The mechanisms of collinear integration

John Cass  
Department of Psychology, University of Sydney, Australia

David Alais  
Department of Psychology, University of Sydney, Australia

Low-contrast visual contour fragments are easier to detect when presented in the context of nearby collinear contour elements (U. Polat & D. Sagi, 1993). The spatial and temporal determinants of this collinear facilitation have been studied extensively (J. R. Cass & B. Spehar, 2005; Y. Tanaka & D. Sagi, 1998; C. B. Williams & R. F. Hess, 1998), although considerable debate surrounds the neural mechanisms underlying it. Our study examines this question using a novel stimulus, whereby the flanking “contour” elements are rotated around their own axis. By measuring contrast detection thresholds to a brief foveal target presented at various phases of flanker rotation, we find peak facilitation after flankers have rotated beyond their collinear phase. This optimal facilitative delay increases monotonically as a function of target–flanker separation, yielding estimates of cortical propagation of 0.1 m/s, a value highly consistent with the dynamics of long-range horizontal interactions observed within primary visual cortex (V1). A curious new finding is also observed: Facilitative peaks also occur when the target flash precedes flanker collinearity by 20–80 ms, a range consistent with contrast-dependent cortical onset latencies. Together, these data suggest that collinear facilitation involves two separate mechanisms, each possessing distinct dynamics: (i) slowly propagating horizontal interactions within V1 and (ii) a faster integrative mechanism, possibly driven by synchronous collinear cortical onset.

Keywords: collinear, contrast facilitation, V1, long-range horizontal connections, feedforward, feedback, uncertainty reduction

Introduction

Neurons constituting the earliest stages of cortical visual processing respond selectively to stimuli presented to a small region of visual space. Despite this fragmented neural representation of the visual world, we routinely perceive and differentiate between objects whose retinal image extends well beyond the spatial limits of individual cortical receptive fields. This implies that the visual system selectively integrates and segregates local information distributed across the visual field. How the visual system accomplishes these long-range interactions is a matter of considerable debate (Angelucci & Bullier, 2003; Stettler, Das, Bennett, & Gilbert, 2002).

One source of environmental information that we readily use to differentiate objects in the real world is collinearity, which is typically afforded by surface edges (Geisler, Perry, Super, & Gallogly, 2001). Related to this is the psychophysical phenomenon known as collinear facilitation, whereby sensitivity to a low-contrast target is enhanced when presented in the context of spatially separated collinear flankers (Freeman, Driver, Sagı, & Zhaoping, 2003; Freeman, Sagı, & Driver, 2001, 2004; Polat & Sagı, 1993; Tanaka & Sagı, 1998; Williams & Hess, 1998). This effect has received considerable attention in the last decade, with accounts generally favoring some form of long-range structural integration of center and surround stimuli, via long-range feedforward, horizontal, or feedback connections (Angelucci & Bullier, 2003; Kapadia, Ito, Gilbert, & Westheimer, 1995), whereas others appeal to higher level, informationally and attentionally (Freeman et al., 2001, 2003, 2004) driven processes. There is, however, little experimental evidence to differentiate between these various models.

Recently, it was demonstrated that the period of exposure required to induce collinear facilitation increased as a function of the visual separation between target and flanking Gabor stimuli (Cass & Spehar, 2005). The slope of this spatiotemporal dependency was consistent with the propagation velocity of long-range horizontal interactions observed across the retinotopic surface of primary visual cortex (0.1–0.2 m/s; Bringuier, Chavane, Glaeser, & Fregnac, 1999; Grinvald, Lieke, Frostig, & Hildesheim, 1994) rather than with cortical feedforward and feedback propagations (Girard, Hupe, & Bullier, 2001), which are an order of magnitude faster. However, this relationship could conceivably be interpreted informationally rather than structurally. Accordingly, collinear surround stimuli could provide target-relevant information, which serves to remind a higher level decision stage (which may or may not be perceptually accessible) of the target feature space. If the number of irrelevant channels being monitored is increased (in this case, increasing target–flanker separation would increase the number of location-selective channels to be monitored), then a process involving the differentiation of target signal from irrelevant noise is...
likely to be more time consuming and, hence, require greater exposure duration.

To differentiate between these possibilities, we developed a novel paradigm to determine whether the spatio-temporal dependency described above (Cass & Spehar, 2005) reflects lateral transmission delay or some more complex temporal compensatory mechanism, possibly resulting from increased spatial uncertainty. To this end, we continuously varied the carrier orientation of the flankers from frame to frame (3.6 deg/frame) and flashed the target for a single frame (10 ms) at different phases of the flanker rotation cycle (Figure 1). The advantage of this method was that we were able to manipulate precisely the timing of target onset relative to the moment of flanker collinearity, while keeping exposure duration constant.

According to the lateral propagation model, collinear surround facilitation results from the simultaneous integration of feedforward and horizontally propagating surround signals in the population of target neurons. Because geniculo–cortico transmission is much faster than long-range intrastriate interactions (Girard et al., 2001; Kandel, Schwarz, & Jessel, 2000), facilitation is predicted when the target “flash” is presented after the moment of flanker collinearity (see Figure 2). This model further predicts that the optimal facilitative delay between flanker collinearity and target onset will increase as a function of target–flanker separation, with the slope of this relationship reflecting the conduction velocity of lateral propagation.

In contrast to the classical finding in which maximum facilitation depends upon physically collinear target–flanker contexts, we find that (i) facilitative peaks are clearly apparent for targets whose onset occurs after flankers have rotated beyond their collinear phase and (ii) this optimal facilitative onset lag increases with greater target–flanker separation, yielding cortical transmission velocity estimates corresponding with physiologically observed long-range intrastriate transmission. This supports the predictions of the lateral propagation model (Figure 2). Remarkably, we also find that facilitation occurs prior to flanker collinearity, which precludes lateral propagation. By conducting an additional experiment to determine whether these instances of collinear precedent facilitation result from perceived target–flanker collinearity, we conclude that these instances of facilitation are more likely to result from contrast-dependent cortical latency differences. Collectively, these results indicate that collinear integration is subserved by two mechanisms, each with distinct dynamics: (i) slow long-range interactions within V1 and (ii) a fast feedforward mechanism, possibly driven by synchronous collinear cortical onset.

**Methods**

**Subjects**

Three males (two authors and one naive observer) participated in this experiment. All had normal or corrected-to-normal vision.

**Materials**

Stimuli were produced on a G5 Macintosh computer using Matlab and Psychophysics Toolbox (Brainard, 1997) software driving an ATI Radeon 9600 Pro video card and displayed upon a 10-bit, gamma-corrected Mitsubishi Diamond Pro cathode ray tube (1,024 × 768 mm, 36.5 × 27.5 deg, mean luminance = 94 cd/m²) operating...
at 100 Hz vertical refresh at a viewing distance of 57 cm in a dark viewing chamber.

Stimuli and procedures

The stimulus used to estimate contrast detection threshold (CDT) was a circular target Gabor patch (\( \lambda = 0.67 \) deg = \( \sigma \); cosine phase; horizontal carrier orientation) presented for 10 ms (temporal square wave) at fixation. High-contrast fixation crosses located 3.2 deg above and below fixation were presented for the duration of each trial. Contrast thresholds were measured by instructing subjects to make a forced-choice judgment on each experimental trial regarding which of two intervals contained the target Gabor (the order of which was randomized across trials). Target contrast was varied from trial to trial in response to subject performance using two randomly interleaved adaptive QUEST (Watson and Pelli, 1983) procedures tracking 75% correct performance. Detection thresholds were computed using pooled data for each subject and condition using a least squares psychometric curve-fitting procedure. Corrective auditory feedback was provided following each response.

Contextual threshold effects were determined by comparing target CDTs measured without surround Gabor patches (baseline condition) with those in which surround Gabors were present. Contextual surrounds consisted of high-contrast flanking Gabor patches equidistantly to the left and right of fixation at target–flanker separations of 3\( \lambda \), 4.5\( \lambda \), or 6\( \lambda \). Target contrast was varied from trial to trial in response to subject performance using two randomly interleaved adaptive QUEST (Watson and Pelli, 1983) procedures tracking 75% correct performance. Detection thresholds were computed using pooled data for each subject and condition using a least squares psychometric curve-fitting procedure. Corrective auditory feedback was provided following each response.

The second experiment employed identical stimuli to those in the first experiment (but with suprathreshold contrast target Gabors, -10 and 0 dB). In this experiment, however, the phase of flanker rotation at which the target onset occurred was manipulated from trial to trial, and perceived collinearity estimates were based on the target onset phase at which 50% of trials were seen as occurring before collinearity. No corrective feedback was provided in this latter experiment.

Results and discussion

Results from our experiments clearly demonstrate the predictions of the lateral propagation model (Figure 3a). The right-hand portion of each graph represents temporal contexts in which the flashed target onset succeeds physical collinearity. A facilitative peak is evident within this temporal window at each separation for every observer (Figure 3a, blue-shaded regions). Furthermore, the latency at which this facilitative peak occurs increases as a function of target–flanker separation between flanker-centered to target-centered neural populations (slope > 0, \( p < .01 \); see blue line, Figure 3b). These latencies imply that this facilitative signal takes time to travel across retinotopic space. Transforming this spatiotemporal dependency into striate coordinates (Horton and Hoyt, 1991; see Equation 1) yields an average linear velocity estimate of 0.1 m/s. Remarkably, this value strongly resembles the velocity of subthreshold activity observed to travel across V1 of several species (Bringuier et al., 1991).
Therefore, based on these postcollinear target onset data, it would seem that collinear facilitation is likely to be mediated by long-range intrastriate connections.

A curious new result can also be seen in the data: Facilitation is evident in many instances in which the target flash precedes collinearity (see left-hand portion of each graph in Figure 3a). Assuming that surround transmission
is slower than feedforward transmission, the lateral propagation model is unable to account for these effects (see Figure 2). One possibility is that these instances of facilitation are the result of temporal coincidence. That is, although the stimuli are not physically aligned, they may still be temporally aligned at a neural level because of differential feedforward latencies for the central target and surround stimuli. Several sources of evidence support this interpretation. Firstly, retino–geniculo–cortico latencies increase by up to 40 ms as luminance contrast is lowered

Figure 3. Results of contrast detection experiment. (a) Target CDTs (y-axes) measured for three subjects (columns) as a function of target–flanker separation (rows) and different phases of flanker rotation (x-axes). The horizontal dotted line in each graph represents target detection threshold measured in the absence of flankers (baseline condition). Contrast facilitation is defined as any threshold measurement that is lower than baseline. Shaded regions identify the maximum facilitative rotation phase associated with target onsets, which precede (red) and succeed (blue) physical flanker collinearity. (b) Average latencies at which maximum target facilitation was recorded prior to flanker collinearity (red line) and after flanker collinearity (blue line) as a function of cortically transformed visual separation (striate distance; see appendix). Independent regression analyses indicate that while peak facilitative latencies increase with target–flanker separation in the context of postcollinear target onsets ($p < .01$; blue curve), facilitative peaks associated with precollinear target onsets do not exhibit significant distance dependence ($p > .05$; red curve). Postcollinear velocity estimate of 0.1 m/s is computed by dividing target–flanker–centered striate distance by facilitative delay. Error bars represent plus and minus one standard error of the between-subject means.
Psychophysical evidence supports this relationship between decreased contrast and increased latency (Solomon & Morgan, 1996). Secondly, V1 latencies are reduced by approximately 40 ms for moving compared with flashed stimuli (Jancke, Erlhagen, Schoner, & Dinse, 2004). Either of these processes, independently or in combination, could increase the latency of the low-contrast flashed target relative to the high-contrast rotating flankers so that neural temporal alignment would occur for targets whose onset physically precedes flanker collinearity. Consistent with this, facilitation preceding physical collinearity is evident within this range of latencies (20–80 ms; see red-shaded regions in Figure 3a and red line in Figure 3b).

Why synchronous cortical collinear onsets would generate target facilitation is not clearly known. A structural interpretation is that the instances of precollinear target facilitation reflect the operation of first-order detectors whose receptive fields are elongated in the direction of the collinear alignment (Morgan & Dresp, 1995) and which are optimally driven by synchronous collinear cortical inputs. Candidate neural substrates for such detectors are extrastriate summation, extrastriate feedback (Angelucci et al., 2002), and/or cortico–thalamo interaction. An alternative, information-based interpretation is that these instances of collinear-precedent facilitation might result from perceived collinear alignment between the target and flankers. Indeed, the information that one perceives to be relevant to the target feature space (e.g., location and orientation) would arguably be more precise when presented in the context of a collinear compared with a noncollinear image, thereby facilitating a reduction in uncertainty.

To determine whether these collinear-precedent instances of target facilitation are due to perceived collinearity, we measured the temporal offset required to induce perception of target–flanker collinearity using equivalent spatiotemporal conditions to those used in the contrast detection experiment described above (but employing suprathreshold rather than near-threshold “target” flashes). According to this interpretation, if the collinear precedent facilitation effects observed in the first experiment (Figure 3) are due to perceived collinearity, then they should exhibit similar spatiotemporal dependencies. Figure 4 demonstrates that, on average, perceived collinearity occurs when the target flash precedes flanker collinearity by approximately 0–50 ms. These latency values appear consistent with the flash-lag phenomenon (Kanai, Sheth, & Shimojo, 2004; (Gawne, Kjaer, & Richmond, 1996). Psychophysical evidence supports this relationship between decreased contrast and increased latency (Solomon & Morgan, 1996).
typically involving motion across retinotopic space as opposed to orientation feature space).

Consistent with the finding that cortical latencies increase with decreasing stimulus contrast (Gawne et al., 1996), a within-subjects ANOVA revealed that our observed flash-lag effects were greater (~20–40 ms) at the lower (flashed) target contrast compared with the high-contrast target ($p < .05$). Curiously, while we found no evidence that the target onset latencies associated with perceived collinearity varied with target–flanker separation (and, therefore, are not inconsistent with the collinear-precedent target facilitation observed in Experiment 1, see red curve in Figure 3b), we did observe a trend toward a decrease in flash lag with greater target–flanker separation ($p = .13$). Why the flash-lag effect would decrease with greater target–flanker separation is unclear, although it is conceivable that cortical latencies may decrease with eccentricity. Given the lack of statistical and neurophysiological support for this interpretation, we conclude that while the instances of collinear-precedent facilitation observed in Experiment 1 may not be due entirely to perceived collinearity, both phenomena are consistent with a latency contingent cortical representation of collinearity.

Conclusions

Collectively, these findings demonstrate that psycho-physical collinear facilitation is likely to be mediated by two sets of mechanisms, each with distinct dynamics: a temporally coincident cortical representation of collinearity and another, involving slow, long-range horizontal transmission within V1. Given that current neurophysiological evidence provides a sufficient account of our collinear facilitation data, we see no reason to appeal to an informational account such as uncertainty reduction. If uncertainty reduction does play a role, however, our results indicate that it is unlikely to rely entirely on perceptual judgments of collinearity.

Equations

Cortical magnification factor

The visual angles subtended by various target–flanker separations were transformed into cortical distance estimates (see Figure 3b) using the integral of the following human cortical magnification factor estimate (Horton & Hoyt, 1991):

$$y = \int \frac{17.3}{E + 0.75} dE = 17.3 \ln(E + 0.75),$$

where $y$ = millimeters across retinotopic striate surface and $E$ = degrees of visual angle.

Acknowledgments

This work was supported by Australian Research Council Grant DP0345797 (to D.A.).

Commercial relationships: none.

Corresponding author: John Cass.

Email: jcass@physiol.usyd.edu.au.

Address: Department of Physiology, University of Sydney, NSW, Australia.

References


Gawne, T. J., Kjaer, T. W., & Richmond, B. J. (1996). Latency: Another potential code for feature binding...


