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An oblique illusion modulated by visibility: Non-monotonic sensory integration in orientation processing

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Orientation perception is known to be anisotropic, with cardinal axes (i.e., horizontal and vertical) being privileged. Indeed, orientation sensitivity is greater near the cardinals, and small deviations from cardinal axes may be illusorily perceived in an exaggerated manner. Here, we quantified this illusory deviation from the cardinals at various visibility levels, by having participants reproduce the orientation of oriented Gabor stimuli whose visibility was manipulated by duration and masking. We found, first, that participants could reproduce quite accurately the orientation of very brief stimuli presented at lowest visibility levels. Second, the magnitude of the deviation followed a non-monotonic pattern, being maximal for stimuli of intermediate visibility, and lower for both the lowest and highest visibility levels. Thus, orientation processing at lowest visibility levels is noisier but paradoxically more faithful to the physical input. This counterintuitive result suggests that categorical processing of sensory information depends on perceptual awareness.

Keywords: perceptual anisotropy, orientation processing, vision, unconscious perception, visual consciousness

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Introduction

Most stimuli in our environment vary continuously along certain physical dimensions. Yet, our perception often introduces anisotropies, enhancing certain physical differences compared to others. Perception of orientations offers a good instance of such an anisotropic character, with cardinal axes (i.e., vertical and horizontal orientations) having a privileged role. However, while some aspects of this advantage for cardinal orientations have been extensively studied (e.g., the *oblique effect*, reviewed in Appelle, 1972, and more recently in Gentaz & Ballaz, 2000), some questions are still open. In particular, the neural dynamics of this perceptual anisotropy are still debated (see Matthews, Rojewski, & Cox, 2005; Westheimer, 2003), and how it might relate to stimulus visibility remains to be investigated. This study addresses the relation between stimulus visibility and anisotropic orientation processing.

People's ability to assess orientation is not uniform over the whole range of orientations. Indeed, early behavioral reports documented that a line slightly tilted from the horizontal or vertical axis is perceived more tilted than it

really is (e.g., Jastrow, 1892; Smith, 1962). Later on, researchers have focused on the oblique effect, which is the greater sensitivity found around the cardinal axes in forced choice tasks such as discrimination of two oriented lines or detection of oriented lines (e.g., Campbell, Kulikowski, & Levinson, 1966; Foster & Westland, 1995; Matthews et al., 2005; Westheimer, 2003). In his canonical review of this oblique effect, Appelle (1972) suggested that the two phenomena (i.e., standard oblique effect and the deviation from cardinals) might be related as they both reflect the underlying perceptual anisotropy for visual orientations.

What are the bases of the anisotropy in orientation processing? Interestingly, the input itself is anisotropic: analyses of orientation statistics over natural visual scenes revealed that cardinal orientations dominate our visual environment compared to non-cardinal ones (Dakin, Mareschal, & Bex, 2005; Dragoi, Turcu, & Sur, 2001; Hansen & Essock, 2004). Accordingly, one could expect cardinal orientations to recruit more processing resources in our visual system, an issue thoroughly addressed by neurobiological investigations. While a retinal locus has been discarded (see Appelle, 1972), cell recording (e.g.,

Li, Peterson, & Freeman, 2003; Mansfield, 1974; Wang, Ding, & Yunokuchi, 2003; Xu, Collins, Khaytin, Kaas, & Casagrande, 2006) and fMRI studies (e.g., Yacoub, Harel, & Ugurbil, 2008) have shown that in the primary visual cortex more neurons are tuned to the cardinal orientations. These neurons might also have a sharper tuning curve (Li et al., 2003; Wang et al., 2003). This neuronal anisotropy in the primary visual cortex may support the behavioral oblique effect.

However, other studies have suggested that more central, cognitive factors might also contribute to the perceptual anisotropy. Indeed, the cardinal advantage in orientation discrimination is more pronounced when the two discriminanda are presented consecutively rather than simultaneously, suggesting an effect of memory (Heeley & Buchanan-Smith, 1992; Matthews et al., 2005; Westheimer, 2003). The oblique effect is also found to depend on perceived orientation rather than physical orientation, when the two are made different by means of a tilt illusion (Meng & Qian, 2005).

Building on these observations, we speculated that stimulus visibility will affect perceptual anisotropies in visual orientations, since it involves both peripheral bottom-up factors and central attentional factors (e.g., Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Enns & Di Lollo, 2000). Interestingly then, as it is generally acknowledged that unconscious perception does not involve recurrent processing to the same extent than conscious perception (Dehaene et al., 2006; Lamme, 2003), assessing conjointly the perceptual anisotropy and stimulus visibility would inform the possible mechanisms of the anisotropy.

Here, we predict more specifically a three-step pattern for the anisotropy: minimal for stimuli of lowest visibility, increasing to a maximum at intermediate visibility, and decreasing for highly visible and fully resolvable stimuli. Two arguments lead us to this prediction. First, while orientations may be processed unconsciously (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Kentridge, Heywood, & Weiskrantz, 2004; Shin, Stolte, & Chong, 2009), there is suggestive evidence that the anisotropy is absent or diminished in low visibility conditions. Indeed, Matthews et al. (2005) used various stimulus durations (from 8 to 200 ms) and found the oblique effect to increase with duration and to be absent for very short stimuli. Stimulus visibility was however not directly assessed in this study. Second, we reasoned that the anisotropic character must perforce plateau or even diminish with visibility. For instance the greater stimulus availability would increase accuracy around the cardinals, thus reducing the illusory deviation from cardinals. In other words, considering the deviation from cardinals as a form of illusory misperception, we might expect it to be maximal at intermediate levels of visibility for which the stimulus is visible but degraded (e.g., Kouider & Dupoux, 2004).

To test these predictions, we asked 49 participants to reproduce the orientation of a Gabor patch presented for a

variable duration (from 20 ms to 1000 ms) and immediately followed by a circular pattern mask (see Figure 1A). Following previous studies (Gentaz et al., 2001; Jastrow, 1892; Smith, 1962), we used the deviation from cardinal axes as a measure of the anisotropic character of orientation perception. On each trial, observers were also asked to rate the visibility of the stimulus on a continuous scale, so as to enable us to correlate their performance on the orientation reproduction task with awareness of the stimulus.

Methods

Participants

Participants were 49 students (age range = 18–25) from Paris universities, reporting normal or corrected-to-normal vision, and paid for their participation. Results from three participants reporting high visibility ratings (>10%) in trials in which there was no stimulus were discarded.

Stimuli

The experiment was run using Matlab and the Cogent 2000 Toolbox (Laboratory of Neurobiology, Functional Imaging Laboratory, and Institute of Cognitive Neuroscience, University College London). Participants viewed stimuli on a 17-in CRT screen (1024 × 768 resolution, 100-Hz refresh rate) at a 60-cm distance. All stimuli were presented on a background gray texture generated randomly on each trial by averaging a binomial random noise on a 20 × 20 pixel (approx. 0.66° × 0.66°) window. A central fixation cross was added to this texture. A randomly oriented, 18% contrast, Gabor patch was added to this texture at a random location 6.5° from fixation. Apart from orientation, the Gabor's parameters were constant (frequency = 1.5 cpd, sigma of the Gaussian envelope = 0.33°). The mask was constituted by 6 black circles (width = 2 pixels, 0.066° of angle, radii = 0.66°, 0.99°, 0.132°, 1.64°, 1.97°, 2.30°) added to the background texture where the Gabor patch appeared (see Figure 1A).

Procedure

All trials (see Figure 1A) began with the apparition of the background noise texture for a variable foreperiod (900–1100 ms), then the Gabor patch was presented for a variable duration (20, 40, 80, 160, and 1000 ms, intermixed randomly), and was immediately replaced by the mask (300 ms). To control for potential biases, in one trial out of 10 the stimulus was absent (contrast set to 0%). When the mask disappeared, there was a blank interval of 400 ms before a randomly oriented blue Gabor patch with only one visible strip (frequency = 3 cpd, sigma = [0.33,

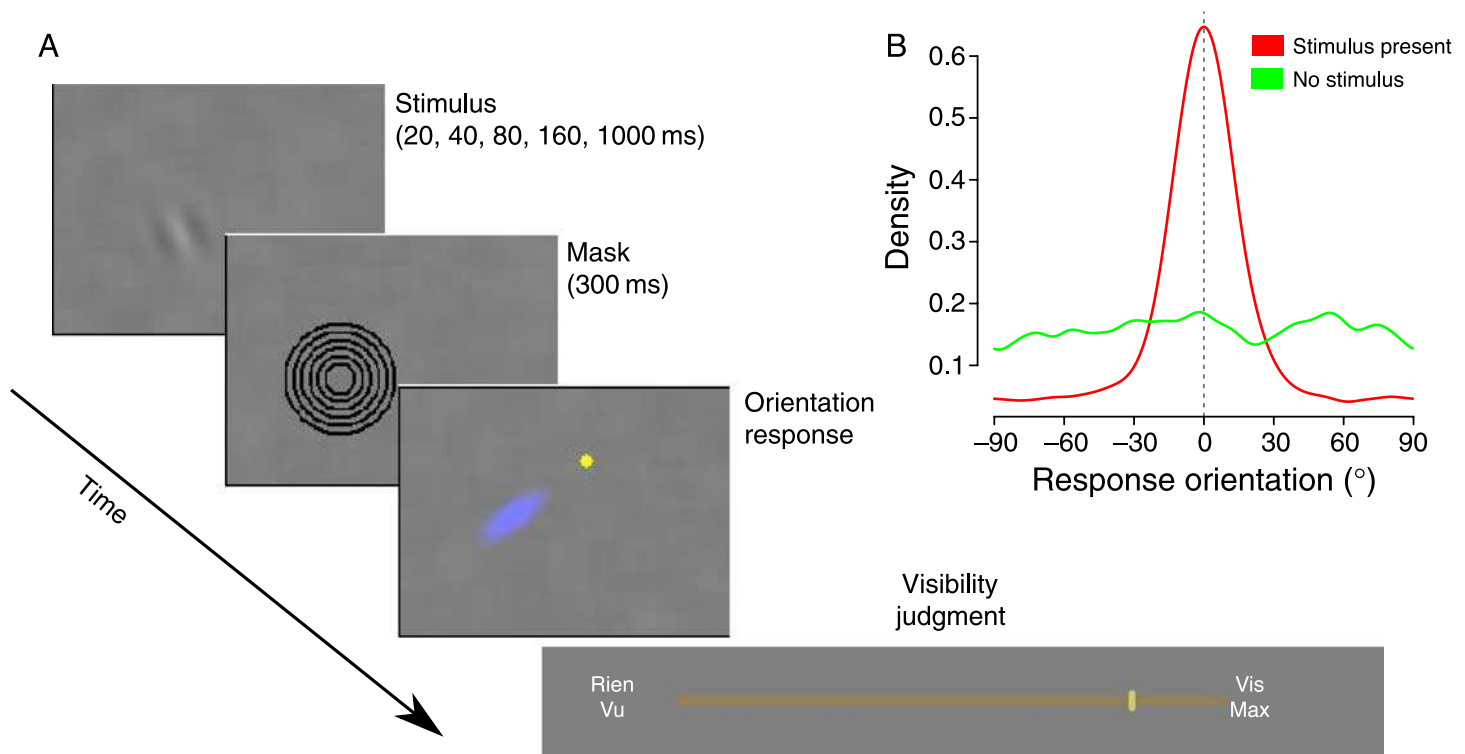


Figure 1. (A) Schematic presentation of the paradigm used in this study. (B) Density of response errors (angular difference between stimuli and responses) when stimulus present shows an overall precision of participants (red curve), and density of response orientation when stimulus absent shows the absence of bias in this case (green curve). Densities are estimated using a von Mises kernel function (bandwidth = 32°).

0.16]) appeared at the stimulus position. Participants adjusted the orientation of this blue strip using the mouse cursor (a yellow dot on the computer screen), so as to reproduce the orientation of the stimulus. Then, they were asked to report their subjective level of visibility for the stimulus, on a continuous scale ranging from “nothing seen” to “fully visible.” When reporting visibility ratings, we use percentages, 0% corresponding to “nothing seen” and 100% to “fully visible.”

A first training used only fully visible stimuli (duration = 1000 ms), with feedback on the orientation task, and no visibility rating. A second training used stimuli of variable visibility (including the no-stimulus condition), to introduce the continuous visibility scale and let participant calibrate their use of the scale. Then, participants had two to four experimental blocks with 120 trials each.

Manipulation of exposure

To assess whether privileged exposure with particular orientations could modulate the influence of cardinal axes, we divided participants in five groups, four of which were presented with randomly oriented patches for 2/3 of the trials and with one particular orientation (horizontal, vertical, right, or left diagonal) in the remaining trials. The fifth group always received randomly

orientated stimuli. Note that we analyzed only the trials with random orientation, which were thus uniformly distributed.

Results

Visibility judgments

We assessed how stimuli’s physical characteristics affected visibility. We averaged visibility judgments for each participant and duration, separately for stimuli closer to cardinals and for stimuli closer to diagonals. A within-subject ANOVA revealed that visibility increased with stimulus duration ($F(4, 180) = 720.64$, $p < 0.001$; mean ratings: 2.3%, 9.0%, 32.3%, 52.4%, 92.9%, respectively, for 20, 40, 80, 160, and 1000 ms), and that it was weakly but significantly reduced around the cardinal axes ($F(1,45) = 6.63$, $p < 0.05$; 37.3% for cardinals vs. 38.3% for obliques). These two effects of orientation and duration did not interact ($F < 1$).

Visibility classes

In further analyses involving visibility, we isolated three classes of trials, defined by conjunction between subjective

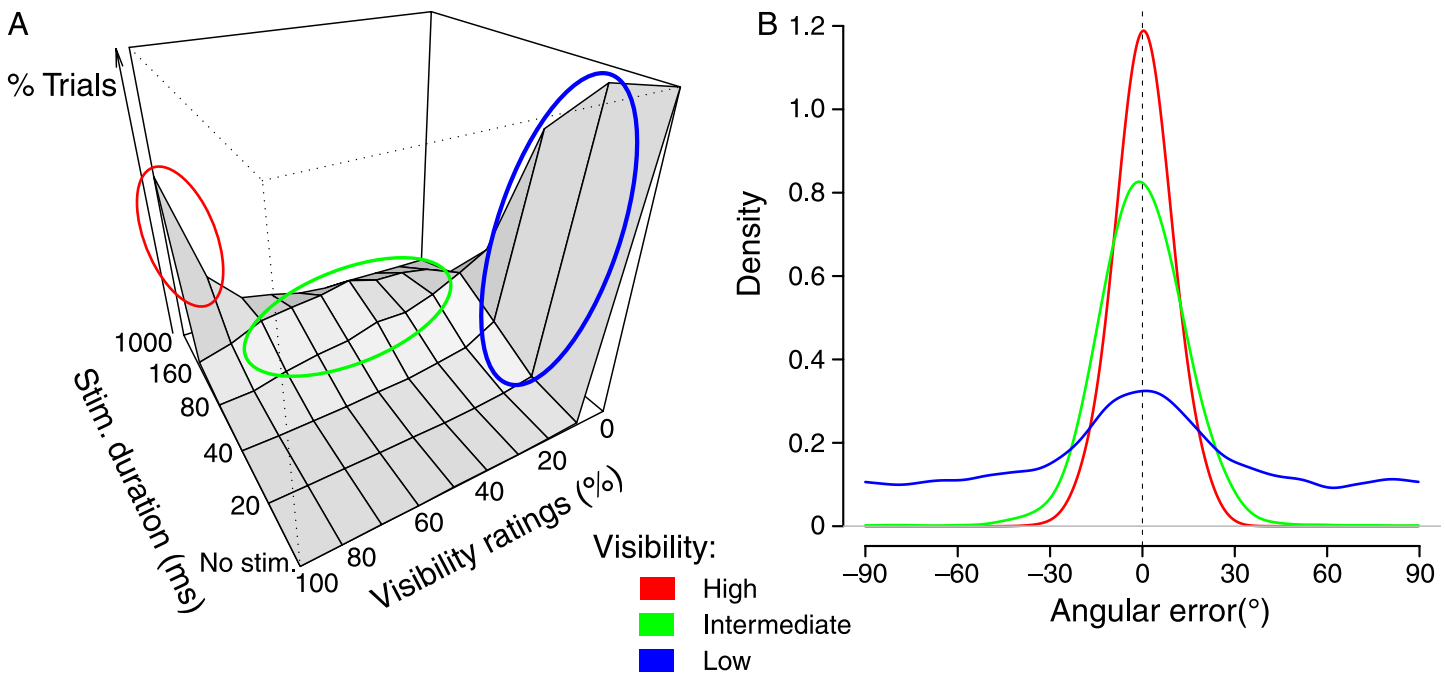


Figure 2. (A) Proportion of trials as a function of visibility ratings for the Gabor patch stimulus (100%: fully visible; 0%: nothing seen), for each stimulus duration. Superimposed on this histogram are the three classes of trials used for subsequent analyses (see main text). (B) Density of response errors assessed in the three classes of trials. Mean responses were always accurate, i.e., centered on the stimulus, although precision increases (i.e., variance decreases) with visibility. Densities are estimated using a von Mises kernel function (bandwidth = 32°).

visibility judgements and objective stimuli durations (see Figure 2A). Low visibility trials (in blue in the figures, 3559 trials) involved shortest stimulus durations (20–40 ms) and lowest visibility ratings (<15%); intermediate visibility trials (green, 2904 trials) involved intermediate durations (80–160 ms) and visibility ratings (15%–85%); and full visibility trials (red, 849 trials) involved 1000-ms duration and highest visibility ratings (>85%). Note that these classes are non-overlapping and that 19% of the trials are cautiously excluded, to discard potential outliers resulting from noise in the visibility ratings. We used this approach to provide a sensible qualification of our data in three homogeneous sets of trials.

Response times

The same analysis of variance with duration and orientation factors was done on median Response Times (RTs) for the orientation matching task (RTs were taken from the onset of the response Gabor patch). Participants were slower for longer stimuli durations ($F(4, 180) = 44.80, p < 0.001$; RT: 915, 1187, 1464, 1580, and 1856 ms for 20-, 40-, 80-, 160-, and 1000-ms durations, respectively), but there was no effect of orientation and no interaction between orientation and duration. A regression between RTs and visibility ratings revealed that RTs increased with higher visibilities ($T(9070) = 21.2, p < 0.001$; Pearson's r :

0.217; RTs for low, intermediate, and full visibility trials were 920, 1411, 1683 ms, respectively; see Figure 4B).

Orientation responses

Overall, observers' responses in the orientation matching task were tracking the stimulus' orientation (Rayleigh's test, $p < 0.001$) and showing no perceptual or response biases in the absence of stimulus (Rayleigh's test, $p > 0.1$; see Figure 1B). Importantly, participants' responses revealed that small deviations from cardinal orientations were overestimated (Figure 3), demonstrating the special status of cardinal axes. For instance, a stimulus tilted a few degrees left to the vertical would make participants' errors be even more to the left of the vertical (Figure 3B, black curve). This pattern was confirmed by sorting trials in two categories depending on whether the stimulus orientation was greater or less than the orientation of the closest cardinal axis (Figure 3B) and finding that participants' errors systematically differed between these two categories of trials ($p < 0.001$, Watson two samples test). From here on, we quantified on each trial this misperception, by assigning a positive sign to response errors reflecting an attraction toward the closest cardinal and a negative sign to response errors reflecting a deviation away from the closest cardinal. Interestingly, the deviation from cardinals was also stronger when

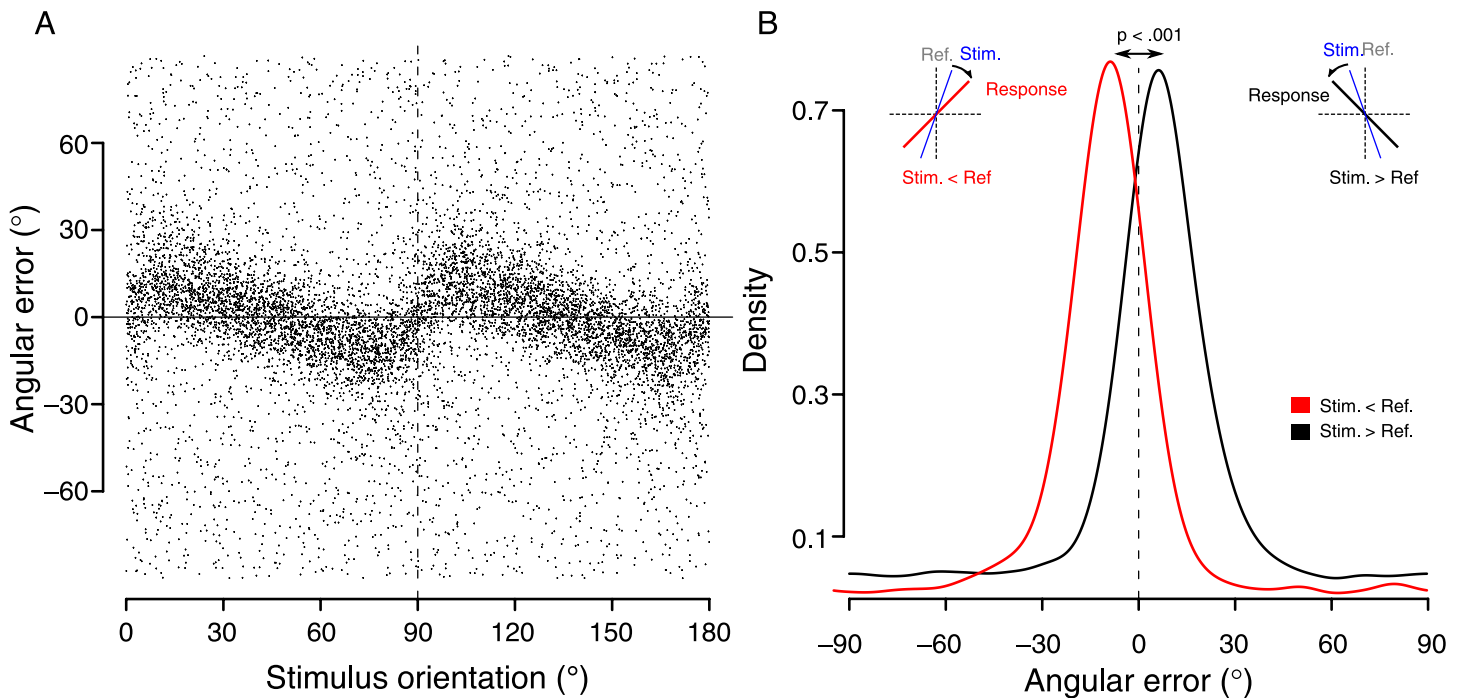


Figure 3. (A) Participants' errors as a function of stimuli orientations. All visibility conditions are included. Errors around 90° and 0°/180° reflect the illusory increased deviations from the cardinal axes. (B) Density of response errors: trials were sorted in two groups, as a function of the sign of the angular difference between the stimulus and the closest reference. In each group of trials, mean participants' errors were of the same sign as this angular difference, showing that stimuli are perceived away from the references. In the insets, the closest reference is the vertical axis, and observers' responses are more tilted than the stimulus. Densities are estimated using a von Mises kernel function (bandwidth = 32°).

stimuli were actually closer to the cardinals than to the diagonals (-6.0° vs. -3.4° , $F(1, 45) = 12.53$, $p < 0.001$), showing additional evidence for the special status of cardinal orientation in visual perception.

Visibility and the anisotropy

We then turn to our main question that is the relation between visibility and perceptual anisotropy quantified as the exaggerated deviation from cardinal orientations. First, and crucially, participants' responses in low visibility trials were not random but actually tracked the orientation of the stimuli ($p < 0.001$, Rayleigh's test), suggesting unconscious processing of orientation although with a low signal-to-noise ratio (see Figure 2B). We could then assess the deviation from cardinals separately for the three classes of trials corresponding to low, intermediate, and high visibility situations (see Figure 4A). The effects were reliable in each class of trials (low visibility: $T(45) = 2.28$, $p < 0.05$; intermediate visibility: $T(45) = 18.04$, $p < 0.001$; high visibility: $T(44) = 12.41$; $p < 0.001$), but differed in magnitude across the three classes ($F(2, 89) = 18.3$, $p < 0.001$). Deviations from cardinals were found to have a non-monotonic profile with minimal deviations for low visibility conditions and maximal deviations for intermediate

visibility (mean deviations = -2.12° , -7.14° , -4.70° for low, intermediate, and high visibilities, respectively). The non-monotonic profile was confirmed by *T*-test comparisons between consecutive classes (low vs. intermediate: $T(45) = 5.4$, $p < 0.001$; intermediate vs. high: $T(44) = -6.37$, $p < 0.001$). Crucially, these results confirmed the critical prediction that the anisotropy is more prominent under conditions of intermediate visibility, in comparison with either unconscious or full perception. This pattern was found in all participant groups (Supplementary Figure 1) and was unaffected by previous exposure during the experiment ($F < 1$).¹

Visibility vs. duration

Subjective visibility ratings and objective stimuli durations being highly correlated, we wanted to ensure that the non-monotonic profile could not be explained only by duration. To do so, we considered two regression models in which the deviation from cardinals was predicted by a quadratic function of either visibility or duration (the clear U-shape of the effect discarded a simple linear function), and we computed the Akaike Information Criterion for these two models. We found a lower AIC for the model based on visibility, showing that visibility

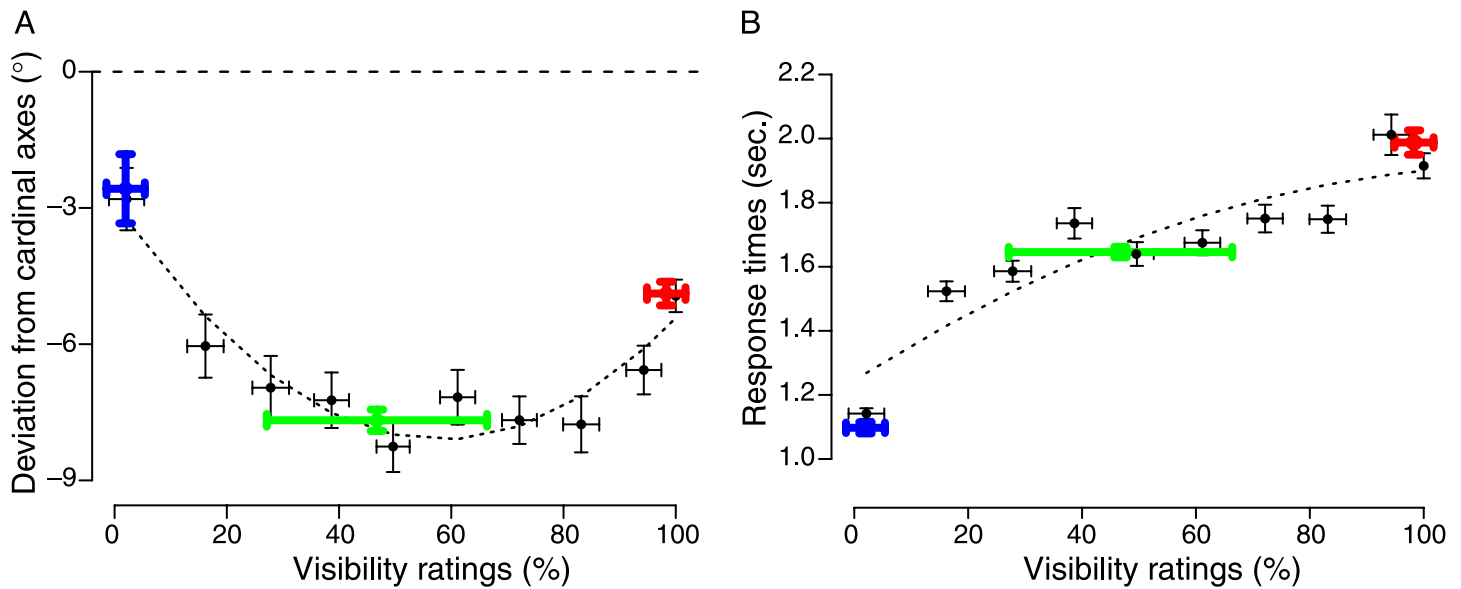


Figure 4. (A) The deviation from cardinals in orientation responses assessed in 10 adjacent bins of trials sorted by visibility ratings, fitted by a quadratic model (dotted curve; $F(2, 7) = 28.6$; $p < 0.001$; $r^2 = 0.86$). (B) Response times in the same visibility bins and the quadratic fit ($F(2, 7) = 16.5$; $p < 0.005$; $r^2 = 0.83$). Superimposed on these graphs are the mean deviation effects and mean RTs in the three classes of lowest (blue), intermediate (green), and highest visibility (red) trials. Vertical error bars represent *SEM* on deviation effects and RTs, horizontal error bars represent *SD* on visibility ratings.

better predicts the effect than duration. This model comparison was reliable across subjects when computing the two AIC separately for each subject ($T(45) = 2.14$, $p < 0.05$). This finding is also consistent with a control experiment showing a similar interaction between visibility and anisotropy, even when visibility of the Gabor patch was manipulated with 4-dot masking, ensuring constant stimulus duration (see [Supplementary Data](#) and [Supplementary Figure 2](#)). Thus, our main result cannot be explained by the stimulus duration alone.

Discussion

In this study, we probed orientation perception and visibility as a function of the stimulus orientation and duration. Overall, observers consistently overestimated small angles around the cardinal axes, an effect previously described (e.g., Jastrow, 1892; Smith, 1962), which reflects the perceptual anisotropy in orientation processing. Crucially, we found that this effect had a non-monotonic profile as a function of visibility, with maximal amplitude for intermediate conditions of visibility involving degraded but still detectable stimuli. Although visibility judgements were correlated with the stimuli durations, a model comparison analysis suggests that the non-monotonic profile is best accounted for by changes in subjective visibility.

This profile was present in all five groups of subjects and unaffected by biasing experimentally the exposure to particular orientations. Thus, it appears that whatever mechanism is responsible for the deviation from cardinals in our experiments, it is immune to recent exposure, suggesting that our manipulation of visibility impacted a mechanism hard wired in the brain. Further studies are needed in order to determine whether visibility has the same kind of influence on less entrenched mechanisms.

Importantly, comparison of the profile of Response Times as a function of visibility suggests that the non-monotonic profile of the deviation effect cannot be simply accounted for in terms of memory. It could be that the perceptual anisotropy depends on the necessity to keep the orientation information in memory, as suggested by previous work on the oblique effect (Heeley & Buchanan-Smith, 1992; Matthews et al., 2005; Westheimer, 2003). Indeed, in these studies, orientation discrimination thresholds exhibited an advantage for cardinal over oblique orientation mainly when the two stimuli to be discriminated were presented successively to the observer, while this advantage was reduced or erased when the two stimuli were simultaneously presented and thus did not require memory. In this perspective, the poorer discrimination around oblique axes would reflect a limited capacity to maintain over time a precise trace of these oblique orientations. However, if memory were to explain our data we would expect a monotonic relation between our effect and response times, as any memory-dependent effect would be modulated by the retention time. However,

fully visible trials are responded slower but yield a smaller deviation than trials with intermediate visibility (see Figure 4), which contradicts an explanation in terms of memory.

Similarly, we may discard a simple sensory-motor interpretation, according to which the anisotropy in perception does not depend on stimulus' visibility, but on the possibility to use real-time information to monitor the response. If so, we would expect the deviation from cardinals to increase monotonically with RT. This, again, is in contradiction with the comparison between intermediate visibility and fully visible trials. Yet, it is true that low visibility trials involve both faster responses and lesser deviations than intermediate visibility trials, which is in accordance with a sensory-motor interpretation. Further studies, using various time constraints on responses or different response modes (e.g., Rossetti & Pisella, 2002) might help clarify the matter.

Our main result is a new characterization of the dynamics of the anisotropy in orientation processing. Not only does it appears gradually and builds up over time, as was previously reported (Matthews et al., 2005), but it also decreases when conditions allow for full processing of the stimulus, and it depends more on subjective visibility than on physical stimulus duration. Importantly, these results suggests that variation in the magnitude of the anisotropy is not due simply to mere feedforward consequences of orientation coding in the primary visual cortex (e.g., Furmanski & Engel, 2000; Mansfield, 1974; Li et al., 2003; Wang et al., 2003). Indeed, this simple scheme would only predict a static or monotonic profile for increasing stimuli durations. Rather, we argue that the present findings support an interaction between the low-level anisotropy in V1 and more central components.

The influence of visibility on the anisotropy in orientation processing might shed some light on the neurobiological and functional distinction between conscious and unconscious visions. In fact, recent accounts in this domain (e.g., Dehaene et al., 2006; Lamme, 2003) have reached the consensus that subliminal, undetected, stimuli only receive bottom-up processing, while supraliminal stimuli receive more integrative processing by means of feedback loops, should they be distributed globally and involve an extended fronto-parietal brain network (Dehaene et al., 2006), or should they be only local loops in sensory regions (Lamme, 2003). In this perspective, one could then consider that the deviation effect observed in the lowest visibility trials is merely a feedforward consequence from anisotropic orientation coding in neurons of the primary visual cortex (V1), and that the anisotropic coding is amplified for visible stimuli as they trigger interactions between V1 and higher regions accessing the orientation information. Interestingly, this potential scenario receives support from physiological studies suggesting that anisotropic orientation coding is supported by intra-cortical lateral interactions among V1 neurons (Li et al., 2003; Ling, Pearson, & Blake, 2009), and that these lateral

interactions are enhanced by top-down attention (Ito & Gilbert, 1999).

One might also consider our results along the anisotropic normalization model of orientation perception (Essock, DeFord, & Hansen, 2003; Hansen & Essock, 2006). In this model, cardinal stimuli trigger lower responses because they receive greater divisive normalization, due to the greater pool of neurons tuned to the cardinals. Note that this greater normalization is observed specifically with broadband stimuli and that our stimuli have relatively low frequencies (1.5 cpd) and included noise that could drive similar effects. With such stimuli, the model predicts better visibility for oblique stimuli, which is also what we observe. In this perspective, for a stimulus slightly tilted from a cardinal the normalization will silence the cardinal units more than the non-cardinal ones, which could produce the illusory deviation from the cardinals. Interestingly, previous modeling work related to the normalization model proposed that anisotropy depends on the stimulus signal-to-noise ratio (Wainwright, 1999): for fully visible stimuli it is optimal to respond equally to all orientations, while when the stimulus becomes harder to see it becomes optimal to privilege some orientations. However, more work is needed to establish these links and to understand why when stimuli are taken to be absent, no such normalization occurs.²

One should carefully acknowledge that the present experiments do not enable us to disentangle visibility *per se* from its consequences. Indeed, as soon as the stimulus is detected, its information can receive more top-down attention and cognitive control and recruit more processing resources. It is thus plausible that an invisible stimulus should not involve many resources for its processing, because the expected accuracy is low. This concurs with the fact that response times are low for invisible stimuli, as was found in a previous study (Sackur & Dehaene, 2009). By contrast, when the stimulus is degraded but *detected*, it may trigger the involvement of top-down resources. Furthermore, we may expect that these will have a great impact, as information from the stimulus itself is noisy or ambiguous. At last, when the stimulus is detected and strong, it may not need additional top-down resources to be processed. Accordingly, the modulation of the anisotropy could stem from various levels of engagement of top-down attention resulting from different visibility conditions. Interestingly then, one could predict that the deviation from cardinals, or the oblique effect, might vary with the reward value associated with accuracy on the task, in particular for visible stimuli, since more attention would be dedicated to stimuli that are worth it. Such differential weighting of top-down information according to stimulus' ambiguity has already been found in sensory-motor processing (e.g., Körding & Wolpert, 2006). Our results extend the notion to the domain of perception and suggest that subliminal stimuli are specific in that they fail to trigger top-down resources.

Importantly, it remains unknown whether this relation between visibility and resource allocation is implemented

implicitly, through unconscious mechanisms reflecting an intrinsic property of the cognitive system, or explicitly, with observers having (conscious) reasoning about resource allocation as a function of visibility. In our paradigm, participants are probably not committing to such explicit strategies. However, assessing the contribution of both explicit and implicit components in the allocation of resources remains in general an open empirical question.

Finally, the pattern of results presented here confirmed the counterintuitive prediction that perception of a stimulus under the lowest visibility conditions, although more affected by noise, can be more faithful to the actual stimulation than perception of visible stimulus. One could wonder whether this property observed for visual orientations might reflect a more general principle of human cognition. Speaking to this issue, it was recently speculated that subliminal stimuli might only receive analog processing, while supraliminal stimuli could benefit from the computational advantages of symbolic processing and in particular from a limited level of noise accumulation across steps of processing (Sackur & Dehaene, 2009). The symbols of perception would be perceptual categories built on anisotropic processing. Interestingly, categorical perception has been proposed for visual orientation, with categories such as “tilted” or “vertical”/“horizontal” (Wolfe, Stewart, Friedmanhill, & Oconnell, 1992). Along these lines, further research capitalizing on categorical perception of colors, faces, or phonemes might attempt to test whether this suggested relation between awareness and non-monotonic (anisotropic) processing also holds true in other domains of cognition.

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Footnotes

¹Additionally, as suggested by an anonymous reviewer, we controlled that this effect was not driven by potential unequal contributions of orientations in the three classes of visibility, by equalizing orientation histograms in each visibility class.

²We thank an anonymous reviewer for suggesting this line of reasoning.

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