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DOI:
10.1016/j.visres.2016.12.016

Document Version
Accepted author manuscript

Individual differences in the dynamics of collinear facilitation?

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Abstract

Collinear facilitation refers to the increase in sensitivity found for a target when aligned between nearby, brighter flankers. Many studies have explored the spatial and temporal aspects of this arrangement, and there is a consensus that two mechanisms could be responsible for this phenomenon; lateral excitation within V1 and extra-striate feedback to V1. There is some debate as to whether facilitation can still occur if the target is presented before the flankers, a manipulation known as backward masking, which could rely on feedback to V1. We shed light on this debate by using forward, simultaneous and backward masking with a relatively large sample of 26 participants. We used short stimulus presentation times (35 ms) and a range of SOAs (stimulus onset asynchronies) (-70, -35, 0, 35 and 70 ms) in order to isolate any feedback facilitation that may occur. We found that collinear facilitation occurred with forward masking (+ve SOAs) in all participants. However, facilitation with backward masking (-ve SOAs) only occurred in 54% of participants. We present a basic model of facilitation that simulates the results of our experiment and could account for differences between previous studies. The model indicates that facilitation with backward masking arises primarily from feedback excitation. Our findings suggest that both lateral connectivity and extra-striate feedback contribute to target facilitation, but in fundamentally different ways and that feedback may be significantly reduced in some participants.

1 Introduction

Over the last twenty-five years, the vertical Gabor triplet (Figure 1B) has featured in many psychophysical investigations concerning the nature of contextual interactions between orientation selective neurons in the primary visual cortex (V1). Since Polat & Sagi (1993) first demonstrated both facilitation and suppression with such an arrangement, a multitude of spatial (Polat & Sagi 1994; Polat 2009; Polat et al. 1998; Zenger-Landolt & Koch 2001; Mizobe et al. 2001; Freeman et al. 2001; Woods et al. 2002; Freeman et al. 2004; Giorgi et al. 2004; Polat et al. 2005; Polat & Sagi 2007; Shani & Sagi 2005; Huang et al. 2006; Huang & Hess 2007; Huang et al. 2012; Huang & Hess 2008; Sterkin et al. 2008; Katkov & Sagi 2010; Wu & Chen 2010; Kéita et al. 2011; Lev & Polat 2011; Jachim et al. 2015) and temporal (Tanaka & Sagi 1998; Polat & Sagi 2006; Cass & Alais 2006; Polat et al. 2007; Huang & Hess 2008; Sterkin et al. 2009; Li et al. 2010; Sterkin et al. 2012) combinations of target and flanker designs have been developed.

One of the key parameters determining whether interactions are facilitatory or suppressive is the distance between the target and flanking Gabors. This distance is usually expressed in terms of the wavelength (λ) of the Gabor (the combined width of a single dark and light stripe), and Polat & Sagi (1993) demonstrated suppression when this distance was less than 2λ. At these short distances, and depending on the spatial frequency of the stimuli, there may be some spatial overlap between the target and flanking Gabors. This suppression, known as overlay suppression (Morrone et al. 1982; Bonds 1989; DeAngelis et al. 1992; Carandini et al. 1997) is thought to be the result of lateral inhibition as the flanking Gabors stimulate inhibitory neurons in the vicinity of the target Gabor (Macknik & Martinez-Conde 2007). As target-to-flanker separation increases, suppression turns to facilitation, with optimal facilitation occurring at a separation of 3λ. Although facilitation decreases as separation increases beyond 3λ, it is still apparent at separations of 12λ (Polat & Sagi 1993). These contextual, facilitatory interactions are thought to be mediated by intrinsic horizontal (lateral) connections in V1 (Rockland & Lund 1982; Gilbert & Wiesel 1983; Livingstone & Hubel 1984; Gilbert & Wiesel 1989; Polat & Sagi 1993) and/or feedback to V1 from higher cortical areas (Hupe et al. 1998; Angelucci et al. 2002; Freeman et al. 2003; Huang & Hess 2008). This paper will focus on studies using a target and flanker separation of 3λ, with the assumption being that interactions at these distances are largely facilitatory rather than suppressive.

The temporal properties of collinear facilitation are less well investigated than its spatial properties. The majority of investigations into collinear facilitation have used simultaneous masking (SM, stimulus onset asynchrony (SOA) = 0 ms (Figure 1B)) in which the target and flankers are displayed simultaneously and have identical presentation times. This temporal arrangement has consistently shown facilitation when target separation is greater than 2λ. Facilitation has also been

shown when the flankers are displayed before the target (forward masking, FM, SOA > 0 ms (Figure 1A)) (Tanaka & Sagi 1998; Polat & Sagi 2006; Polat et al. 2007; Li et al. 2010). However, experiments with the reverse temporal configuration, i.e. in which the target is displayed before the flankers (backward masking, BM, SOA < 0 ms (Figure 1C)) have delivered mixed results (Polat & Sagi 2006; Sterkin et al. 2009; Huang & Hess 2008).

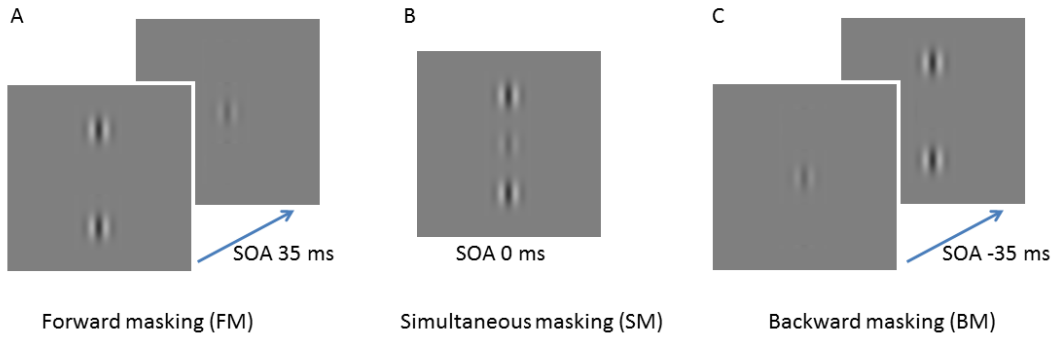

Figure 1 Presentation sequence of target and flankers for the different masking arrangements. (A) With forward masking the target is presented after the flankers. (B) With simultaneous masking the target is presented at the same time as the flankers. (C) With backward masking the target is presented before the flankers. Note that backward masking is distinguished from forward masking by a negative SOA.

The temporal characteristics of mechanisms responsible for facilitation will depend upon the dynamics of underlying neural excitatory connections. Two different types of excitation – driving and modulating are thought to contribute to facilitation at the target site in V1. Feed-forward stimulus-driven excitation is a fast-onset and transient *driving* influence that can cause the target neurons to fire. This is in contrast to the slow-onset and sustained *modulating* influence of the horizontal excitation, which makes target neurons more susceptible to firing (Sherman & Guillery 1998; Spratling 2013). In addition, it has been shown that feedback excitation to V1, long assumed to have a modulating influence, can also have a driving influence (De Pasquale & Sherman 2011; Covic & Sherman 2011). Examining facilitation with FM and BM is important because they are thought to rely on different mechanisms, FM making use of lateral connections, and BM making use of feedback connections (Huang & Hess 2008). We suggest that lateral connectivity plays little part in facilitation with BM for short duration stimuli, since the modulating influence of the horizontal connections would arrive at the target site after target activation has ceased.

Polat & Sagi (2006) conducted a series of experiments examining the effect of different temporal masks on collinear facilitation. Using a two interval forced choice (2IFC) design, they presented target and flankers at a wide range of spatial separations (2λ -12λ) and a variety of temporal configurations, including FM, SM and BM. For FM and SM they found typical patterns of facilitation i.e. suppression at separations that were less than 2λ, maximum facilitation at 3λ, and a

reduction in facilitation as separation increased. However, in the BM condition, facilitation was not evident at any separation including 3λ. They also presented a descriptive model of collinear facilitation mediated by lateral connections in V1. In a further study of the temporal properties of collinear interactions involving both psychophysical and visually evoked potential (VEP) experiments, Polat et al. (2007) examined the effect of FM, SM and BM on target and flanking Gabors at separations of 2λ and 3λ. Their results echoed those of the previously described study, with facilitation found for FM and SM, but not for BM. In each of these studies, the display duration of the target and the flanking pair was 60 ms and, in the BM condition, the target was presented 120 ms before the flankers. Polat and colleagues interpret these results as an indication that collinear facilitation relies predominantly on lateral connections and that, in the case of BM, horizontal connections cannot enhance a target that is no longer active (Figure 2A).

However, in a later study examining the dynamics of collinear facilitation, Huang & Hess (2008) demonstrated significant BM facilitation in a 2IFC design with target and flanker separations of 3λ. The presentation time of their target and flankers was 50 ms, and facilitation was measured over a range of SOAs that included FM, SM and BM at multiples of 50 ms. Peak facilitation was estimated to occur when the target preceded the flankers by 30 ms (BM). No significant facilitation was found when the target-to-flanker SOAs exceeded ±150 ms. Huang and Hess suggest that collinear facilitation cannot rely on horizontal connections alone, but may also involve a rapid, orientation specific interaction based on feedback connections from V2 (Girard et al. 2001) (Figure 2B).

The primary difference in the methods used by Polat and colleagues compared to Huang and Hess was the length of SOA. In order for feedback facilitation to occur, the target and flanker sites in V1 must be activated simultaneously (Angelucci et al. 2002; Cass & Alais 2006; Huang & Hess 2008). This 'window of integration' is dependent on the SOA and the fact that lower-contrast target signals take longer to reach V1 than higher-contrast flanker signals, a phenomenon known as contrast dependent onset latency (CDOL) (Sestokas & Lehmkuhle 1986; Reich et al. 2001). For these reasons we suggest that Polat et. al may have used SOAs that were too long to allow-BM to occur (Figure 2B). A long BM SOA would mean that the target site was stimulated before the flanker sites, despite the fact that, due to CDOL, low-contrast target signals arrive later in V1 than the higher contrast flanker signals. Consequently, we suggest that the *target delay* (TD), i.e. the extra time it takes for target signals to reach V1 compared to flanker signals (Figure 2) is the key to understanding the differences in previous findings.

In the current study, we investigate the temporal dynamics of collinear facilitation in a relatively large group of adults (N = 26 compared to previous studies reported above that used 3-5

participants). We varied the SOA between target and flanking Gabors separated by a distance of 3λ. We used SOAs that were shorter than those used by Polat and colleagues (-70 ms, -35 ms, 0 ms, 35 ms and 70 ms), and expected to find facilitation for all temporal conditions tested. Such a finding would suggest that facilitation occurs at some SOAs without lateral interactions, with the implication that feedback processing is exerting a contextual influence. Finally, we present a model combining both lateral and feedback facilitation that can successfully predict the results of our experiment and, to a certain extent, the conflicting data found in previous studies.

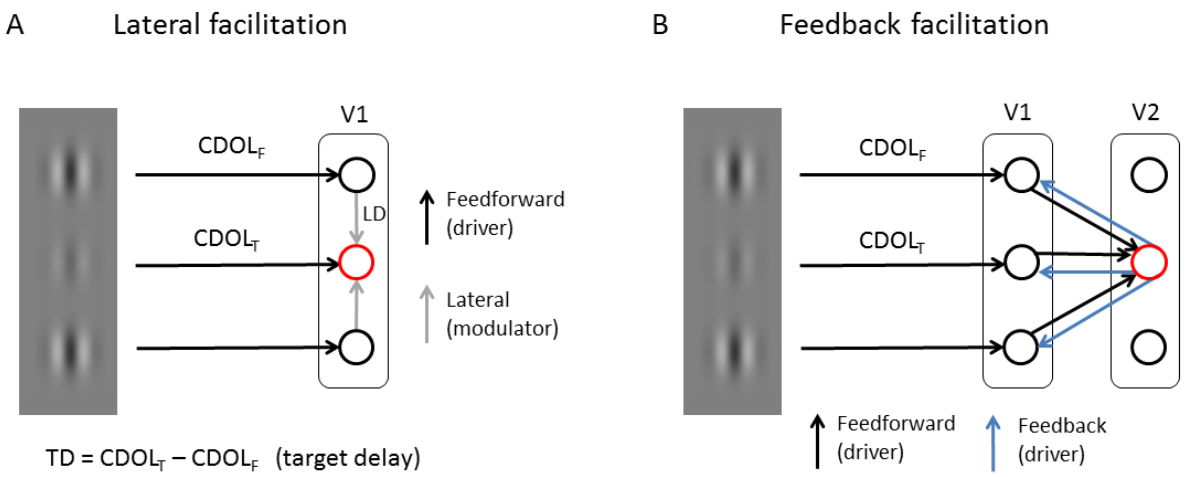

Figure 2 Sites of signal integration (red circles) in V1 and V2, thought to be responsible for collinear facilitation. The vertically aligned Gabor-triplet stimulus that generates the retinal and cortical activity is shown as a greyscale image. (A) Lateral facilitation is thought to occur at the target site in V1 (red circle) when the arrival of modulatory signals from the flanker sites coincides with the arrival of driving signals from the target stimulus. The time taken for the lateral modulatory signals to arrive equals the contrast dependent onset latency of the flanker ($CDOL_F$) plus the lateral delay (LD) due to the slow conduction rate of the unmyelinated lateral fibres (Grinvald et al. 1994). The time taken for the driving signals from the target to reach the integration site equals the contrast dependent onset latency of the target ($CDOL_T$) plus the SOA (which can be negative). (B) For feedback facilitation, the site of integration is extra-striate (V2 for example). Transfer from V1 to V2 is fast because inter-cortical axons are myelinated (Grinvald et al. 1994). Optimal feedback facilitation is thought to occur when driving signals from the target and flankers arrive simultaneously at the integration site (red circle). This can be achieved if the target is presented before the flankers (a negative SOA), in which case the SOA can cancel out the target delay (TD). This synchronous activation in V2 (or extra-striate areas) is thought to cause facilitatory feedback to the target and flankers in V1.

2 Methods and materials

2.1 Participants

A total of 26 participants (eleven female) were recruited via the University of Manchester's volunteer website. Mean age (±SD) of the participants was 27.9 ± 6.3. All had normal or corrected-to-normal vision (6/6, reduced Snellens) and 60' stereoacuity (TNO stereotest). Written informed consent was obtained from each participant. The study had the approval of the University of Manchester Research Ethics Committee (Ref: 12013), and was accordant with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2 Apparatus

Target and flanking Gabors were displayed on a gamma-corrected Iiyama MA203DT Diamondtron NF-CRT monitor having a screen resolution of 1600 x 1200 and a refresh rate of 85 Hz. The maximum luminance of the monitor was 81 cd/m^2. The actual screen dimensions were 407 x 304 mm, giving a pixel density of 3.93 pixels per mm. Participants were seated in a dimly lit room at a distance of 105 cm from the monitor. An adjustable plinth ensured that the centre of the screen was elevated to the participant's eye-level and a chinrest minimised head movement. The mean display luminance was 40 cd/m^2. The VGA output channels of the computer were used to drive a video attenuator device (Video Switcher, Xiangrui Li, Los Angeles, CA) to enable 12-bit precision in the grey-scale luminance values (Li et al. 2003). Participant responses were recorded via a standard computer keyboard.

2.3 Stimuli

The target and flanker Gabors were generated and presented with MATLAB (MathWorks 2005) and Psychtoolbox (Brainard 1997; Pelli 1997) (Fig 1). Each Gabor had a wavelength λ = 12 pixels giving a spatial frequency of 6.0 cpd at the viewing distance of 105 cm. Each Gabor was modulated by a Gaussian envelope with standard deviation (σ) = 4.7 pixels giving a bandwidth of 1.5 octaves. The flanking Gabors had a Michelson contrast of 80%. The distance between the target and each flanker was 3λ. Within the stimulus interval that contained the target (Figure 3A), the flankers always appeared at 105 ms with a duration of 35 ms. The target occurred at five different SOAs (-70 ms, -35 ms, 0 ms, +35 ms, +70 ms) with a duration of 35 ms. The inclusion of a baseline (no flankers) condition gave six experimental conditions. Each stimulus presentation was attended by an audible beep (245 ms), this helped to aid target location in the no flanker condition.

2.4 Procedure

The stimuli sequence is shown in Figure 3A. Each trial consisted of a blank screen for 1010 ms, followed by a fixation cross (752 ms) then a blank screen (752 ms), the first stimulus presentation (245 ms, see Figure 3A), a blank 800 ms inter-stimulus interval and finally the second stimulus presentation (245 ms). Each stimulus presentation was attended by an audible beep (245 ms). The central target Gabor could occur in either the first or second stimulus presentation. Participants had unlimited time in which to respond and indicated the interval in which the target appeared in by pressing a left-arrow or right-arrow key on the keyboard. Within the stimulus interval that contained the target, the flankers always appeared at 105 ms with a duration of 35 ms. The target occurred at five different SOAs (-70 ms, -35 ms, 0 ms, +35 ms, +70 ms) with a duration of 35 ms. The inclusion of a baseline (no flankers) condition gave six experimental conditions. Each of the six conditions were randomly interleaved in blocks of six, therefore each condition occurred once every six trials. Participants were unaware of the temporal manipulation. Each condition occurred fifty times, giving a total of 300 trials. Target contrast thresholds were determined by the Psi-method (Kontsevich & Tyler 1999) using routines from the Palamedes toolbox (Kingdom & Prins 2009) for MATLAB.

2.5 Analysis

The Psi-method returned target contrast threshold estimates based on the Weibull distribution (81.6% correct performance level). Facilitation is calculated in decibel units (dB), which is -20 x log10 (contrast ratio), where the contrast ratio is defined as the flanked-target threshold divided by the baseline-target threshold (Polat & Sagi 1994). Significant facilitation was determined using paired samples t-tests comparing baseline (no facilitation, dB = 0) to facilitation at each SOA, and Bonferroni corrections were used for multiple comparisons.

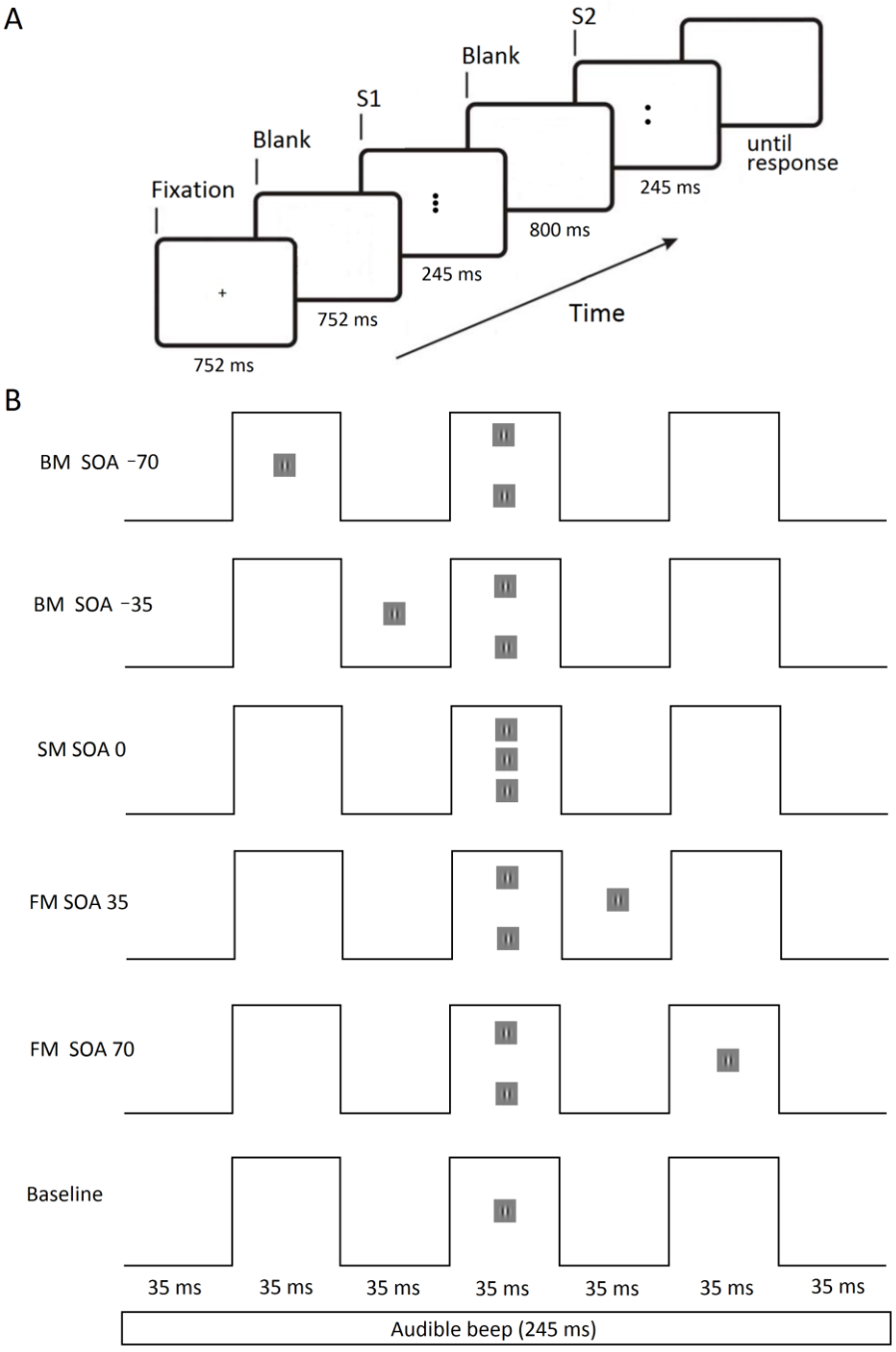

Figure 3 (A) Timeline for the 2IFC experimental procedure. S1 is the first stimulus presentation period, separated by an ISI of 800 ms. The temporal breakdown of S1 and S2 is shown in B. (B) Temporal sequencing of the six conditions showing the relationship between the target and flankers in the different masking scenarios (BM ,SM and FM). Target and flanker presentation times were 35 ms. The flankers appeared at the same time in each trial; 105 ms after the audible beep onset.

3 Results

We calculated collinear facilitation in dBs at five different target-to-flanker SOAs for 26 participants. A one-way repeated measures ANOVA (Figure 4A) determined that facilitation differed significantly across SOAs ($F(4,100) = 19.87$, $p < 0.001$, $\eta_p^2 = .44$). Post hoc tests using the Bonferroni

correction revealed that, when compared to baseline (0 DB), there was no significant facilitation for BM at -70 ms (M = .74, SD = 1.70) (t(25) = 2.23, p = .175). However, significant facilitation was found at all other SOAs; -35 ms (M = 2.53, SD = 2.03) (t(25) = 6.37, p < .001), 0 ms (M = 4.21, SD = 1.65) (t(25) = 12.98, p < .001), 35 ms (M = 3.42, SD = 1.78) (t(25) = 9.82, p < .001), 70 ms (M = 2.02, SD = 1.63) (t(25) = 6.34, p < .001).

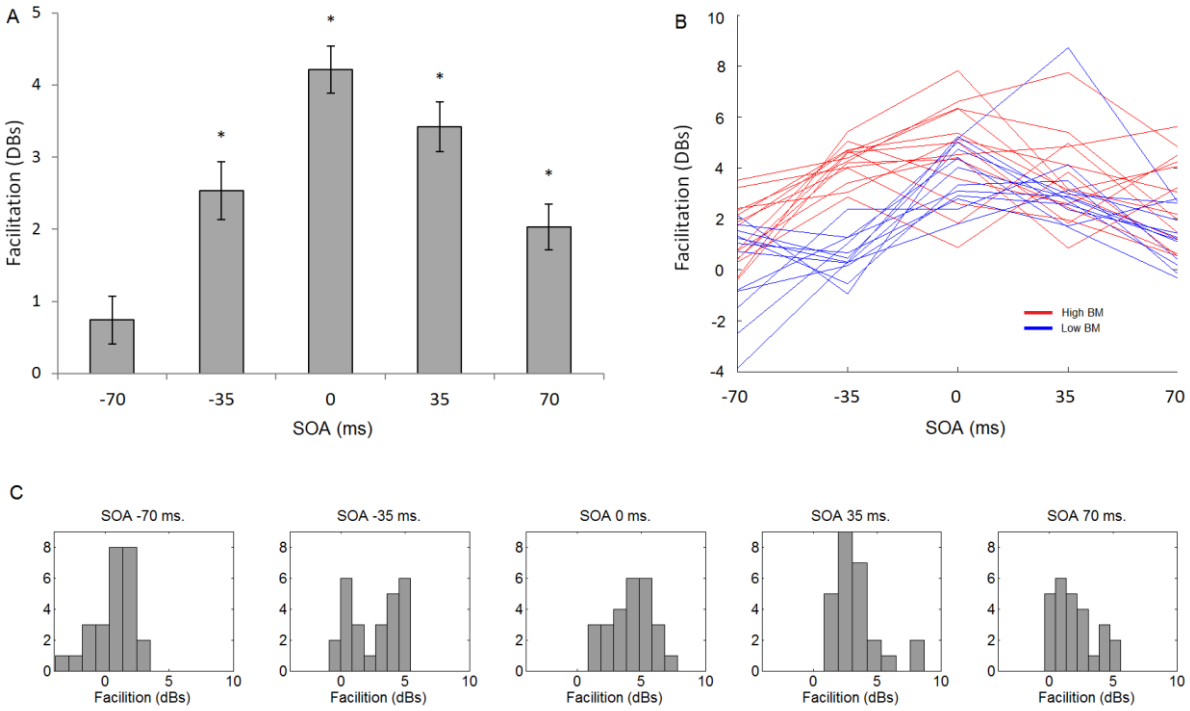

Figure 4 (A) Collinear facilitation in dBs as a function of target SOA for all participants. Negative values indicate backward masking (BM), zero indicates simultaneous masking (SM) and positive values indicate forward masking (FM). Error bars represent SEM. (B) Combined facilitation line plots for all participants. Clustering can be seen at an SOA of -35 ms, with grouping around the 4dB and 0dB levels. (C) Histograms showing the number of participants grouped by facilitation for each of the SOAs used. There is a bi-modal distribution for an SOA of -35 ms, with a no facilitation group of 12 participants and a facilitation group of 14 participants.

Interestingly, plotting the facilitation results for individuals (Figure 4B) gives some indication of two groups of participants for whom facilitation is either present or absent at SOA = -35ms. This is illustrated further in Figure 4C which shows the bimodal distribution of data is observed at this SOA. We investigated this further using a bimodality test, to check whether any of the distributions were in fact bimodal (Schwaiger et al. 2013). The result of the test was significant only at an SOA of -35, (p = .007). For this condition the test revealed a mixture ratio of .443 for two groups (M = .40, SD = .68 and M = 4.11, SD = .95). Using this ratio, we split the main group into two separate groups (low-BM = .443 x 26 = 11.52, high-BM = .557 x 26 = 14.48), a low-BM facilitation group consisting of 12 participants, and a high-BM facilitation group consisting of 14 participants. We compared the

performance of the two groups using a mixed ANOVA (Figure 5) which revealed a significant main effect of SOA ($F(4,96) = 46.47$, $p < .001$, $\eta_p^2 = .50$), a significant interaction ($F(4,96) = 5.47$, $p = .001$, $\eta_p^2 = .19$) and a significant group difference ($F(1, 24) = 21.97$, $p < .001$, $\eta_p^2 = .48$). Post hoc tests using the Bonferroni correction revealed one significantly different comparison at an SOA of -35. The high-BM group showed higher facilitation ($M = 4.23$, $SD = .73$) than the low-BM group ($M = .55$, $SD = .73$) ($t(24) = 11.69$, $p < .001$).

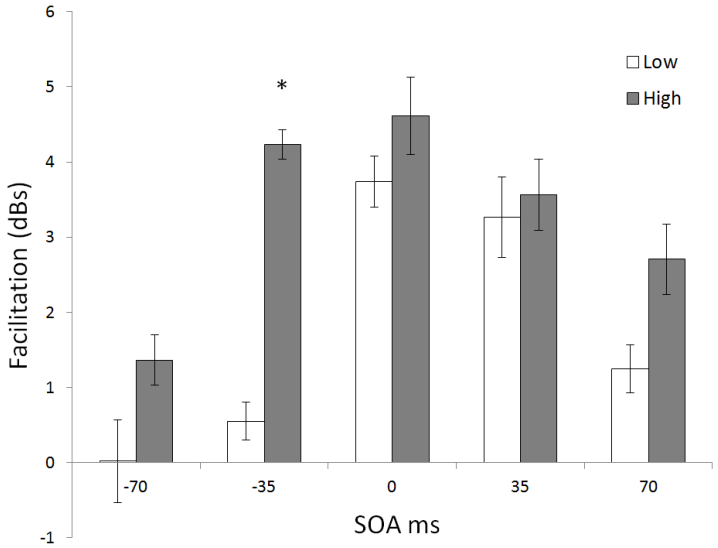

Figure 5 Comparison of high and low facilitation groups. Participants were split into a high facilitation group (N = 14), and a low facilitation group (N = 12), using the mixture ratio returned from the bimodalitytest. Bonferroni corrected t-tests reveal a significant group difference at an SOA of -35 ms ($p < .001$).

In order to explore potential causes of the individual differences observed in BM we looked for evidence of relationships between BM facilitation and three other variables; contrast sensitivity, age and psychophysical experience. Pearson product-moment correlation coefficients were computed (Bonferroni corrected for multiple tests such that alpha = 0.0167). Using the baseline (no flankers) value as a convenient measure of contrast sensitivity we found there was no correlation between BM facilitation and contrast sensitivity to the target alone, $r = -0.341$, $n = 26$, $p = 0.088$. Nor was there a significant correlation between BM facilitation and age, $r = -0.417$, $n = 26$, $p = 0.034$. Most of the participants had no experience of collinear facilitation experiments. However, five had taken part in a previous collinear facilitation experiment (Jachim et al. 2015) and three participants had experience of several collinear facilitation experiments. However, we found no correlation between BM facilitation and experience of collinear facilitation experiments, $r = -0.139$, $n = 26$, $p = 0.498$. The correlation results have been summarised by the scatterplots in Figure 6.

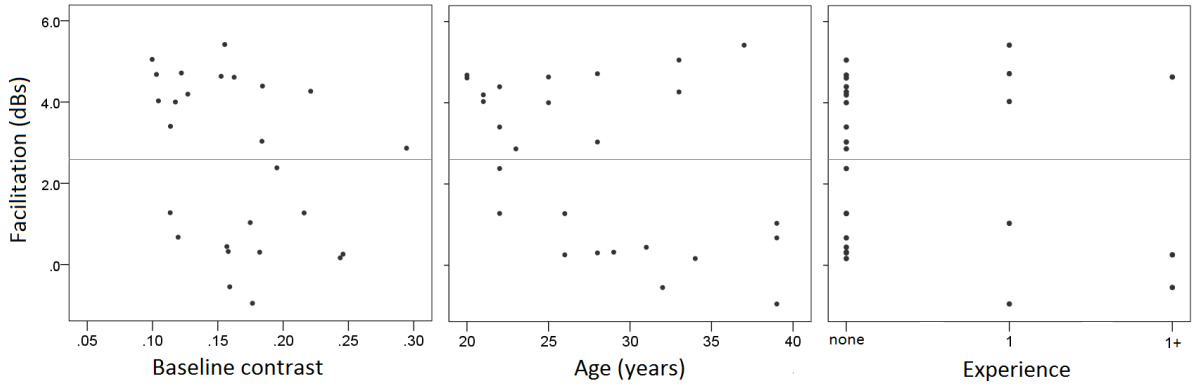

Figure 6 Scatterplots summarizing the results of the three correlation tests. We tested the relation between facilitation at an SOA of -35 ms and baseline contrast (contrast sensitivity), age and experience of collinear facilitation experiments. None of the three measures of individual differences proved to be significant. The horizontal lines separate the high and low facilitation groups.

4 A Dual Facilitation Model

It has been suggested that collinear facilitation may result from the combination of two independent facilitatory mechanisms (Cass & Alais 2006; Huang & Hess 2008), mediated by lateral and feedback connections, in and to V1. Here, we present a simple model of excitatory facilitation comprising lateral and feedback components. Our model assumes that the profile of excitatory signals (i.e. the onset and decay) for both slower, sustained modulatory horizontal excitation (Sherman & Guillery 1998), and faster, more transient feedback excitation (Girard et al. 2001) can be modelled by a gamma function. There is some evidence that the spiking activity of V1 cells in monkeys exhibit a broadly gamma shaped onset and decay profile (Reich et al. 2001; Kim et al. 2012).

Fundamental to this model is the idea that facilitation depends primarily on the temporal overlap (i.e. coincident activity) of target and flanker signals at the target site. For lateral facilitation to take place, we assume that the target neurons need to be active when impulses from the flankers are arriving at the target site (Polat & Sagi 2006). Similarly, for feedback facilitation to take place, we assume that the target and flanker sites are active at the same time (Angelucci et al. 2002; Cass & Spehar 2005), thus driving neurons at higher cortical levels. Under these assumptions a number of key parameters are likely to affect facilitation by modifying the degree of overlap. These parameters include:

- Stimulus Duration (*SD*) – increasing the duration increases the chance of temporal overlap between target and flankers

- SOA – shifts the temporal alignment of target and flanker signals thereby affecting their overlap
- Lateral Delay (LD) – the time it takes for facilitatory signals from the flankers to reach the target site, which depends on target-to-flanker separation.
- Target delay (TD) – the extra time it takes for target signals to reach V1 compared to flanker signals, which depends on the relative contrast between target and flankers ($CDOL_F$ – $CDOL_T$ (Figure 2)).

The results of Cass & Spehar (2005), and Huang & Hess (2008) provide an insight to the LD parameter. In a series of SM, 2IFC collinear facilitation experiments, Cass & Spehar (2005) showed that the minimum stimulus presentation time necessary for facilitation increases with distance between the target and flankers, suggesting that collinear facilitation is mediated by lateral connections. They demonstrated this effect over a range of separations and spatial frequencies and were able to estimate the velocity of cortical propagation at 0.10 - 0.23 m s^{-1}. A faster estimate was reported by Huang & Hess (2008). In a collinear facilitation experiment comparing peak facilitation at a number of different target-to-flanker separations, they estimated a mean propagation rate of 0.32 m s^{-1} for their subjects. A somewhat faster velocity of 0.57 m s^{-1} has been reported for propagating waves in the primary visual cortex of awake monkeys (Muller et al. 2014). We use an intermediate figure of 0.3 m s^{-1} for the lateral propagation rate to calculate LD. In the current study, the visual angle of separation between the target and flanking Gabors is 0.5^{o}, equating to a horizontal separation in V1 of approximately 8.5 mm [*log*(0.5 + 1.05)*19.3] (Schira et al. 2010). With a lateral propagation rate of 0.3 ms^{-1} it would take approximately 28 ms for signals to travel from the flanker to the target site. We therefore initially estimated LD to be 30 ms.

In a study that provides an insight into the TD parameter in humans, Cass & Alais (2006) used a novel collinear facilitation design with which they were able to estimate a value for CDOL. They used Gabor flankers that rotated about their own axis and a flashing target Gabor to introduce temporal lag. Unexpectedly, they found facilitation when the target flash occurred *before* the rotating flankers aligned collinearly with the target, and they raise the possibility that target onset latency may thus result in target and flanker synchronisation that induces feedback facilitation. They estimate the onset latency to be 20-80 ms, a range that is consistent with delays of around 40 ms, measured intracellularly, for primates viewing low contrast stimuli (Gawne et al. 1996; Reich et al. 2001). For modelling purposes, we therefore initially estimated TD to be 40 ms.

We modelled 25 delay combinations ranging from lateral propagation rates of 0.16-0.40 ms^{-1} (lateral delays of 10, 20, 30, 40 and 50 ms) and TDs of 20, 30, 40, 50 and 60 ms. Based on these

values, the best fitting gamma PDFs for many of the TD and LD combinations produced poor fits to the data, or were not consistent with previous neurophysiology i.e. fast-onset curves for lateral facilitation or slow-onset curves for feedback facilitation (see Figure 7 for examples of these curves). We centred our main analysis on LD and TD values of 30 and 50 ms respectively because this combination produced plausible parameter estimates that resulted in good facilitation estimates (Appendix). The fixed and free parameters used by the model are listed in Table 1.

Table 1 Fixed and free model parameters ($_{LAT}$ = lateral facilitation, $_{FBK}$ = feedback facilitation). This table shows fixed parameters for one of the twenty-five LD and TD combinations.

Symbol	Description	Unit	Quantity	Type	Reference
SOA	Stimulus onset asynchrony	ms	-70, -35, 0, 35, 70	Fixed	
SD	Stimulus duration	ms	35	Fixed	
LD	Lateral delay	ms	30	Fixed	Huang & Hess (2008)
TD	Target delay (Figure 2)	ms	50	Fixed	Polat, Sterkin & Yehezkel (2007)
SA_{LAT}	Signal asynchrony (Eq. 1)	ms	-50, -15, 20, 55, 90	Fixed	
SA_{FBK}	Signal asynchrony (Eq. 2)	ms	-20, 15, 50, 85, 120	Fixed	
k_{LAT}	Gamma shape parameter		estimated	Free	
Θ_{LAT}	Gamma scale parameter		estimated	Free	
S_{LAT}	Scaling parameter		estimated	Free (≥ 0)	
k_{FBK}	Gamma shape parameter		estimated	Free	
Θ_{FBK}	Gamma scale parameter		estimated	Free	
S_{FBK}	Scaling parameter		estimated	Free (≥ 0)	

4.1 Model details and estimates

We assume that collinear facilitation depends on the temporal overlap of neural signals in V1 for lateral facilitation and V2 (or extra-striate areas) for feedback facilitation. We further assume that the time course of both lateral and feedback facilitation can be modelled using a gamma probability distribution (eq. 3) and that the facilitation over a given time period is proportional to the integral under the distribution over that time period (the accumulation of excitatory impulses). Since probability distributions are constrained to integrate to one, the facilitation *f* is obtained by scaling the gamma distribution by parameter *s*. Because the model makes the assumption that LAT and FBK excitation is facilitatory (not suppressive), *s* is constrained to be non-negative.

$$f(t; k, \theta, s) = s\, p(t; k, \theta) \qquad (3)$$

where

$$p(t;k,\theta) = \frac{t^{k-1}e^{-\frac{t}{\theta}}}{\theta^k \Gamma(k)}$$

is the gamma PDF defined by shape (k) and scale (θ) parameters with $\Gamma(k)$ being the gamma function evaluated at k.

The range over which to integrate the facilitation is determined as the temporal overlap between the signals arriving at the target site due to the target and flanker stimuli. We refer to this overlap as the Signal Asynchrony (SA). SA depends upon the fixed parameters outlined in the previous section (SOA, TD and LD) and the flow of signals illustrated in Figure 2.

$$SA_{LAT} = SOA + TD - LD \quad (1)$$

$$SA_{FBK} = SOA + TD \quad (2)$$

Equations 1 and 2 are used to calculate the relative time difference between target and flanker signals arriving at the site of lateral integration (Figure 2A) and feedback facilitation (Figure 2B).

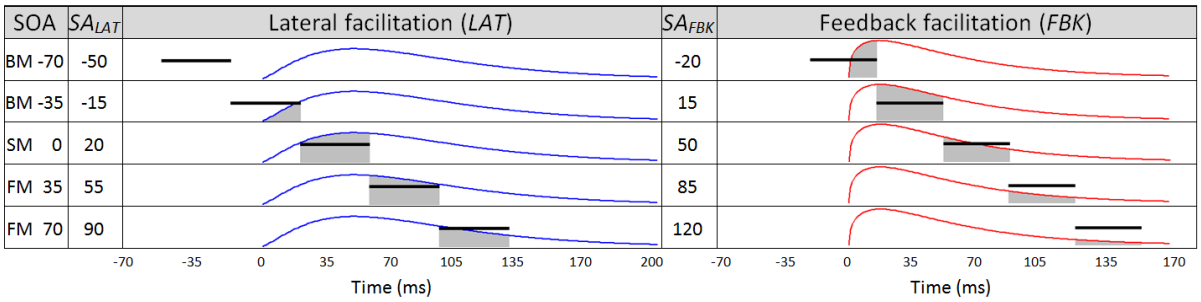

Figure 7 An illustration of signal asynchronies (*SA*s) calculated for each SOA using LD = 30 ms and TD = 50 ms (the best fitting gamma parameters, Appendix C14). The shaded areas under the curves represent the integration of target driven and flanker induced excitation. The blue line is the scaled gamma curve for lateral facilitation, representing the approximate modulatory effect of lateral facilitation. The red line represents the approximate effect of feedback facilitation. The black bars represent the time that the target signals drive the integration site (*SD* = 35 ms). It can be seen that, at an SOA of -70 for feedback facilitation which has an SA of -20 (Eq. 2), integration will occur for 15 ms of overlap (*SA* + *SD* = -20 + 35 = 15 ms).

Given the overlap region (SA) we then define the lateral (*LAT*) and feedback (*FBK*) facilitation over the stimulus duration period (Figure 7) as:

$$LAT = \int_{SA_{LAT}}^{SA_{LAT}+SD} f(x; k_{LAT,}\, \theta_{LAT,}\, S_{LAT})dx \qquad (4)$$

$$FBK = \int_{SA_{FBK}}^{SA_{FBK}+SD} f(x; k_{FBK,}\, \theta_{FBK,}\, S_{FBK})dx \qquad (5)$$

Finally, we calculate the total facilitation as the sum of the LAT and FBK components

$$F = LAT + FBK \qquad (6)$$

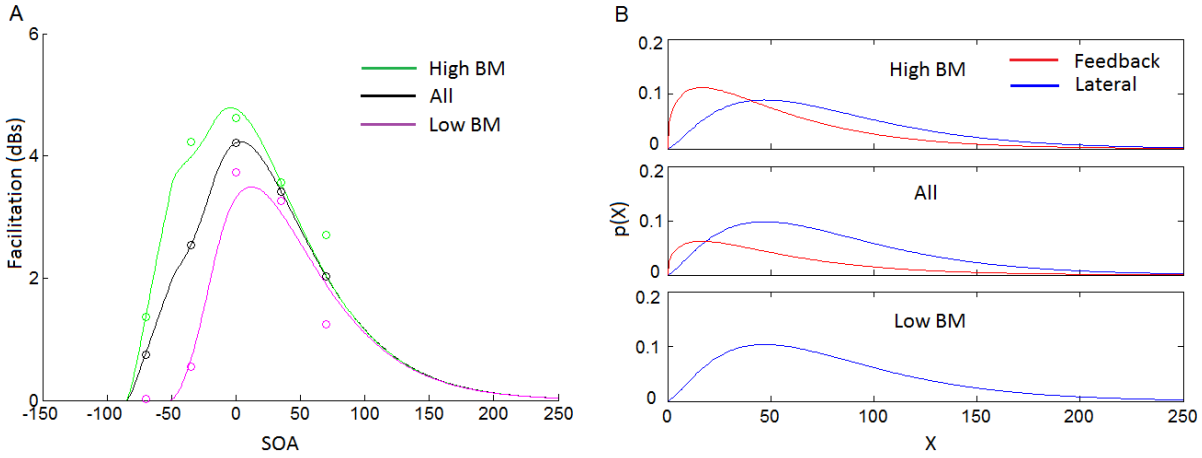

Figure 8 The results of model fitting with LD = 30 ms and TD = 50 ms. (A) Model predictions (lines) and mean participant data (circles) for all, low-BM and high-BM participants. (B) Gamma PDF curves estimated by the fitting process for the different groups. The blue curves shows the modulatory curve estimated for lateral facilitation, scaled by S_{LAT} , and the red curves shows the faster-onset curve estimated for feedback facilitation scaled by S_{FBK}. (scaling from Table 2).

To summarise, for a given set of six fixed parameters (SOA, SD, LD, TD, SA_{LAT}, SA_{FBK}) obtained from previous research and the conditions of our experiment, and six free parameters (k_{LAT}, Θ_{LAT}, S_{LAT}, k_{FBK}, Θ_{FBK}, S_{FBK}), the model estimates overall facilitation. Using the Matlab (Mathworks, Inc.) fminsearch routine we found the free parameters which minimised the least squares error between our model prediction and the observed facilitation data (Figure 4 and Figure 5). The six free parameters were fit to 130 data points (5 SOAs x 26 participants) and the results of the fitting process are shown in Figure 8A (solid black line) and 8B (middle panel) for LD = 30ms and TD = 50 ms. The corresponding best fitting parameter estimates for all participants are shown in the first line of Table 2. Note that best fitting parameters of the model have produced gamma curves which

appear to be consistent with previous neurophysiology, i.e. LAT facilitation is relatively slower and sustained whereas the FBK facilitation has a more rapid onset.

Table 2 Estimates for the free parameters described in Table 1. The parameters shown in light-gray were fixed in order to generate the S_{LAT} *and* S_{FBK} values for the high and low-BM groups.

Group	k_{LAT}	Θ_{LAT}	S_{LAT}	k_{FBK}	Θ_{FBK}	S_{FBK}
All	2.42	33.12	10.28	1.44	37.64	4.61
High-BM	2.42	33.12	9.34	1.44	37.64	8.29
Low-BM	2.42	33.12	10.80	1.44	37.64	0.00

Given that we found evidence for two different groups with low and high-BM performance we sought to fit these two groups separately. To do this we assumed that the gamma shape and scale parameters recovered in the first analysis reflect the underlying modulatory and driving rates of decay for all participants. Consequently, we fixed these parameters and reduced the number of free parameters in the model from six to two. We then refit to the sub-groups identified by the bimodality test (Figure 4C). The facilitation scaling factors then reflect the contribution that lateral and feedback facilitation make to overall facilitation. The results are shown in Figure 8A (magenta and green lines) and 8B (top and bottom panels). Best fitting parameters are presented in Table 2 (rows 2 and 3). It can be seen that S_{LAT} remains relatively unchanged, indicating lateral facilitation is consistent for the low and high-BM groups. However, the best fitting S_{FBK} clearly differs between groups and is in fact completely absent for the low-BM group. Facilitation estimates returned by the model for all group subdivisions are shown in Table 3.

5 Discussion

This study was partially motivated by what appeared to be conflicting findings in previous studies, reporting that collinear facilitation was either present (Huang & Hess 2008) or absent (Polat et al. 2007) during backward masking. In an attempt to resolve this issue we used Gabor targets and flankers with similar spatial characteristics as those used by Polat et al. (2007), but with shorter SOAs, predicting that the long SOAs used by Polat et al. prevented target and flanker sites to be activated simultaneously. As expected and in keeping with previous results (Tanaka & Sagi 1998; Polat & Sagi 2006; Polat et al. 2007; Li et al. 2010), we found significant collinear facilitation with SM and FM. However, unlike Polat et al. (2007) who found no facilitation when BM was employed, we found significant facilitation at an SOA of -35 ms. Our results suggest that their SOA was too long (120 ms (ISI 60 ms)), and target activity had ceased before the overlap between target and flanker excitation necessary for feedback facilitation could take place. This idea is supported by the results

of our study and the study of Huang & Hess (2008), who did find facilitation with BM using *shorter* SOAs. Huang & Hess (2008) suggest that facilitation when the target is presented before the flankers (BM), rules out an explanation that is solely reliant on horizontal connections, and we agree, incorporating feedback connections too in our model.

Although we have suggested two different sources of facilitation, it is possible that lateral facilitation alone could account for the BM facilitation found. In a recent comprehensive paper exploring the relationship between lateral masking and crowding, Lev & Polat (2015) suggest that participants with lower "contrast thresholds" (i.e. higher facilitation) may have longer integration times as a result of reduced levels of inhibition. In accordance with this, there is evidence to suggest that increased stimulus contrast leads to greater levels of inhibition (Polat et al. 1998). It is possible therefore that what we propose as being due to individual differences in the amount of feedback facilitation actually reflects variability in integration time, based on participant contrast thresholds. Alternatively, individual differences in contrast threshold could lead to differences in the time for which significant levels of inhibition are present (i.e. variability in inhibition decay times), which might also affect the likelihood of observing facilitation in our BM conditions. Irrespective, if contrast thresholds were at the root of the observed differences in our experiment, we might expect participants with lower baseline contrast thresholds to show higher facilitation, due to there simply being lower levels of inhibition present for low contrast targets. However, a comparison of the baseline contrast thresholds (Michelson contrast) between the Hi (M=0.153, SD=0.055) and Lo (M=0.178, SD=0.042) groups revealed no such significant difference ($t(24)=1.314$, $p=.201$). Nonetheless, we cannot rule out the possibility that facilitation with BM is the result of a single lateral facilitation process, based on individual differences in the amount of inhibition present or the time course of that inhibition. While our model provides a parsimonious account of the data, it does not currently include inhibition and so it is difficult to make predictions about its effects. With this in mind, in future modelling we aim to incorporate both inhibitory and excitatory effects (rather than just 'net' excitation).

One surprising finding was the two-group split revealing that approximately half of the participants did not show collinear facilitation with backward masking. This finding raises the possibility that a further reason for lack of collinear facilitation during backward masking in previous studies may be that they have investigated a predominantly low-BM facilitating group of participants. The group difference can be parsimoniously explained by the absence or presence of feedback facilitation (Figure 8B). It would be interesting to determine the stability of this characteristic before commenting on its origin. However, based on the performance of two researchers who helped to test the experimental design, facilitation with BM seemed consistent

across sessions spanning several days suggesting that this may be a stable characteristic of participants. In the following paragraphs, we speculate tentatively on possible factors that could underpin the differences in behaviour observed in our study.

As noted above, one possibility is that the two groups have differences in the balance between excitation and inhibition across implicated visual areas. For example, the Hi-BM group might have relatively more excitatory activity in V2 for example, than the Lo-BM group, leading to greater levels of facilitatory feedback to V1. Of relevance here is recent work by Greenhouse et al. (2016) suggesting that there are reliable individual differences in GABA concentration between cortical areas. Furthermore, there is evidence that individual differences in GABA in early visual areas can predict performance in a psychophysical task (Edden et al. 2009). Consequently, it may be that the observed differences in our data reflect regional variation in GABA concentration between groups; More specifically, the hi-BM group may have lower levels of GABA in V2 or higher cortical areas.

In a second possibility, the observed differences may reflect variability between participants in the prevalence of top-down signals more generally, with for example, greater top down influence in the hi-BM group. It has been suggested that collinear facilitation plays a role in higher-level contour integration (see Loffler (2008) for a review). When target and flankers are presented simultaneously (SM), top down signals based on the expectation that there is a single object present might drive facilitation to enhance the target and integrate the Gabor elements to make a coherent line (Blake & Lee 2005). In this case robust levels of facilitation were seen by both groups. However, if the target is presented before the flankers (BM), it is less likely that the elements arise from the same object and the top-down facilitation might therefore be significantly weaker or absent; the extent of this effect might vary between our groups.

A third possibility is that observed differences relate to variability in critical time parameters across individuals. For example, participants without BM might require longer stimulus duration to engage feedback facilitation mechanisms. It certainly appears that collinear facilitation (SM) is dependent on stimulus duration. At 3λ, Lev & Polat (2015) found no facilitation with a 30 ms stimulus duration. Cass & Spehar (2005) found little facilitation at 20 ms, but robust facilitation with a 40 ms stimulus duration. In this study, we found robust facilitation with a 35 ms stimulus duration. It is possible therefore that feedback facilitation also has a lower stimulus duration limit and that the bimodal split simply reflects a critical stimulus duration threshold at which not all participants have yet had time to initiate feedback facilitation.

We also present a model which attributes facilitation to two sources, lateral and feedback excitation, and successfully described the responses of our participants. One of the strengths of this

model is its simplicity, using fixed parameters with experimentally determined dimensions. However, a weakness is its reliance on a relatively high number of free parameters for the initial determination of the gamma curves that represent the dynamics of excitation. The fits are also based on a limited number of target and flanker SOAs. We suggest that the model can be tested more thoroughly by increasing the number of SOAs for the forward and backward masking conditions and by using shorter stimulus presentation times. More SOA conditions would increase the number of data-points for model fitting, and adjusting the presentation time may help to further segregate the different types of facilitation, by reducing the potential for temporal overlap.

The present model is constrained such that the scaling factors (S_{LAT}, S_{FBK}) are non-negative. This constraint was imposed in the interests of model simplicity and the assumption that suppression is minimal at separations of 3λ. However, in future work it should be possible to extend the model to explore suppression effects at shorter target-flanker separations, (e.g. 2λ).To do this we could reduce the value of LD in Eq. 1 to account for shorter target to flanker signal delay, and allow the scaling factors to be unconstrained, so that they may go negative and thus incorporate suppression.

As has been seen, this modelling technique has the potential for revealing the transmission velocities employed in lateral facilitation, by estimating facilitation using different combinations of lateral and target delays (Appendix), although this depends to some extent on how accurately the gamma PDFs reflect the dynamics of modulatory and excitatory onset and decay. There is some evidence that the spiking activity of V1 cells in monkeys can exhibit a broadly gamma shaped onset and decay (Reich et al. 2001; Kim et al. 2012). In modelling collinear facilitation as a dual component function we have shown that feedback facilitation may have a rapid onset, and that lateral modulation is likely to be more persistent, enduring after the flanker signals have ceased.

5.1 Summary

In summary, we have shown that facilitation can occur with BM at shorter SOAs, but crucially, not for all participants. Using our estimates, significant facilitation with BM is likely to be a feedback phenomenon, with lateral facilitation making no contribution at -70 ms and a low contribution at -35 ms (Table 3).

Table 3 Facilitation estimates returned by the model (in dBs), for the contribution (%ages) that lateral and feedback facilitation make at each SOA for all participants and both subgroups (LD = 30 ms, TD = 50 ms).

		SOA									
Group	Facilitation	BM (-70 ms)		BM (-35 ms)		SM (0 ms)		FM (35 ms)		FM (70 ms)	
All	Lateral	0.00	0%	0.65	26%	3.16	75%	2.92	85%	1.81	89%
High-BM	Lateral	0.00	0%	0.59	15%	2.87	60%	2.65	74%	1.64	80%
Low-BM	Lateral	0.00	0%	0.69	100%	3.32	100%	3.06	100%	1.90	100%
All	Feedback	0.74	100%	1.88	74%	1.06	25%	0.51	15%	0.23	11%
High-BM	Feedback	1.34	100%	3.39	85%	1.90	40%	0.91	26%	0.41	20%
Low-BM	Feedback	0.00	0%	0.00	0%	0.00	0%	0.00	0%	0.00	0%

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Appendix: Modelling facilitation with a range of different target and lateral delay rates

The following page has two groups of plots; Figure A1, a set of gamma curve estimates, and Figure A2, a set of modelling estimates.

The Figure A1 plots show the gamma PDFs estimated by the model for lateral (blue) and feedback (red) facilitation at a variety of lateral delay (LD) and target contrast dependent onset latency delay (TD) combinations (C1 thru C25).

The Figure A2 plots show model predictions using the gamma PDFs from above (C1 thru C25). The Y-axis shows facilitation in dBs, the X-axis shows SOA in ms. The lines show estimated facilitation, the circles show experimental data (participants: green = high-BM participants, magenta = low-BM participants, black = all participants). An estimate of the goodness of fit is indicated by the SSE, which is the sum of the sum of the squared errors of prediction (SSE) for each curve, divided by the number of participants.

The central combination (C13 both Figures) show estimates for our initial guesses at LD (30 ms) and TD (40 ms). We expect realistic delay combinations to produce (i) gentle onset and sustained (modulatory) lateral PDFs (blue) (ii) fast onset (excitatory) feedback PDFs (red) (iii) have a low SSE and (iv) not appear to be over-fitted, as in combination C14.

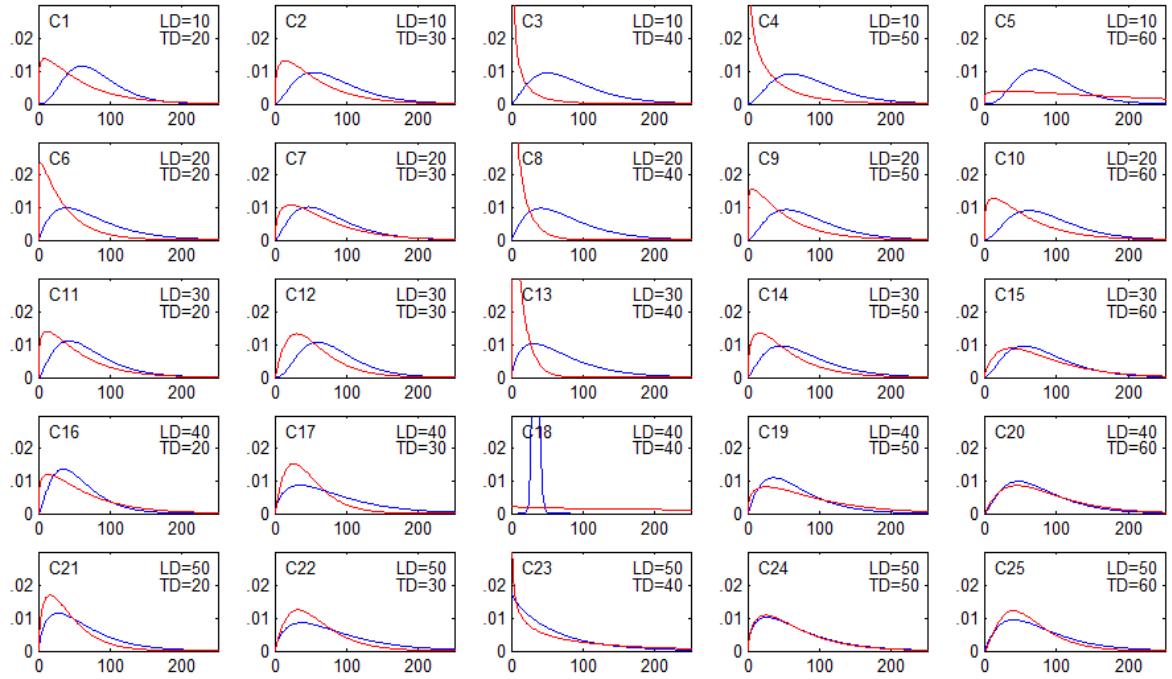

Figure A1. Estimated gamma PDFS returned by the model for lateral (blue) and feedback (red) facilitation for 25 lateral delay (LD) and target delay (TD) combinations. Y-axes show probability as a function of X.

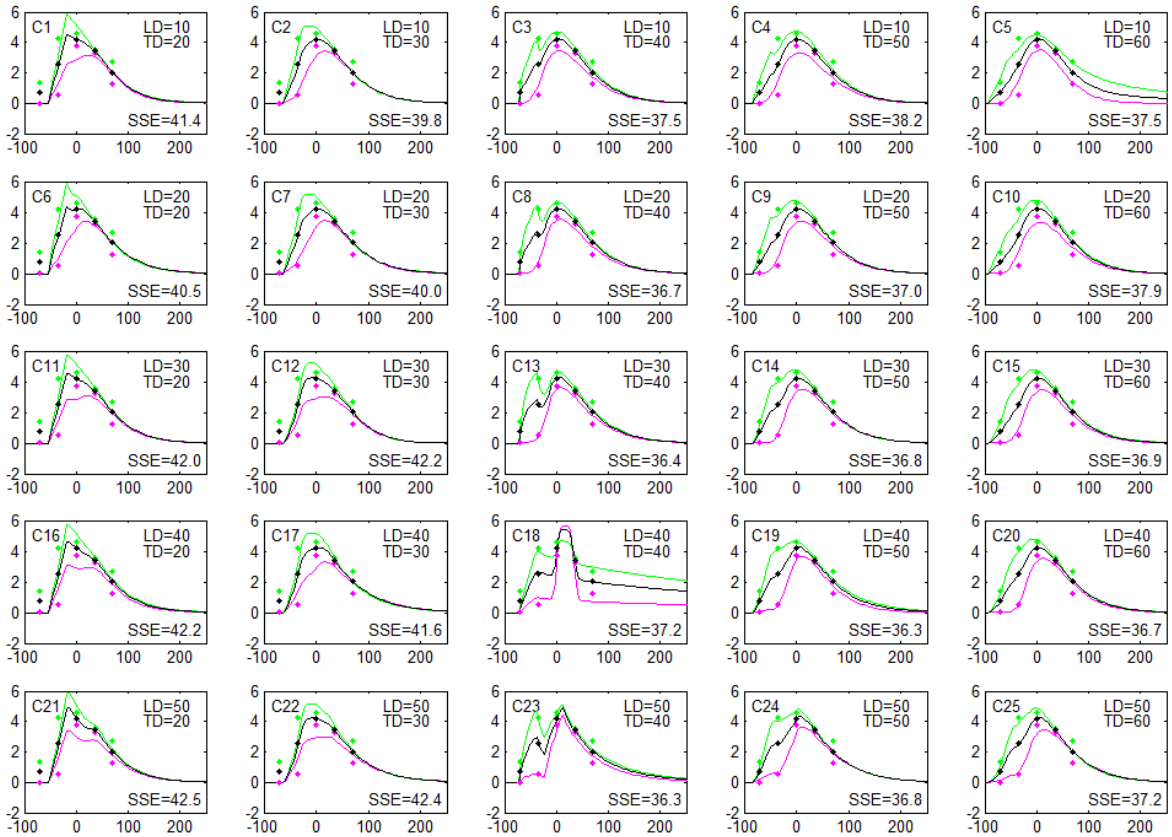

Figure A2. Estimated facilitation based on lateral and feedback PDFs above. Dots represent mean (N = 26) participant data (green = high-BM participants, magenta = low-BM participants, black = all participants).