# The use of optimal object information in fronto-parallel orientation discrimination 

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#### Abstract

When determining an object's orientation an implicit object axis is formed, based on local contour information. Due to the oblique effect (i.e., the more precise perception of horizontal/vertical orientations than oblique orientations), an object's orientation will be perceived more precise if the axis is either horizontal or vertical than when the axis is oblique. In this study we investigated which object axis is used to determine orientation for objects containing multiple axes. We tested human subjects in a series of experiments using the method of adjustment. We found that observers always use object axes allowing for the highest object orientation discrimination, namely the axes lying closest to the horizontal/vertical. This implies that the weight the visual system attaches to axial object information is in accordance with the precision with which this information is perceived.


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## 1. Introduction

In order to interact with the environment, an observer needs information about object attributes such as shape, location, and orientation. Along the pathways of visual information processing elementary visual features like local and global contour orientation, color, texture, etc., are integrated into higher order representations up until a point where semantic and contextual properties are attributed (Jeannerod, 1997).

Detection of elementary visual features must occur sufficiently early along the pathways of visual processing to select objects, and interact with them (Boutsen \& Marendaz, 2001). An example of fast detection and processing of object attributes can be found in the literature regarding saccadic localization. Saccades directed to simple twodimensional target shapes, where the instruction is to look at the target as a whole, land near the center of gravity

[^0](COG) of the object (Vishwanath \& Kowler, 2003). This even happens when this COG is outside the object itself and thus outside the region of retinal stimulation. The result by Castiello and colleagues even suggested that object-shadow processing in humans is outside conscious awareness (Castiello, Lusher, Burton, \& Disler, 2003). These findings imply a mechanism for fast and unconscious detection of specific object attributes, such as size, orientation, mass, and shadow.

### 1.1. Perception of orientation

An interesting phenomenon occurs when oblique object orientations are processed. It is well documented that the processing of orientation information is anisotropic, i.e., the veridical orientations along cardinal axes $\left(0^{\circ}\right.$ and $\left.90^{\circ}\right)$ are perceived more precise than oblique orientations (oblique meaning anything other than the cardinal orientations). This oblique effect has been confirmed in various behavioral studies in man (Appelle, 1972) and not only for visual perception. For example, Kappers (2001)
describes that for a haptic orientation matching task on the horizontal plane, deviations belonging to oblique reference orientations are significantly larger than for cardinal reference orientations. The effect seems elementary as it has also been found in several animals (Bonds, 1982; Emerson, 1980).

Early theories attributed the oblique effect to frequent micro saccades along the Cartesian axes, damped oscillations of the eye would lead to preferential vibrations in the horizontal and vertical planes (Higgins \& Stultz, 1950). However, these theories were refuted by experimental data, suggesting that these physical factors cannot contribute significantly to the oblique effect (Higgins \& Stultz, 1950; Nachmias, 1960). Furthermore, no difference between the accuracy of horizontal/vertical and oblique saccades was found (Becker \& Jürgens, 1990). Coppola, Purves, McCoy, and Purves (1998) showed a prevalence of vertical and horizontal orientations in indoor, outdoor, and even entirely natural settings. The authors reason that since visual experience is known to influence the development of visual cortical circuitry, the real world orientation anisotropy is related to the enhanced ability of humans and other animals to process contours in the cardinal axes. Perhaps by stimulating the development of a greater amount of visual circuitry devoted to processing vertical and horizontal contours. This suggests that the oblique effect has a cortical basis, rather than retinal sampling.

Recent research has elaborated on this neuronal explanation. Furmanski and Engel (2000) reported that functional magnetic resonance imaging (fMRI) responses in V1 were reliably greater for cardinally oriented gratings than for oblique gratings. However, optical imaging studies of V2 have shown that orientation anisotropies are also found outside area V1 (Wang, Ding, \& Yunokuchi, 2003). Also, Coppola et al. (1998) measured the amount of cortical space activated by differently oriented gratings in the ferret and found that on average $7 \%$ more area of the exposed visual cortex was activated by cardinally oriented gratings than by gratings having an oblique orientation.

These findings raise the question as to how the brain determines (object) orientation. What object information is used to determine orientation? Furthermore, when multiple sources of information are present, is there a preference for a specific information source?

### 1.2. Local and global orientation processing

When determining the object's orientation an implicit object axis is formed, based on local contour information (Found \& Müller, 1997). This finding was corroborated by three experiments by Boutsen and Marendaz (2001) who found that orientation search asymmetry (i.e., a faster detection of a tilted target among vertical distractors than the reverse) in a visual search task depended on the orientation of a global axis, rather than on the orientation of local contours. The orientation of this axis then determines the accuracy with which the object's orientation is per-
ceived. If the axis is either horizontal or vertical, the object's orientation will be perceived more precisely than when the axis is oblique.

Symmetrical objects also contain a cue based on local contour information, which can be used to determine the overall object orientation: the axis of symmetry. De Kuijer, Deregowski, and McGeorge (2004) showed that when using simple flat objects (lamellae) the orientation of the axis of symmetry had the single highest influence affecting the reproduction of a symmetrical stimulus. To the best of our knowledge, there are no reports on which object information observers use to determine fronto-parallel object orientation.

In this study, our aim is to investigate which object information is used in determining fronto-parallel object orientation. An example is shown in Fig. 1. Important cues to determine object orientation are the sides of the square and the axes of symmetry. However, the questions on what criteria observers select these axes or sides is still unanswered. That is, do observers apply a specific strategy in determining object orientation?

### 1.3. The optimized visual system

As is illustrated in Fig. 1a, the orientation of two axes of symmetry are $0^{\circ}$ and $90^{\circ}$, the other axes of symmetry have an orientation of $45^{\circ}$ and $90^{\circ}$, respectively, with all sides' orientations being either $0^{\circ}$ or $90^{\circ}$. Fig. 1 b shows the same object, in an orientation of $45^{\circ}$. Again the orientations of two axes of symmetry are $45^{\circ}$ and $90^{\circ}$, and two axes of symmetry are oriented $0^{\circ}$ and $90^{\circ}$, all sides are oriented either $45^{\circ}$ or $135^{\circ}$.

If observers use the oblique axes of symmetry or the sides to determine global object orientation for the $45^{\circ}$ orientation (Fig. 1b), the prediction is that precision for judging this object orientation will be significantly lower than when observers would use (any of) the cardinal axes of symmetry, due to the lower sensitivity of the visual system for oblique information.

If on the other hand observers select the axis or side lying closest to the horizontal/vertical, it seems that the visual system attaches more weight to cardinal information than to oblique object information. Thus, the weight the visual sys-


Fig. 1. Square oriented $0^{\circ}$ (a) and $45^{\circ}$ (b). Axes of symmetry are represented by dashed lines.
tem attaches to specific stimulus information would correlate with the overall informativeness of stimulus information, i.e., the precision with which object orientation can be determined. When object information yields high precision, this information would then be weighed higher, lower weights would be attached when object information yields low precision. An optimized orientation judgment system, would therefore always select the axis or side lying closest to the horizontal/vertical, since this strategy allows for the highest precision in judging object orientations.

This optimization process closely resembles the findings of Schrater and Kersten (2000). They describe a Bayesian approach to depth cue integration, based on the premise that a fundamental goal of a visual system is to make optimal statistical estimates of scene variables. The authors show that human observers' decisions are near optimal for certain depth representations, in that subjects weight cue information in accordance with their informativeness. Furthermore, Ernst and Bülthoff (2004) describe the Modality Precision Hypothesis which states that in situations of modality conflicts, discrepancies are always resolved in favor of the more precise or more appropriate modality.

The above mentioned examples seem general principles that govern the human sensory system when dealing with situations in which multiple sources of (conflicting) information are present. The human visual system seems to apply a strategy allowing to cope with these situations in a near optimal fashion.

### 1.4. Dot stimuli

To test the hypothesis that observers have a preference for using object information that yields high orientation precision, we designed an experiment in which observers had to adjust the fronto-parallel orientation of a test stimulus to a reference stimulus. In order to minimize interference between local and global contours, we chose to use dot stimuli, since these contain no global contour information. Li and Westheimer (1997) have shown that thresholds for detecting the angle of rotation for stimuli containing contours without luminance contrast (using a stimulus consisting of two dots) were almost as low as those for an actual vertical line. They dubbed this implicit orientation discrimination. This further supports our choice for using dot stimuli.

Experiment 1 was designed to validate our stimulus and ascertain the existence of an oblique effect using a dot stimulus. In Experiments 2 and 3 we used a square and an equilateral triangle stimulus, respectively, both consisting of dots.

## 2. Methods

### 2.1. Observers

Three observers took part in Experiment 1. All observers were experienced in visual psychophysics experiments but were naive as to the purpose of this experiment. The age range of the observers was 24-30 years, all had normal or corrected to normal vision.

### 2.2. Apparatus and stimuli

The experiments were performed using an Apple G4 Power Mac computer and an Iiyama Visionmaster Pro 454 CRT screen (vertical refresh rate of 80 Hz and a resolution of $1024 \times 768$ pixels). Stimuli were presented using Matlab 5.2 using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

Stimulus displays consisted of two dots, each dot measured $0.53^{\circ}$ in diameter and was presented with a luminance of $25.2 \mathrm{~cd} / \mathrm{m}^{2}$, with a background luminance of $0.0 \mathrm{~cd} / \mathrm{m}^{2}$. The distance between the two dots was $4^{\circ}$. See Fig. 2 for an example of the "two dot line" stimulus.

### 2.3. Design and procedure

Observers looked straight ahead, using a chin-rest located 57 cm from the computer screen. The experiment was performed in a dark room. A black cloth with a circular aperture was draped over the monitor to prevent the light of the screen illuminating the edges of the monitor. Each trial started with the presentation of the 'line' stimulus in the center of the screen for 500 ms . This stimulus had an orientation randomly chosen per trial out of 5 standard orientations: $0^{\circ}, 22.5^{\circ}, 45^{\circ}, 67.5^{\circ}$, and $90^{\circ}$. After the initial 500 ms presentation a white circular mask with a diameter of $8.5^{\circ}$ was presented for 1500 ms . This was to make sure no information could be derived using the phosphor excitation (afterglow) of the stimulus on the monitor at the time the test stimulus appeared (see Fig. 3). After this 1500 ms interval, the test stimulus appeared. This stimulus was rotated a random amount of degrees with respect to the reference stimulus and randomly chosen per trial to be clockwise or counter-clockwise, within a range of $10-20^{\circ}$ from the orientation of the reference orientation.

Observers were instructed to adjust the orientation of the test stimulus to the reference stimulus by pressing the 5 (counter-clockwise rotation) or the 6 key (clockwise rotation) on the computer's keyboard.

Also, the position of the test stimulus was translated a random number of degrees (with a minimum of $1.42^{\circ}$ and a maximum of $2.14^{\circ}$ ) for both the $x$ and the $y$ position as compared to the reference stimulus. This stimulus shift was introduced to exclude that observers perform the task using the location shift of one single dot. Fig. 4 illustrates this stimulus shift. The reference orientation is shown in grey, with the test stimulus shown in black. In Fig. 4a the test stimulus is rotated $45^{\circ}$ counter-clockwise, with no stimulus translation. The upper dot of the test stimulus now moves to the left with respect to the upper dot of the reference stimulus. This excludes that observers attend only to the location of one of the stimulus dots to determine the amount of rotation of the test stimulus with regards to the reference stimulus. In Fig. 4b, we show the stimulus translation. Although the upper dot of the test stimulus is in the exact same position as in 4 a , it does not correspond to the same $45^{\circ}$ counter-clockwise rotation.

Our variable of interest is the standard deviation of the adjustment errors, i.e., the standard deviation of the difference between the obser-ver-adjusted test stimuli and reference stimuli for each condition. When


Fig. 2. An example of the "two dot line" stimulus used in Experiment 1. Each stimulus dot measures $0.53^{\circ}$ in diameter, with the distance between dots being $4^{\circ}$.


Fig. 3. Stimulus presentation, the circular mask (with a diameter of $8.5^{\circ}$ ) was used to compensate for stimulus afterglow on the monitor due to phosphor excitation.


Fig. 4. Stimulus shift. Reference stimuli are shown in grey, test stimulus is shown in black. (a) The test stimulus rotated $45^{\circ}$ counter-clockwise but not translated on screen. (b) A clockwise rotation of $45^{\circ}$ with a translation. This stimulus shift was introduced to force observers to attend overall stimulus orientation instead of attending only to the location of one of the stimulus dots.
observers were convinced that the test stimulus had the same orientation as the reference stimulus they pressed the space bar to start the next trial. A total of 30 trials was collected for each reference stimulus orientation.

## 3. Results

### 3.1. Experiment 1

Experiment 1 was designed to test for the existence of an oblique effect using dot stimuli. As described earlier, a two dot 'line' stimulus was presented in various orientations. The results are shown in Fig. 5. As expected, the lowest standard deviations of the adjustment errors were found for the cardinal object orientations (i.e., $0^{\circ}$ and $90^{\circ}$ ) while the highest standard deviations were found for the oblique object orientations (i.e., $22.5^{\circ}, 45^{\circ}$, and $67.5^{\circ}$ ). Standard deviations ranged from $0.77^{\circ}$ for the cardinal orientations to $5.4^{\circ}$ for the oblique orientations. For each observer both $0^{\circ}$ and $90^{\circ}$ differed significantly from all oblique orientations (Levene test for equality of variances, $p<.001$ ).

### 3.1.1. Results and discussion

The results from Experiment 1 indicate that there is an oblique effect for dot stimuli. The lowest standard deviations are found for the cardinal object orientations for each observer, while the highest standard deviations are found for the oblique object orientations. This means that we can proceed with Experiments 2 and 3 where we test whether observers apply the aforementioned strategy of selecting optimal (horizontal and vertical) object information to determine object orientation.

### 3.1.2. The model

To test the hypothesis that observers have a preference for using object information yielding high orientation precision, we constructed a model based on the data obtained in Experiment 1. This model simulates a "winner takes all" strategy to determine an object's orientation. We have used the following parabola to model observers' performance, based on the data from Experiment 1:
$y=-0.0022(x-45)^{2}+5.4$
The horizontal and vertical positions of the parabolas' vertex are determined by the data from Experiment 1. The horizontal position of the vertex is determined by the reference orientation in Experiment 1 yielding the highest $S D$ (the $45^{\circ}$ condition), and the height of the vertex is determined by the $S D$ corresponding with this reference orientation.

For each orientation of a given dot stimulus the model then estimates which combination of stimulus dots or axes of symmetry yields the lowest $S D$. This lowest $S D$ is then selected by the model to represent the modelled threshold for this particular stimulus orientation. Since the lowest $S D$ determines the modelled threshold for a given stimulus orientation, this is termed a "winner takes all" strategy. Fig. 6 shows the modelled threshold for a dot 'square', based on the threshold data from Experiment 1.


Fig. 5. Results for Experiment 1. Individual data for three subjects are shown. $S D$ s are plotted on the $y$-axis, the $x$-axis shows the orientation of the reference stimulus.

Fig. 7 shows the model's thresholds for the 'triangle' stimulus, obtained similarly as the modelled thresholdcurve for the square. We then ran Experiments 2 and 3 to see if the model is an appropriate description of the observer's behavior.

### 3.2. Experiments 2 and 3

The same conditions from Experiment 1 were applied to both Experiments 2 and 3. Experiments 2 and 3 consisted of a four dot 'square' stimulus and a three dot equilateral 'triangle' stimulus, with sides measuring $4^{\circ}$ for both the 'square' and 'triangle' stimulus. We will refer to these stimuli as the 'square' and 'triangle' stimuli, respectively. In each trial the 'square' had an orientation randomly chosen out of 5 standard orientations $\left(0^{\circ}, 22.5^{\circ}, 45^{\circ}, 67.5^{\circ}\right.$, and $90^{\circ}$ ). Similarly, the 'triangle' had an orientation randomly chosen out of 7 standard orientations $\left(0^{\circ}, 22.5^{\circ}, 30^{\circ}, 45^{\circ}\right.$,


Fig. 7. Modelled triangle $S D$ s using a "winner takes all approach".
$60^{\circ}, 67.5^{\circ}$, and $90^{\circ}$ ), in which the $0^{\circ}$ orientation had the 'triangle' pointing upwards. Orientations of the 'square' were chosen so that in three of the 'square' orientations the


Fig. 6. Modelled thresholds for a square using a "winner takes all" approach. The first graph shows $S D$ s for a two dot 'line' stimulus, low $S D$ s when this stimulus is either $0^{\circ}$ or $90^{\circ}$, and higher $S D$ s when the stimulus is oblique. The solid line in the second graph shows $S D$ s for the horizontal and vertical axis of symmetry of a square, with low $S D$ s when the orientation of this axis is $0^{\circ}$ or $90^{\circ}$, and higher $S D$ s when the orientation of this axis is oblique. The dashed line in the second graph represents $S D$ s for the diagonal of the square. When the square is oriented $45^{\circ}, S D$ s for the diagonal are low, and when the square is $0^{\circ}$ or $90^{\circ}, S D$ s for the diagonal are higher. The final third graph represents the modelled graph for a dot square. For each orientation of the square, $S D$ s are plotted that yield the highest orientation discrimination accuracy, i.e., lowest $S D$ s.
sides, the axes of symmetry, or the diagonals were either horizontal or vertical. For the 'triangle' stimulus four orientations were chosen so that one of the sides and one of the axes of symmetry was aligned with either the horizontal or the vertical. Also, three orientations were chosen such that the sides and the axes of symmetry were oblique.

### 3.2.1. Results: Experiments 2 and 3

Experiments 2 and 3 were designed to find out whether observers select object information lying closest to the horizontal/vertical in order to determine global object orientation. As described earlier, a 'square' and a 'triangle' stimulus were presented in various orientations. Results for Experiment 2 are shown in Fig. 8, lowest $S D$ s were found not only for the $0^{\circ}$ and $90^{\circ}$ object orientations, but also for the $45^{\circ}$ object orientation. $S D$ s range from $0.71^{\circ}$ for the $0^{\circ}, 45^{\circ}$, and $90^{\circ}$ object orientation, to $4.9^{\circ}$ for the $22.5^{\circ}$ and $67.5^{\circ}$ object orientation, a similar order of magnitude as in Experiment 1. For each observer the SDs for the $0^{\circ}, 45^{\circ}$, and $90^{\circ}$ object orientations (in which at least one of the object axes was horizontal/vertical) were significantly lower than for the oblique object orientations (Levene test for equality of variances, $p<.01$ ).

Results for Experiment 3 are shown in Fig. 9. SDs range from $0.9^{\circ}$ to $4.6^{\circ}$. Although there are individual differences, a pattern similar to that found in Experiment 2 emerges: low $S D$ s for the $0^{\circ}, 30^{\circ}, 60^{\circ}$, and $90^{\circ}$ object orientations and higher $S D$ s for the $22.5^{\circ}, 45^{\circ}$, and $67.5^{\circ}$ object orientations. For observers JB and MS the $S D$ s for the $0^{\circ}, 30^{\circ}$, $60^{\circ}$, and $90^{\circ}$ object orientations (in which at least one of the object axes was horizontal/vertical) were significantly lower than for the oblique object orientations (Levene test for equality of variances, $p<.01$ ). For observer CP this was not the case for the $30^{\circ}$ object orientation, which did not differ significantly from the $S D$ s for the oblique object orientations.

### 3.2.2. Discussion: Experiments 2 and 3

The results of Experiments 2 and 3 show that observers are more precise in judging object orientation for orientations in which either the object axis or the side is horizontal/vertical. The low $S D$ s when the stimulus' sides are either horizontal or vertical $\left(0^{\circ}\right.$ and $\left.90^{\circ}\right)$, and when the axis of symmetry is either horizontal or vertical illustrate that observers indeed apply a strategy that favors information closest to the horizontal/vertical. Observers determine an


Fig. 8. Results for the "square stimulus" Experiment 2. Individual data for three subjects are shown. SDs are plotted on the $y$-axis, the $x$-axis shows the orientation of the reference stimulus. Observers show a significant increase in orientation matching for the $45^{\circ}$ reference orientation.


Fig. 9. Results for the "triangle stimulus" Experiment 3. Individual data for three subjects are shown. SDs are plotted on the $y$-axis, the $x$-axis shows the orientation of the reference stimulus. Observers show a significant increase in orientation matching performance for the $30^{\circ}$ and $60^{\circ}$ reference orientations, with the exception of observer CP for the $30^{\circ}$ reference orientation.
object's orientation based on object information that allows for the highest orientation precision.

## 4. General discussion

Observers were asked to adjust the fronto-parallel orientation of a test stimulus to a reference stimulus in three experiments. All three experiments concerned the method of adjustment, with the variable of interest being the standard deviation of the difference between the adjusted test stimulus and the reference stimulus. We found that the visual system always selects object information that allows for the highest orientation matching precision. That is, axes lying closest to the horizontal/vertical are selected to determine an object's orientation.

In Experiment 1, which was designed to validate our dot stimulus, we found a convincing oblique effect. Standard deviations for the oblique stimulus orientations were significantly greater than for the horizontal/vertical orientations. This is a replication of an experiment by Westheimer (2003), in which the author showed a convincing oblique effect for virtual line segments, with small circles demarcating the endpoints, indicating that overt oblique line segments are not a necessary condition for the oblique effect. The data we obtained in Experiment 1 were then used to construct a "winner takes all" model. This model was used to predict an ideal observer's performance on our adjustment task for the four dot "square" stimulus, and the three dot 'triangle' stimulus we used in Experiments 2 and 3.

Observers' performance in Experiments 2 and 3 supported this model and showed that observers indeed perform the task using object axial information lying closest to the horizontal/vertical. Observers showed high task precision for all object orientations in which object axes are horizontal/vertical, and low precision for all object orientations in which object axes were oblique. This strategy of always selecting object information lying closest to the horizontal/vertical suggests that the visual system has prior knowledge about the sensitivity with which object orientation is perceived.

Our findings fit in with results obtained by Schrater and Kersten (2000), and Ernst and Bülthoff (2004) as described in our Introduction. Their findings suggest a general principle that governs the human sensory system when dealing with situations in which multiple sources of (conflicting) information are present. Our experiment shows that in determining object orientation, object axial information is weighed in accordance with it's informativeness. Horizontal/vertical object information yields the highest precision in orientation discrimination, and is thus weighed accordingly. Our findings reflect a coping mechanism of the visual system to deal with orientational sensitivity anisotropies.

The use of two-dimensional stimuli may not necessarily generalize to real world (three-dimensional) objects. However, since observers only manipulated the fronto-parallel orientation of our stimulus, we have no reason to suspect
differences between fronto-parallel orientation matching for the stimulus we used and three-dimensional objects.

Our findings of an oblique effect using dot stimuli has a further, neurophysiological implication pertaining to the discussion whether the oblique effect originates solely in V1. Research by Merigan, Nealey, and Maunsell (1993) suggests a strong role for V2 in the perceptual grouping of objects. Since the stimuli we used in our experiments are dot stimuli, which are possibly grouped by V2, the origin of the oblique effect seems to extend beyond V1. The study of Merigan et al. (1993) indicate dramatic reductions in feature grouping of dot stimuli when V2 is lesioned in macaque. Macaques were presented with a task that involved the discrimination of the orientation of two parallel lines of five colinear dots each. Orientation of the parallel lines was either horizontal or vertical, with the number of background masking dots controlled with a one-up onedown staircase. Macaques had to push either the left button for horizontal parallel lines, or the right button for vertical parallel lines. Results indicate a threshold reduction for the number of background masking dots when lesions in V2 are applied. Colinearity detection is therefore disrupted by V2 lesions, indicating the role V2 plays in perceptual grouping. The findings of Merigan et al. (1993) are supported by a study by Woelbern, Eckhorn., Frien, and Bauer (2002). Woelbern et al. (2002) supply more evidence suggesting the role V2 plays in perceptual grouping and fig-ure-ground segregation. In a figure-ground task in which a rhesus monkey had to indicate whether two parallel rows of blobs were present amidst distractor blobs, neuron activity in V2 was recorded. Only in the frequency band (35$90 \mathrm{~Hz})$ did the authors find a highly significant effect in V2: a short phase-coupling before correct perceptual responses. These are first indications that a short synchronous burst in V2 may support perceptual grouping and fig-ure-ground segregation.

However, the already mentioned study by Furmanski and Engel (2000) shows that fMRI responses only in V1 and not V2 were reliably greater for cardinally oriented gratings than for oblique gratings, this can be explained by Neumann \& Sepp (1999) term 'recurrent processing'. Neumann and Sepp proposed a computational model for recurrent contour processing between V1 and V2, in which normalized activities of orientation selective contrast cells are fed forward to a next processing stage, forming a context-dependent gain control mechanism. The sensitivity anisotropies of orientation selective cells in the first stage ( V 1 ) would therefore propagate to the second stage (V2), without the orientation selective cells in V2 having to display the same orientation anisotropies as the cells in the first stage.

Further evidence suggesting the importance of recurrent processing is supplied by a study by Hupé et al. (1998). They studied the role of feedback connections in macaque area MT/V5. When area MT/V5 was inactivated by cooling, a substantial decrease in single neuron activity was found for cell responses to an optimally oriented moving bar in areas V1, V2, and V3. Results from a second exper-
iment, where a moving bar on a stationary background was used, showed that feedback connections from area MT/V5 have a facilitatory effect on the responses of neurons in areas V1, V2, and V3.

So, in sum we have shown in three experiments that observers always use object axes in orientation discrimination that allow for the highest precision in determining object orientation. The weight the visual system attaches to axial object information is in accordance with the precision with which this information is perceived.

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