz, 1996). In these models, iso-orientation
suppression would cause units responding to the frame
to suppress units responding to whichever class of
elements (target or distractor) is parallel to it.

So we have two ways in which the sides of the frame
might compete with stimulus elements parallel to it in a
bottom-up manner: firstly, by providing additional stim-
ulus features with the same orientation as the target, so
that attention might be diverted to the frame before the
target; secondly, by actively inhibiting the responses to
the elements parallel to the frame (iso-orientation sup-
pression). We refer to these two processes collectively as
iso-orientation competition (not to be confused with iso-
orientation suppression). The first process (diversion of
attention) would be expected to provide competition
whatever the distance of the target from the frame: If
anything, there should be more competition for greater
target-frame distances, because attention would be
diverted further from the target. In contrast, the second
process (iso-orientation suppression) should decline in
strength with increasing distance, because this process is
thought to be mediated by long-range horizontal cortical
connections, which, despite being several times longer
than the diameter of the classical receptive field, are still
limited in their extent (Gilbert & Wiesel, 1979, 1983,
1989; Rockland & Lund, 1983). In Experiment 2, we test
the predictions of these two bottom-up iso-orientation
competition processes.

The effect of the frame could also be mediated by top-
down mechanisms; for example, the frame could provide
a “frame of reference” against which vertical is defined.
Marendaz’s (1998) results suggest that bottom-up iso-
orientation competition between the target and the frame
is not solely responsible for the frame effect. But does iso-
orientation competition play any role in the frame effect at
all, or is the effect entirely due to higher-level configural
cues? And, if iso-orientation competition is involved,
which of the two processes outlined above mediates this
effect? To answer these questions, we designed two
experiments in which the nature of the frame was
manipulated. In Experiment 1, we investigated the effect
of removing the iso-orientation competition, while keep-
ing the configural cues to orientation. In Experiment 2, we
attempted to minimize the configural cues, while keeping
the iso-orientation competition. Experiment 2 allowed us
to test the predictions of the two hypothesized iso-
orientation competition processes.

**Methods**

**Apparatus**

All experiments were run on a Dell PC with a VSG 2/5
graphics card (Cambridge Research Systems). Experi-
ments were controlled using software written in MAT-
LAB (The MathWorks, Inc.). Bitmap images were
generated in MATLAB, and these were linearly scaled
to fit the range 0–255 and stored in an 8-bit frame store on
the VSG card. Stimuli were then scaled to the correct
contrast and gamma corrected by mapping the 8-bit values
onto 15-bit values. An analogue input to the monitor was
generated from these 15-bit values using two 8-bit digital-
to-analogue converters on the VSG card. Stimuli were
displayed on a Sony CPD-G520P monitor at a frame rate
of 80 Hz. The system was configured to generate a screen
display that measured 1024 pixels (40 cm) horizontally by 769 pixels (30 cm) vertically. In front of the screen was placed an opaque, rectangular, black board of width 101.5 cm and height 76 cm, which contained a central circular hole 26.8 cm in diameter. This hole was centered on the center of the screen, and provided a circular window surrounding the stimuli. Subjects sat in a darkened room and viewed the screen binocularly from a distance of 60 cm. At this distance, the circular window subtended a visual angle of 25.2 deg. Responses and reaction times (RTs) were recorded using a CB6 response box (Cambridge Research Systems) connected to the VSG card.

Experiment 1

Subjects

Experiment 1 used three male subjects (AI, AJ, and AJA), and two female subjects (LZ and NG). All subjects were naive to the purposes of the experiment except for LZ, who is an author on this paper. All subjects had normal or corrected-to-normal vision.

Stimuli

Figure 1 gives several examples of the different types of stimulus used in Experiment 1. Stimuli consisted of 12 black bar elements on a mid-gray background, surrounded by one of three different types of frame (also black). The bar elements were either vertical or tilted 18° anticlockwise. For target-absent stimuli, there were either 12 vertical bars or 12 tilted bars; for target-present stimuli, there were 11 tilted distractors and 1 vertical target, or 11 vertical distractors and 1 tilted target. To prevent jagged edges, and to allow positioning with sub-pixel accuracy, the edges of the bars had a half-period sine profile, with width subtending a visual angle of 4.2 arcmin (just over 2 pixel-widths). The bars were rectangles 42 arcmin long by 8.4 arcmin wide (measured from the mid-points of the sine edge profiles). Informal inspection of the stimuli on the screen indicated that the tilted bars did not look jagged, and had a very similar appearance to the vertical bars.

The bars were presented within a square region that could be either vertical or tilted 18° anticlockwise. The sides of this region had a length of 5.6 degrees of visual angle. Depending on the frame condition, two or more sides of this square region were visible black lines, with the same cross-sectional profile as the bar elements. There were three different frame conditions: “Complete” (all four sides visible), “L&R” (just the left and right sides visible), and “T&B” (just the top and bottom sides visible).

Figure 1. Examples of the three types of frame used in Experiment 1: “Complete” frame (all sides present), “L&R” frame (only left and right sides present), and “T&B” frame (only top and bottom sides present). The top row shows “vertical” frames, and the bottom row shows frames tilted 18° anticlockwise from vertical. Each of these examples contains vertical distractors and an 18° tilted target. Other conditions had tilted distractors and vertical target, or just vertical or tilted distractors with no target present. The circular window was created by placing a large board in front of the screen with a circular hole cut into it. The frames and bar elements in this figure were generated using the same software that was used to generate the stimuli in the experiment.
The positions of the 12 bars within the square region were determined one by one. For each bar, we selected a random location at least 31.5 arcmin from all of the sides of the square region, and then checked that the center of the bar was not within 63 arcmin of the center of any bar that had already been inserted into the display. If it was, the location was rejected and another one was chosen; this process was repeated until a satisfactory location could be found. This method of generating the stimulus arrays prevented a regular structure that would have emerged from inserting the bar elements into a grid of cells (e.g., Field, Hayes, & Hess, 1993).

The L&R and T&B frames had missing sides, but they still defined the same square region as the Complete frame, by amodal completion. Therefore, it is likely that the high-level configural cues that might have provided a frame of reference were similar for all three frame types. In contrast, iso-orientation competition would have occurred only for the Complete and L&R frames: Only the left and right sides of the frame could be parallel to the bar elements, so the Complete and L&R frames should both have given rise to the same amount of iso-orientation competition, while the T&B frame should have generated none. The T&B condition therefore gave a pure measure of the effect of configural cues provided by the frame, while the other two frame conditions reflected the combined effects of configural cues and iso-orientation competition. From these assumptions, we can derive the predictions of three hypotheses:

1. The effect of the Complete frame arises only from configural cues, which provide a “frame of reference”: This predicts that all three frame types will have an effect of the same size.
2. The effect of the Complete frame is caused only by iso-orientation competition: This predicts that only the Complete and L&R frames will have an effect.
3. The effect of the Complete frame is caused by both configural cues and iso-orientation competition: This predicts that the Complete and L&R frames will have an effect of the same size, while the T&B frame will have a smaller, but still significant, effect.

**Design**

The experiment had a factorial design with four within-subject factors: distractor orientation (0° or 18° anticlockwise from vertical), frame orientation (0° or 18° anticlockwise from vertical), frame type (Complete, L&R or T&B), and target presence (present or absent). The target (when present) had an orientation of 0° for 18° distractors, and 18° for 0° distractors. Each of the 24 combinations of levels of the different factors appeared 12 times within a session, with a random order of presentation. Each subject performed 5 similar sessions, giving 60 trials per condition, and 1440 trials over the whole experiment.

**Procedure**

On each trial, subjects saw a circular black fixation dot (9 arcmin in diameter) on a mid-gray screen for 700 ms, after which the fixation dot was overwritten by the stimulus. The stimulus remained visible until the subject responded to indicate target presence (left button) or absence (right button). Subjects were instructed to respond as soon as possible while maintaining a low error rate. During the presentation of the stimulus, subjects were allowed to make whatever eye movements they wanted. The RT (from target onset to response) was recorded. No feedback was given regarding correctness of response. The next trial began automatically after a short delay.

The use of RT as a measure of search time is compromised by the fact that the subjects are free to choose whatever speed-error tradeoff they want, and there is no well-established theory for interpreting RTs in a quantitative manner. Because of these problems, instead of measuring reaction times, some researchers present the stimuli for a controlled duration, followed by a post-stimulus mask. Search difficulty can then be measured by analyzing the yes/no responses for a single stimulus duration using standard signal detection theory (e.g., Doherty & Foster, 2001; Foster & Ward, 1991a, 1991b), or by using a number of different stimulus durations and finding the duration corresponding to a chosen threshold level of performance (e.g., Meigen, Lagreze, & Bach, 1994). The latter approach involves the implicit assumption that the post-stimulus mask terminates processing of the stimulus, but this assumption has recently been questioned (Smithson & Mollon, 2006): The mask might pursue the stimulus through the processing stream for some time before catching up with it, so the stimulus could still be available for processing after the mask onset. During this time, the mask could still interfere with processing of the stimulus because visual neurons integrate over time as well as space, but this interference would probably be more complex than simple termination of processing. Therefore, the duration threshold may not be a more valid measure of search time than RT. The alternative approach, used by Foster and colleagues, in which a single fixed stimulus duration is used, has failed to replicate gravitational frame-of-reference effects (Doherty & Foster, 2001) that had previously been found using an RT paradigm (Marendaz et al., 1993). It is possible that results obtained using a short, fixed, stimulus duration reflect the activity of very fast-acting mechanisms that are not susceptible to frame-of-reference effects (see the Discussion for further elaboration of this point). Given that this method was potentially insensitive to the effects that we wanted to study, and that all previous
studies showing an effect of a surrounding frame had used RTs (Marendaz, 1998; Treisman, 1985; Treisman & Gormican, 1988), we decided to use RTs as a measure of search difficulty in our experiments. If error rates show a similar pattern to the RTs, or show no substantial difference between the conditions being compared, then RT differences between conditions must reflect differences in search difficulty, rather than different speed-error tradeoffs.

Experiment 2

Subjects

Experiment 2a used one male subject (AJ, who also participated in Experiment 1), and four female subjects (LZ and NG from Experiment 1, and two further subjects, JSH and LJ). Experiment 2b used two male subjects (AI from Experiment 1, and a new subject, ASL), and three female subjects (LJ, LZ and NG, all of whom participated in Experiment 2a). LJ performed Experiment 2b before Experiment 2a, while LZ and NG performed Experiment 2a first. All subjects were naive to the purposes of the experiments except for LZ. All subjects had normal or corrected-to-normal vision.

Stimuli

In Experiment 2, we attempted to minimize the configural cues, while maintaining the possibility of iso-orientation competition. The stimuli are illustrated in Figure 2. Instead of a frame, there was a single line that bisected the circular window. We refer to this line as the “axis”. The axis orientation was 0° or 18° anticlockwise from vertical (Experiment 2a) or 0° or 18° anticlockwise from horizontal (Experiment 2b). The circular window was the same size as in Experiment 1, but was now filled with bar elements (with a similar density to the stimuli in Experiment 1) so that each stimulus had the appearance of a circular object, rather than a square one. We hoped that this might reduce any configural cues that could generate a frame of reference.

As in Experiment 1, the target and distractors were either 0° or 18° anticlockwise from vertical. Therefore, we would expect iso-orientation competition from the axis only in Experiment 2a; in Experiment 2b, the axis was never parallel to any of the elements, analogous to the T&B frame condition in Experiment 1.

We can define three hypotheses, analogous to those in Experiment 1:

1. The effect of the axis arises only from configural cues, which provide a “frame of reference”: This predicts that Experiments 2a and 2b will show the same size effect of axis orientation.

2. The effect of the axis is caused only by iso-orientation competition: This predicts that only Experiment 2a will show an effect of axis orientation.

3. The effect of the axis is caused by both configural cues and iso-orientation competition: This predicts that the axis orientation will have an effect in both Experiments 2a and 2b, but the effect will be larger in Experiment 2a.

We also took the opportunity to test between the two suggested iso-orientation competition processes outlined earlier: (1) diversion of attention by additional stimulus features parallel to the target; (2) iso-orientation suppression. The first process predicts that there should be more competition for greater target-frame distances, because attention would be diverted further from the target; the second process predicts that the effect of axis orientation should decline with increasing target-axis distance. To test between these predictions, we systematically manipulated the distance between target and axis in Experiments 2a and 2b. This manipulation was facilitated by the use of a
single line (the axis), rather than the square frame that had been used in Experiment 1: With a square frame, as a bar element moved away from one side, it would move closer to the opposite side, and the combined effect of changes in iso-orientation suppression from the two sides would be difficult to predict without knowing exactly how the strength of iso-orientation suppression varied with distance. For example, if the strength of iso-orientation suppression fell linearly with distance across the width of the frame, then the reduction in suppression as the target moved away from one side would be exactly cancelled by the corresponding increase in suppression from the opposite side.

The stimuli were constructed as follows. A line (the “axis”) with the same cross-sectional profile as the bar elements and sides of the frame from Experiment 1 was inserted so that it passed through the center of the circular window, and extended past the edge of the window on each side: The axis was therefore seen to extend right across the visible screen area. For target-present stimuli, a target element with the same form as in Experiment 1 was inserted on one side of the axis. The center of the target was positioned by first finding a random position along the axis within 4 degrees of visual angle from the center in either direction (flat probability distribution), and then moving perpendicularly away from the axis, so that the center of the target was 1, 2, 3, or 4 degrees of visual angle from the axis. 184 distractor elements were then placed one by one within the circular window. The center of each element had to be at least 63 arcmin from the center of all previously placed elements, and at least 31.5 arcmin from both the axis and the edge of the circular window. For each distractor, we kept generating random locations until we obtained one that satisfied these constraints. For target-absent stimuli, there were 185 distractors and no target; the distractors were positioned using the same method as for the target-present stimuli.

Because the axis always went through the center of the stimulus, the target-axis distance was confounded with mean target eccentricity. In Appendix A, we rule out the possibility that our pattern of results was caused by differences in target eccentricity, rather than target-axis distance per se, by showing that there was no effect of target eccentricity for a particular target-axis distance.

**Results for the Complete and L&R frames were very similar.**

**Experiment 1**

Figure 3 shows the RTs and error rates from Experiment 1. The data were analyzed for each subject as follows. For each condition, we discarded all the trials for which the response was incorrect. From the correct-answer trials, we calculated the mean RT and population standard derivation estimate for each condition, and discarded any outlying trials with RTs more than 3 standard deviations from the mean for that condition. From the remaining trials, we recorded the mean and standard error, which are displayed for each condition and for each subject in the top five rows of Figure 3.

Results for the Complete and L&R frames were very similar. For both types of frame, and for all subjects, RTs...
were shorter for tilted targets when the frame was vertical, and shorter for vertical targets when the frame was tilted; the advantage for tilted targets in a vertical frame was stronger than the advantage for vertical targets in a tilted frame, which probably reflects the general advantage for tilted targets in the absence of any frame. For the T&B frame, the interaction between frame tilt and target tilt was weaker: There was an advantage for tilted targets in a vertical frame while, in a tilted frame, the target orientation had little effect.

Figure 3 also shows the error rates, averaged across subjects. These data showed interactions in the same direction as for the RT data, with a strong advantage for tilted targets in a vertical frame, but little or no advantage for vertical targets in a tilted frame. This shows that the interactions seen in the RT data largely reflect differences in task difficulty, rather than differences in the speed-error tradeoff between conditions.

For each subject and frame type (i.e. each panel from the top five rows of Figure 3), we quantified the interaction between frame tilt and target tilt using Equation 1:

\[
I = \left( \frac{RT_{0,0} - RT_{0,18}}{RT_{0,0} + RT_{0,18} + RT_{18,0} + RT_{18,18}} \right) \left( \frac{1}{2} \right),
\]

where \(I\) is the interaction strength, and \(RT_{a,b}\) is the mean reaction time for frame orientation \(a\) and target orientation \(b\). This equation gives zero when there is no interaction (i.e. if the two lines in a panel in Figure 3 have the same slope), and gives a positive value for the interactions observed in Experiment 1. The mean interaction strengths across subjects are shown in Figure 4. Differences in interaction strength between conditions were assessed using two-tailed \(t\)-tests. There were three possible pairwise comparisons, so the criterion of significance for each individual test was Bonferroni corrected to \(0.05/3 = 0.0167\), ensuring that the probability of a Type I error across all three tests was no higher than 0.05. The T&B frame showed a significantly smaller interaction than either of the other two frames (T&B vs. L&R frame: \(t = 4.83, \text{d.f.} = 4, p = 0.00848\); T&B vs. Complete frame: \(t = 4.00, \text{d.f.} = 4, p = 0.0162\)). The difference between the L&R and Complete frames did not approach significance (\(t = 0.664, \text{d.f.} = 4, p = 0.543\)). Although the T&B frame showed a significantly smaller interaction than either of...
the other two frames, the interaction for this frame was still very significantly above zero (t = 20.7, d.f. = 4, p (two-tailed) = 3.19 \times 10^{-5}).

Mori and Kataoka (2004) carried out an analogous manipulation to our L&R and T&B frames, although they put a small frame around each element, instead of one large frame around the whole display. They obtained similar results, in that the T&B frame had some effect, but not as much as the L&R frame. It is difficult to know whether their procedure was tapping the same mechanisms as ours. Firstly, unlike us, they failed to find any effect of a global frame with their setup; secondly, their frames would have given rise to crowding, because all the stimulus elements were about 5 degrees of visual angle from fixation, and the distance between the center of each element and its frame (0.65 degrees of visual angle) was much less than half the eccentricity, which is the critical spacing below which crowding starts to occur (Bouma, 1970; Pelli, Palomares, & Majaj, 2004). Thus, the interactions between frame and elements in Mori and Kataoka’s (2004) study may have been of a different nature to the interactions that gave rise to our results.

Experiment 2

The results of Experiment 2a (axis at or close to vertical) and 2b (axis at or close to horizontal) were analyzed in the same way as Experiment 1, and are displayed in Figures 5 and 6, respectively. For each target-axis distance, the interaction between axis tilt and target tilt was calculated separately for each subject, using Equation 1. The mean interaction strengths across subjects are plotted in Figure 7 and the numerical values are given in Table 1.

Experiment 2a showed a strong interaction when the target was 1 degree of visual angle from the axis, but the interaction strength dropped rapidly to around zero

Figure 4. Strength of interactions between frame tilt and target tilt in Experiment 1, calculated using Equation 1 for each individual subject, and then averaged across subjects. The frame types are displayed along the horizontal axis (left-to-right: Complete frame, L&R, and T&B). Error bars (in black) indicate ±1 standard error of the mean across the five subjects for each frame type.

Figure 5. Results of Experiment 2a (axis at or close to vertical), analyzed and displayed in the same way as Experiment 1 (Figure 3), except that each column represents a different target-axis distance.
as the target-axis distance increased. For Experiment 2b, the interaction strength was close to zero for all target-axis distances.

Two-tailed $t$-tests were used to test whether the interaction strength in each of the eight conditions from Experiments 2a and 2b was significantly different from zero. The criterion of significance for each individual test was Bonferroni corrected to $0.05/8 = 0.00625$, ensuring that the probability of a Type I error across all eight tests was no higher than 0.05. Using this criterion of significance, only one condition was significantly different from zero: the target-axis distance of 1 degree of visual angle in Experiment 2a. For a target-axis distance of 2 degrees of visual angle in Experiment 2a, the interaction strength had a $p$-value of 0.0309, which would have been significant at the 0.05 level without the correction for multiple comparisons. None of the other conditions of Experiment 2a, that the probability of a Type I error across all eight tests was no higher than 0.05. Using this criterion of significance, only one condition was significantly different from zero: the target-axis distance of 1 degree of visual angle in Experiment 2a. For a target-axis distance of 2 degrees of visual angle in Experiment 2a, the interaction strength had a $p$-value of 0.0309, which would have been significant at the 0.05 level without the correction for multiple comparisons. None of the other conditions of Experiment 2a,
or any of the conditions of Experiment 2b approached even the uncorrected 0.05 level of significance.

Discussion

In Experiment 1, we observed significant interactions between frame tilt and target tilt for all three frames types; the interactions for the Complete and L&R frames were not significantly different from each other, but were both significantly stronger than for the T&B frame. Referring back to the three hypotheses that we outlined when describing the stimuli, we can see that these results are consistent with the hypothesis that the effects of the frame can be mediated by two different mechanisms: (1) a high-level mechanism that derives a “frame of reference” from configural cues provided by the frame, and is equally effective across all three frame types; (2) an additional bottom-up iso-orientation competition mechanism that is only seen when the frame contains components that are parallel to the target or distractors (i.e. the Complete and L&R frame conditions).

The different stimulus layout used in Experiment 2 appeared to be successful in abolishing any high-level configural cues that could have generated a frame of reference from the axis: We obtained an interaction between axis tilt and target tilt only when the axis was parallel to the target or distractors (Experiment 2a). This suggests that the effect of the axis in Experiment 2a was entirely due to bottom-up iso-orientation competition.

Note that both kinds of mechanism outlined above generate an orientation asymmetry from signals provided by the frame or axis; we term these influences “display-dependent” effects. But the orientation asymmetry can also occur without a surrounding frame, with the stimuli presented within a circular window (Doherty & Foster, 2001; Marendaz, 1998; Marendaz et al., 1993; Treisman & Gormican, 1988). This suggests that there must be additional mechanisms generating an orientation asymmetry from factors not contained in the visual stimulus itself; we term these influences “non-display-dependent” effects. Our experiments only address the nature of the display-dependent effects caused by the frame or axis. However, they do provide evidence for non-display-dependent effects because, collapsing across frame or axis orientation, the RTs were generally lower for tilted targets.

In Experiment 2, we tested between two different iso-orientation competition processes by manipulating the target-axis distance. ISO-orientation competition caused by diversion of attention by additional stimulus features parallel to the target would be manifested at all target-axis distances, and would be likely to increase in strength with increasing target-axis distance, whereas iso-orientation competition that arises from iso-orientation suppression should only be seen for short target-axis distances. In Experiment 2a, we found that the interaction between axis tilt and target tilt declined rapidly to zero with increasing target-axis distance: There was a significant interaction for a target-axis distance of 1 deg, and a hint of an interaction for a target-axis distance of 2 deg, which failed to reach significance because of the correction for multiple comparisons; for the two larger distances, the interaction was close to zero, and did not approach significance. Since there was no indication of an interaction at target-axis distances longer than 2 deg, we conclude that the iso-orientation competition in Experiment 2a was entirely due to iso-orientation suppression between nearby units tuned to the same orientation.

We cannot be completely sure that the iso-orientation competition mechanism identified in Experiment 1 was the same as that in Experiment 2a, but we consider this to be a strong possibility. Although there were many more stimulus elements in Experiment 2a than Experiment 1, the spatiotemporal characteristics of the stimuli were the same in many other respects: For example, the elements were identical and had similar densities within the stimuli, and the axis in Experiment 2a was the same as the left and right sides of the frame in Experiment 1 (except in length). The differences between the stimuli in Experiments 1 and 2a are quite minor compared with the heterogeneity found in sets of natural images, and it would be computationally and anatomically inefficient to have several different iso-orientation competition mechanisms to carry out the same process in different visual environments, when one would suffice. So it seems likely that the effects of the Complete and L&R frames in Experiment 1 were caused by one quite well-understood mechanism (bottom-up iso-orientation suppression between nearby units), and one poorly understood mechanism that imposed a frame of reference using high-level configural cues derived from the frame.

It is instructive to compare the spatial extent of the iso-orientation suppression with the size of the receptive fields that would have responded best to the bar elements. Most orientation-selective V1 simple cells have receptive fields that contain 2 or 3 regions of high response (see, for example, Jones & Palmer, 1987a, 1987b), so we can assume that the receptive fields employed here had a width of about 2 or 3 times that of the bar elements. Most orientation-selective V1 simple cells have receptive fields that contain 2 or 3 regions of high response (see, for example, Jones & Palmer, 1987a, 1987b), so we can assume that the receptive fields employed here had a width of about 2 or 3 times that of the bar elements, i.e. about 17–25 arcmin. From Figure 7, it appears that the strength of the iso-orientation suppression drops to zero at a target-axis distance of around 2.5 degrees of visual angle, which is about 6–9 times the expected receptive field size. This range of values is highly compatible with the ratios of long-range horizontal connection length to receptive field size found in striate cortex (Gilbert & Wiesel, 1989). These horizontal connections usually mediate iso-orientation suppression (e.g., Blakemore & Tobin, 1972; Jones, Wang, & Sillito, 2002; Kastner, Nothdurft, & Pigarev, 1997; Knierim & Van Essen, 1992; Nelson & Frost, 1978; Nothdurft, Gallant, & Van...
Essock, 1999; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995). A few cells have been found for which the suppressive effect of the surround is sharply tuned to orientations orthogonal to the classical receptive field (see, for example, Jones et al., 2002, Figure 1F), but the influence of this kind of mechanism in the current experiments is ruled out by the lack of an effect of axis orientation in Experiment 2b.

The finding that the spatial extent of iso-orientation suppression in Experiment 2a matches the length of the long-range horizontal connections in V1 is particularly supportive of models of bottom-up visual attentional selection that utilize these horizontal connections to compute a saliency map in V1 (e.g., Li, 1999a, 1999b, 2000, 2002), although the drop in iso-orientation suppression with increasing target-axis distance would be predicted (at least qualitatively) by any model of visual attentional selection in which mutual inhibition between units with the same orientation preference declined with increasing distance between their receptive field centers (e.g., Itti et al., 1998; Koch & Ullman, 1985; Wolfe, 1994, 2007; Wolfe & Gancarz, 1996). On the other hand, without modification or extension, none of these models would predict the effect of the T&B frame in Experiment 1. Given the lack of an effect of the horizontal or near-horizontal axis in Experiment 2b, it seems likely that the effect of the T&B frame is caused by high-level or top-down mechanisms that extract the global orientation of the object under consideration. The finding that attentional selection is biased by tilt relative to the object containing the target is consistent with the view that competition for attention can be object-based (Duncan, 1984, 1993). It is not clear why this bias should exist. One possibility is that, although natural images generally have fewer image components tilted relative to gravity (Baddeley & Hancock, 1991; Hancock, Baddeley, & Smith, 1992; Hansen & Essock, 2004; Keil & Cristóbal, 2000), it may be that, within an object, components tilted relative to the object’s principal axis are less common; for example, the texture of bark on a tree trunk is usually dominated by features that are parallel (e.g. oak) or perpendicular (e.g. silver birch) to the principal axis of the trunk, even if the trunk itself is tilted. If this hypothesis is correct, then targets tilted relative to the object containing them would be more novel, and would benefit from the well-known top-down bias for novelty in attentional selection (see Desimone & Duncan, 1995, pp. 200–202).

Finally, we return to the basic orientation asymmetry found without a surrounding frame (the “non-display-dependent” effect described earlier). This phenomenon may have several different causes that all contribute to the effect. One possibility is the top-down bias for novelty, because features tilted relative to gravity are, ceteris paribus, less common than vertical or horizontal ones. A novelty bias in favor of tilted image components might also be built into very early stages of visual processing, such as visual area V1 (Essock, DeFord, Hansen, & Sinai, 2003; Hansen & Essock, 2004, 2006). Essock and colleagues showed that, although performance levels on a number of tasks using narrowband stimuli are found to be inferior for oblique orientations (the standard “oblique effect”: Appelle, 1972; Essock, 1980), performance levels on stimuli that are fairly broadband in both orientation and spatial frequency show the opposite effect, with best performance for oblique orientations. They argued that the superiority of oblique orientations results from an anisotropy in divisive normalization caused by a corresponding anisotropy in the numbers of neurons tuned to different orientations, which, in turn, appears to be caused by an anisotropy in the relative frequencies of occurrence of different orientations in natural scenes (Hansen & Essock, 2004). In their proposed model, each neuron is normalized by dividing its output by a signal pooled from neurons with similar preferred orientations and spatial frequencies (similar to the iso-feature suppression seen in most models of visual attentional selection). Because there are fewer neurons tuned to oblique orientations (Li, Peterson, & Freeman, 2003), the normalization signal will be weaker for neurons with preferences close to oblique, so the neurons will be less suppressed, leading to better performance at oblique orientations, especially on tasks involving judgments of salience (Essock et al., 2003; Hansen & Essock, 2006), which has been associated with the response level of neurons in V1 (Jingling & Zhaoping, 2008; Koene & Zhaoping, 2007; Li, 1999a, 1999b, 2000, 2002; Zhaoping, 2008; Zhaoping & May, 2007; Zhaoping, May, & Koene, 2009). Hansen and Essock (2006) found that the superiority of oblique orientations only occurred for fairly broadband stimuli, and they argued that this was because the normalization pool was only large enough to show its effect when the stimuli contained a sufficient number of components in the local neighborhood in Fourier space (see discussion of this point in Hansen & Essock, 2006, pp. 4399–4400). By an analogous argument, the anisotropy in normalization should also be evident when there are many similarly oriented stimulus elements that are spatially close to each other, as with the distractors in visual search stimuli. The level of divisive normalization between neurons responding to the distractors should therefore be lower when the distractors are tilted (and the target is vertical) than when the distractors are vertical (and the target is tilted); tilted distractors should therefore be more salient than vertical ones, which would explain the orientation asymmetry shown in visual search without a surrounding frame.

Another explanation of the non-display-dependent orientation asymmetry is Foster and Ward’s (1991a) model, which contains two filters broadly tuned to horizontal and vertical orientations. It is natural to ask whether it might be possible to reconcile this well-supported model with other models containing a range of more sharply tuned filters spanning the whole range of orientations—for
example the model of Li (1999a, 1999b, 2000, 2002), which is based on known properties of V1 cells, and is also well-supported psychophysically (Jingling & Zhaoping, 2008; Koene & Zhaoping, 2007; Zhaoping, 2008; Zhaoping & May, 2007; Zhaoping et al., 2009). Foster and Westland (1998) presented results showing that this may be the case; their results suggested that Foster and Ward’s (1991a) two broadly tuned orientation channels reflect processing that occurs very shortly after stimulus onset whereas, for longer stimulus durations, performance reflects the activity of a whole range of channels tuned to different orientations. In the latter scenario, which would be more likely to occur in reaction time experiments, a non-display-dependent orientation asymmetry could still arise from a bottom-up multi-orientation-channel model such as Li’s because of the possible anisotropy in iso-orientation suppression proposed above.

The effects of postural-gravitational manipulations reported by Marendaz et al. (1993) and Stivalet et al. (1995) suggest that, even if one or both of the bottom-up mechanisms proposed above contribute to the non-display-dependent orientation asymmetry, there is also a contribution from higher-level mechanisms. It is possible that the relative contributions of different mechanisms vary with the experimental protocol, and this could explain Doherty and Foster’s (2001) failure to replicate Marendaz et al.’s (1993) effect of supine posture. Doherty and Foster always used very short stimulus durations, even in a reaction time version of their experiment, whereas Marendaz et al.’s stimuli remained visible until the subject responded (typically between 500 ms and 1000 ms). Therefore, Doherty and Foster’s orientation asymmetry could have arisen from a very fast-acting bottom-up mechanism that was insensitive to gravitational cues, whereas Marendaz et al.’s orientation asymmetry may have been caused by slower top-down mechanisms that were able to integrate cues from a variety of sources, including vestibular, proprioceptive, and somatosensory sense organs. A similar dissociation seems to apply to the standard oblique effect found with isolated stimuli, whereby performance on a number of different tasks is poorest for oblique orientations. Essock (1980) distinguished between two classes of oblique effect. Class 1 effects (found in, for example, measurements of contrast threshold, acuity, vernier acuity, and visual evoked potentials) appear to result from early visual processing, and are tied to a retinal frame of reference (Banks & Stolarz, 1975; Corwin, Moskowitz-Cook, & Green, 1977; Findlay & Parker, 1972; Frost & Kaminer, 1975; Lennie, 1974); class 2 effects (found in tasks requiring more complex processing than simple detection, often tested using reaction times) reflect higher-level processing, and are characterized by a frame of reference that can be influenced by the gravitational vertical (Attneave & Olson, 1967) as well as voluntary control (Attneave & Reid, 1968).

Conclusions

The results of Experiment 1 suggested that the frame effect is caused by a combination of (1) a high-level mechanism that derives a “frame of reference” from configural cues provided by the frame, and (2) bottom-up iso-orientation competition from the sides of the frame parallel to the bar elements. Experiment 2 used a single line (the “axis”) instead of a frame to isolate the iso-orientation competition mechanism. In this experiment, the effect of the axis declined rapidly to zero with increasing target-axis distance, suggesting that the iso-orientation competition process consists entirely of iso-orientation suppression between nearby neurons tuned to similar orientations; the lack of any effect of the axis for the larger target-axis distances casts doubt on the alternative possibility that the presence of axis or sides of the frame parallel to the target might have diverted attention to the axis or frame before the target.

Appendix A

The near-vertical and near-horizontal conditions of Experiment 2 were run as separate experiments (Experiments 2a and 2b, respectively), with different numbers of trials per session and only partially overlapping sets of subjects. In this appendix we provide analyses that rule out these differences as explanations of the differences between the results of the two experiments. We also rule out the possibility that it was the greater target eccentricity, rather than the greater target-axis distance per se, that led to the decline in the effect of the axis with increasing target-axis distance in Experiment 2a.

Differences in session length between Experiments 2a and 2b

Experiment 2a was divided into 5 sessions of 320 trials, whereas Experiment 2b was divided into 25 sessions of 64 trials. One possibility was that the interaction shown in Experiment 2a only appeared towards the end of a long session, when the subjects were fatigued; if this were the case, then subjects would never have reached a sufficient level of fatigue in the shorter sessions of Experiment 2b, and this could account for the difference in the results. To rule out this possibility, we analyzed the results of Experiment 2a as in the main Results section, except that we only took the first 64 trials from each session. As shown in Figures A1 and A2, and Table A1, the results showed exactly the same pattern as the analysis of the full sessions: The interaction was significant for the shortest target-axis distance, and non-significant for each other.
condition. If the difference in session length between Experiments 2a and 2b had been responsible for the difference in the results, then the significant interaction in Experiment 2a should not have been detectable in this analysis; instead its magnitude and significance were both stronger.

**Different subjects in Experiments 2a and 2b**

The possibility that the different results were caused by the different sets of subjects can be ruled out because the same pattern of results emerges if we only take the data from the three subjects who performed both experiments. Figures 5 and 6 show that, for these subjects (LJ, LZ and NG), there was a negligible interaction between axis tilt and target tilt for all conditions except the shortest target-axis distance in Experiment 2a, for which the interaction was substantial. Figure A3 plots the mean interaction strengths for these three subjects. A comparison with Figure 7 (which plots the mean interactions across all subjects) shows that excluding the subjects who only performed one of the experiments made little difference to the pattern of results. However, because there were only three subjects in this analysis, it was not powerful enough

### Table A1

<table>
<thead>
<tr>
<th>Target-axis distance</th>
<th>Interaction strength</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.0912</td>
<td>9.06</td>
<td>0.000824*</td>
</tr>
<tr>
<td>2</td>
<td>0.0546</td>
<td>2.93</td>
<td>0.0428</td>
</tr>
<tr>
<td>3</td>
<td>-0.0253</td>
<td>1.30</td>
<td>0.264</td>
</tr>
<tr>
<td>4</td>
<td>-0.0101</td>
<td>0.826</td>
<td>0.455</td>
</tr>
</tbody>
</table>

Table A1. Analysis of the first 64 trials of each session of Experiment 2a, analyzed and presented in the same way as in Table 1. We used the same criterion of significance as before (0.00625).
to yield any significant differences from zero. Because of this, we carried out a different test of the interaction: Instead of using Equation 1 to calculate the strength of the interaction, we performed separate analyses of variance (ANOVAs) on each subject’s raw RT data, to test the significance of the interaction for each individual subject.

For these analyses, we used the same sets of RTs as were used for the previous analyses of the data plotted in Figures 5 and 6, using the same exclusion criteria. For each target-axis distance (i.e. each panel in the top five rows of Figures 5 and 6), there were four cells of data, with a $2 \times 2$ factorial arrangement: One factor was axis tilt, and the other was target tilt. Each cell contained the raw RTs that remained after applying the exclusion criteria. Before performing an ANOVA, we equalized the number of trials in the four cells by including only the first $N$ trials to have occurred (chronologically in the experiment) on each condition, where $N$ was the smallest number of included trials out of the four cells. We then performed a $2 \times 2$ independent samples ANOVA. Similar analyses were applied to each of the four target-axis distances for Experiments 2a and 2b for each subject, making 40 ANOVAs in total. Tables A2 and A3 give the $F$-ratio and associated $p$-value for the interaction between axis tilt and target tilt for each of these 40 ANOVAs. The criterion of significance for each individual interaction was Bonferroni corrected to $0.05/40 = 0.00125$, ensuring that the probability of a Type I error across all 40 ANOVAs was no higher than 0.05. Using this criterion, there were only three significant interactions, and all of these were for the shortest target-axis distance in Experiment 2a (subjects AJ, LJ, and NG). The remaining two subjects (JSH and LZ) also showed similar interactions on this condition, with low $p$-values (0.00294 and 0.0199, respectively), but they failed to reach significance because of the very strict criterion that we applied to correct for multiple tests. In contrast, the lowest $p$-value out of all 20 interactions in Experiment 2b was 0.122 (subject: ASL; target-axis distance: 3 deg) which, even without the Bonferroni correction, did not approach the 0.05 level (and, in fact, this non-significant interaction was in the opposite direction to the significant ones found in Experiment 2a). Two of the subjects who showed significant interactions in Experiment 2a (LJ and NG) also performed Experiment 2b, and showed no significant interactions there, showing that the difference between the two

<table>
<thead>
<tr>
<th>Target-axis distance</th>
<th>Subject</th>
<th>Interaction F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 deg</td>
<td>AJ</td>
<td>$F(1, 160) = 23.9$</td>
<td>$2.44 \times 10^{-6}$*</td>
</tr>
<tr>
<td></td>
<td>JSH</td>
<td>$F(1, 188) = 9.08$</td>
<td>0.00294</td>
</tr>
<tr>
<td></td>
<td>LJ</td>
<td>$F(1, 164) = 40.7$</td>
<td>$1.70 \times 10^{-9}$*</td>
</tr>
<tr>
<td></td>
<td>LZ</td>
<td>$F(1, 184) = 5.52$</td>
<td>0.0199</td>
</tr>
<tr>
<td></td>
<td>NG</td>
<td>$F(1, 188) = 24.1$</td>
<td>$2.02 \times 10^{-6}$*</td>
</tr>
</tbody>
</table>

Table A2. Interactions between axis tilt and target tilt in Experiment 2a, assessed using an ANOVA on the raw RT scores for each subject and target-axis distance. The criterion of significance was set to 0.00125, giving a maximum Type I error rate of 0.05 across the 40 interactions in the two experiments (2a and 2b). Significant interactions (indicated by an asterisk) only occurred for the shortest target-axis distance.

<table>
<thead>
<tr>
<th>Target-axis distance</th>
<th>Subject</th>
<th>Interaction F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 deg</td>
<td>AJ</td>
<td>$F(1, 164) = 2.77$</td>
<td>0.0979</td>
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<tr>
<td></td>
<td>JSH</td>
<td>$F(1, 188) = 6.75$</td>
<td>0.0101</td>
</tr>
<tr>
<td></td>
<td>LJ</td>
<td>$F(1, 148) = 0.995$</td>
<td>0.320</td>
</tr>
<tr>
<td></td>
<td>LZ</td>
<td>$F(1, 188) = 0.489$</td>
<td>0.485</td>
</tr>
<tr>
<td></td>
<td>NG</td>
<td>$F(1, 192) = 4.48$</td>
<td>0.0357</td>
</tr>
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</table>

<table>
<thead>
<tr>
<th>Target-axis distance</th>
<th>Subject</th>
<th>Interaction F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 deg</td>
<td>AJ</td>
<td>$F(1, 164) = 1.82$</td>
<td>0.179</td>
</tr>
<tr>
<td></td>
<td>JSH</td>
<td>$F(1, 184) = 7.41$</td>
<td>0.00710</td>
</tr>
<tr>
<td></td>
<td>LJ</td>
<td>$F(1, 156) = 5.69$</td>
<td>0.0182</td>
</tr>
<tr>
<td></td>
<td>LZ</td>
<td>$F(1, 188) = 2.32$</td>
<td>0.130</td>
</tr>
<tr>
<td></td>
<td>NG</td>
<td>$F(1, 188) = 0.382$</td>
<td>0.537</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Target-axis distance</th>
<th>Subject</th>
<th>Interaction F-ratio</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>4 deg</td>
<td>AJ</td>
<td>$F(1, 164) = 1.38 \times 10^{-4}$</td>
<td>0.991</td>
</tr>
<tr>
<td></td>
<td>JSH</td>
<td>$F(1, 180) = 2.56$</td>
<td>0.111</td>
</tr>
<tr>
<td></td>
<td>LJ</td>
<td>$F(1, 156) = 0.00676$</td>
<td>0.935</td>
</tr>
<tr>
<td></td>
<td>LZ</td>
<td>$F(1, 184) = 0.0736$</td>
<td>0.786</td>
</tr>
<tr>
<td></td>
<td>NG</td>
<td>$F(1, 184) = 0.339$</td>
<td>0.561</td>
</tr>
</tbody>
</table>

Table A3. Interactions between axis tilt and target tilt in Experiment 2b, analyzed in the same way as for Experiment 2a (Table A2). None of the interactions approached significance.
Experiments was not caused by using different sets of subjects. In addition, we can rule out order effects, because NG performed Experiment 2a before Experiment 2b, while LJ performed Experiment 2b first.

Effect of target eccentricity

In Experiment 2, target-axis distance was confounded with mean target eccentricity. Although the subjects were free to move their eyes during the trial, they were fixating on the center of the stimulus at the start of each trial, and it may have been that the increased eccentricity of the targets with greater target-axis distance caused the reduced effect of the axis, rather than the target-axis distance per se. If this were true, it would undermine our conclusion that the results reflected the action of iso-orientation suppression between nearby units.

To rule out this possibility, we took the trials from the 1 deg target-axis distance condition in Expt 2a (the only condition that showed a significant effect), and categorized them according to the displacement, d, along the axis direction (measured in degrees of visual angle). Data points give the mean interaction strength across subjects. Error bars indicate ±1 standard error of the mean.

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higher than those in the eccentric categories, where the target eccentricities were comparable to the eccentricities for the higher target-axis distances in Experiment 2 (i.e., those target-axis distances that showed no interactions). We combined the data from the two eccentric categories, giving two categories with approximately similar numbers of trials: central (0 ≤ |d| ≤ 2) and eccentric (2 < |d| ≤ 4). For these two categories, we calculated the interaction strength for each subject, using Equation 1; the mean interactions are plotted in Figure A5. Rather than being smaller, the interaction for the eccentric category was slightly higher (although not significantly so). Two-tailed t-tests were used to compare the mean interaction in each category against a hypothesized population mean of zero. The significance was substantially stronger for the eccentric condition (central: mean = 0.0610, t = 3.75, d.f. = 4, p = 0.0200; eccentric: mean = 0.0717, t = 7.12, d.f. = 4, p = 0.00205). These results comprehensively rule out the hypothesis that it was the greater target eccentricity that caused the drop in interaction strength with increasing target-axis distance.

Acknowledgments

This work was supported by a grant from the Gatsby Charitable Foundation and a Cognitive Science Foresight grant BBSRC #GR/E002536/01.

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