

THEORETICAL NOTE

A Comparison of Two Lateral Inhibitory Models of Metacontrast

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Metacontrast, an apparent reduction in brightness of a target that is followed by a non-overlapping mask, has been modeled with simulated neural nets incorporating either recurrent lateral inhibition or forward and backward inhibition with lateral components. A one-layer lateral inhibitory model (B. Bridgeman, 1971, *Psychological Review* 78, 528–539) and a six-layer model (G. Francis, 1997, *Psychological Review* 104, 572–594) both simulate the basic metacontrast effect, showing that stimulus-dependent activity that reverberates for some time in the model after stimulus offset is essential to simulate metacontrast. The six-layer model does not simulate monotonic masking with low response criterion, an essential property of metacontrast; the lateral inhibitory model uses duration of reverberation to simulate the criterion. Each model simulates several variations of masking, such as changing the relative energy of target and mask, but neither can handle effects of practice or attention that apparently engage higher processing levels. © 2001 Academic Press

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Metacontrast is of special interest because it seems to work backward in time. A target and mask, such as a disk and a surrounding ring, are both seen clearly if they are flashed simultaneously: the subject simply sees a bull's-eye-like pattern. But if the target begins about 60–90 msec before the mask, the target's apparent brightness decreases. Under optimal conditions the target region has the same apparent brightness as the background and may not be visible at all. The stimulus onset asynchrony (SOA) of the optimal effect is much longer than the latency of arrival of stimulus-locked signals at the primary visual cortex; the first stimulus-driven activity in cortical neurons begins about 30 msec after stimulus onset (Spinelli, Pribam, & Bridgeman, 1970), yet that stimulus can be driven to near-invisibility by an event that will not reach the retina until 30–60 msec later. Metacontrast

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shows that the early stages of neural coding are vulnerable, subject to destruction by subsequent activity if that activity is appropriately structured. Thus metacontrast offers a tool to investigate the temporal aspects of visual coding.

A critical property of metacontrast is that the target does not completely disappear. Rather, its presence remains detectable even as its apparent brightness drops to zero. In a high-criterion task, such as a brightness judgment, the masking function is U-shaped, with a minimum of visibility at a positive SOA. But in a low-criterion task such as forced-choice detection of the target presence, masking is weaker and becomes monotonic (defined in terms of the appearance of the positive-SOA side of the masking curve), peaking at an SOA of 0 (Kahneman, 1968). Further, the latency of responding to a masked target does not change even as its apparent brightness decreases (Fehrer & Raab, 1962; Fehrer & Biederman, 1962). These properties of metacontrast are difficult to explain with simple activation models of stimulus coding. They motivated a generation of more complex proposals (Weisstein, 1968; Bridgeman, 1971; Breitmeyer & Ganz, 1976), all of which dealt with the criterion issue in different ways.

These two properties of metacontrast (vulnerability long after the stimulus has been presented and sensitivity to response criterion) present a challenge to modelers. But as a result of modeling these surprising and nonintuitive psychophysical effects, models of metacontrast promise to teach us more about visual coding than models of more commonplace psychophysical phenomena.

Two mathematical models of metacontrast explicitly invoke lateral inhibition (Bridgeman, 1971; Francis, 1997). Both simulate the basic phenomena of metacontrast, optimal masking at a SOA of about 60 msec, but little or no masking at an SOA of 0. Each model also simulates several other properties of metacontrast, such as more nearly monotonic masking with decreased target luminance, but fails or was not tested on others, such as practice and context effects. Both models are homeomorphic, each component of the model corresponding to a definable component of the underlying physiology, and are parsimonious in that the basic model architecture was developed for more general purposes than modeling masking. Their capability of modeling metacontrast is based on lateral spread of information among simulated neurons and reverberation of activity in the network after stimulus offset. Backward masking can be simulated because signals in the modeled networks resonate after the physical stimulus has disappeared.

A comparison of the properties, design, strengths, and weaknesses of the two models is informative about what makes them work, which features are essential, and what remains to be done. The principal result of the current analysis is that U-shaped masking is a general property of networks with the properties described below, and several variations of the metacontrast paradigm are also general. The shift to monotonic masking with a change in criterion, a property that has motivated many attempts at modeling metacontrast, is more difficult and less frequently modeled and is dependent on the linking hypothesis.

DESIGNS OF THE TWO MODELS

The Francis (1997) simulation is based on models developed to account for various properties of visual pattern recognition (Grossberg & Mignolla, 1985). The

metacontrast model is an application of a boundary contour system used to model cortical dynamics of boundary segmentation (Francis & Grossberg, 1996a) and of motion and motion illusions (Francis & Grossberg, 1996b). The model has a six-layered architecture with varying neural receptive fields. The Bridgeman (1971) model also modifies a simulation originally written for another purpose, in this case to simulate recurrent lateral inhibition in the lateral eye of the horseshoe crab *Limulus* (Ratliff, Hartline, & Lange, 1966).

Ironically, the six-layer model uses no lateral inhibition, defined as the inhibition of neurons by other neurons in the same processing layer (Ratliff, 1965). (A layer in this definition is a two-dimensional array of identically connected cells, not the far more complex anatomical “layer” of the cortex.) The model includes both forward inhibition, targeting neurons in a subsequent layer, and backward inhibition, targeting neurons in a previous layer. These connections have lateral components, so that information can move laterally as it migrates through the network. Specifically, neurons in Francis’s level 5 project excitatory and inhibitory connections to neurons with large receptive fields in level 6 (Francis, 1997, Fig. 1: layer 6 is at the top). These neurons in turn excite some of the neurons from which the excitation came, as well as inhibiting other neurons in layer 5. Modeled rise times inject a delay into this inhibition. Thus a functional indirect lateral inhibition can be identified in the net. Target and mask representations can interact through inhibition and excitation.

It is logically necessary that effects in models simulating metacontrast must spread laterally. Otherwise, target and mask representations would never interact, because the two stimuli do not overlap spatially in the world. Similarly, representations must spread in time, so that neural representations can interact even though the stimuli that elicit them do not overlap in time. This was already noted by Martin (1975). In the six-layer model, the spread results both from the bottom-up spread of forward inhibition and from inhibitory feedback originating in the very large receptive fields of layer 6.

The Bridgeman model is structurally simpler, invoking lateral inhibition among identical simulated cells in a single layer. Each neuron is excited by external input and is inhibited by the earlier activities of six nearby neurons, each multiplied by an inhibitory coefficient $0 < k < 1$. The original model used a linear interaction among its elements. After a critique by Weisstein, Ozog, and Szoc (1975) and resimulation, a second-generation model (Bridgeman, 1977, 1978) added a non-linear lower bound to neural responses and Gaussian noise after each iteration of inhibition to simulate neural noise. The “lateral inhibitory model” below refers to the 1978 simulations.

A new analysis by Francis (2000) uses a differential equation as a general framework for analyzing several models; the source of spatial interaction is the fact that both target and mask have terms in the equation. The analysis shows that all published models use a phenomenon called mask-blocking to obtain U-shaped masking. The target blocks the mask’s inhibitory effects at $SOA = 0$.

Relating the output of a small nerve network to the perceptual appearance of a target requires a “linking hypothesis” (Weisstein, 1968), a relationship between a model’s output and psychophysically measured apparent brightness, detectability,

or location. The linking hypothesis in the six-layer model is the duration of activity after stimulus offset in a layer-6 neuron. Short durations correspond to low apparent brightness or poor visibility. In the simulation of metacontrast, a psychophysical reduction of an order of magnitude in apparent brightness is modeled as an 11% reduction in boundary duration, from 135 to 120 msec. The model thus depends on a questionable linking hypothesis, that a response with a 135-msec boundary duration will be recognized while one with a 120-msec boundary duration will not. With a more linear linking hypothesis, the model yields much weaker masking. Presumably an unmodeled later stage of the visual system examines these durations and considers after-activity of 120 msec or less to represent an absence of a stimulus or a severe reduction of its visibility. There is no physiological evidence that an after-discharge of anything like this duration is necessary to pass information to another layer.

The lateral inhibitory model, in contrast, uses a distributed code to represent a stimulus presence in the simulated network, anticipating the later development of parallel distributed processing models. At each iteration of inhibition, two modeling runs of the entire network's activity are correlated, one from the target only and one from the target-mask combination. Low correlation of the two is taken as evidence that the target would not be seen. The similarity measure is average squared correlation across iterations, representing the proportion of variance in network activity attributable to the target at each time iteration. Squared correlations range from 0.2 at the peak of masking (60 simulated msec SOA) to 0.85 when the mask appears 240 msec after the target. Correlations of a mask-only run with the target-mask run remain high throughout the simulation, and this occurs for every SOA, reflecting continuous visibility of the mask.

The current manuscript complements Francis' findings by exploring the physical characteristics of two of these models and identifying commonalities and differences at a more specific level.

SIMULATING METACONTRAST—COMMONALITIES

Both models do a good job of modeling the basic U-shaped backward masking function of metacontrast, if their linking hypotheses are accepted (Fig. 1): Their masking curves fall within the range of psychophysically measured curves. The conclusion for modeling, and for stimulus coding in general, is that metacontrast masking is a very general property of lateral inhibitory networks. Details of connectivity, number of layers, etc., are not critical as long as inhibition has a lateral component and occurs with a time delay. Francis (1997, p. 575) models metacontrast in interactions between excitatory feedback and lateral inhibition; the similarity of performance of the six-layer model with the lateral inhibitory model implies that it is the lateral interactions, not the excitatory feedback, that are responsible for the metacontrast-like effects, since the lateral inhibitory model lacks excitatory feedback but simulates metacontrast. Lateral inhibition does not merely damp activity in a nerve net so much as it reorganizes the activity.

Both Bridgeman (1978) and Francis (1997) simulate nine properties of metacontrast under varying stimulus conditions. But each simulates a different list of

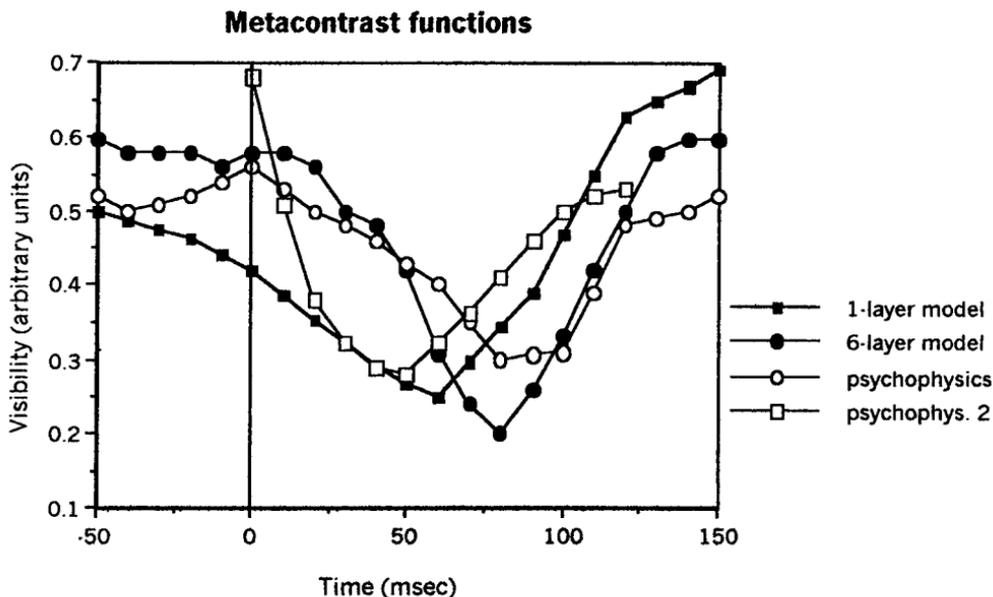


FIG. 1. Metacontrast masking functions for the one-layer lateral inhibitory model of Bridgeman (1978), the six-layer model of Francis (1997, subsampled from Fig. 5), and two empirical studies. Filled symbols display simulated results; open symbols display empirical psychophysical results. Values for the one-layer simulation were calculated from the model at 30-msec steps, and intermediate values were interpolated. The curve labeled “psychophysics” (round symbols) is from Growney *et al.* (1977); “psychophys. 2” (square symbols) is from Bridgeman and Leff (1979) for 5 subjects and a disc-ring configuration of 0.38 deg outside diameter presented on the fovea. The latter data are fitted here to a third-order polynomial and intermediate values are interpolated (this fit was not included in the source paper). The two empirical masking curves give an impression of the variability of masking curves in the literature. The arbitrary units on the vertical axis are squared correlations from the lateral inhibitory model; amplitudes of the other curves are adjusted to approximately match the amplitude of masking in that model. Both models reproduce the empirical curves fairly well, although neither model attempts to simulate every detail of the metacontrast masking functions.

properties, so that only five variations are common to both lists. Empirical masking data for each of the variations are reviewed in the earlier papers. Simulations of the lateral inhibitory model are numbered in Bridgeman (1978, pp. 615–620). Numbered properties of the six-layer model are indexed in Francis (1997, p. 573).

A property beyond U-shaped backward masking that both models simulate is a shift of the peak of masking toward shorter SOAs as mask luminance increases (Simulation 6; Property 2). This nontrivial result occurs because the target’s metaphotic activity (a term defined by Stigler, 1910, to indicate information that persists in the nervous system after stimulus offset) is quickly overwhelmed by the stronger mask activity.

Metacontrast decreases sharply as the distance between target and mask increases (Growney, Weisstein, & Cox, 1977), a property already noted in the paper where the name metacontrast was coined (Stigler, 1910). Both models also handle this variant, because the metaphotic codes interact less strongly when they are more separated in a topographic representation (Bridgeman, 1978, Simulation 3; Francis, 1997, Property 4). These variants, then, seem intrinsic to models incorporating long-duration metaphotic activity and lateral spread of

information in their networks, regardless of the details of connectivity or linking hypothesis.

Two other properties, simulated only for the six-layer model, are easily predicted results of the lateral inhibitory model as well. Increasing target duration leads to better detection of the target (Property 3), while increasing mask duration increases the strength of masking (Property 5). In the lateral inhibitory model, increasing target duration exposes the simulation to the target for more iterations of lateral inhibition, increasing correlations of the masking runs with the target-only runs. Increasing the mask duration adds power to the mask representation, reducing the target's contribution to the composite activity and thus increasing the masking.

In another theoretically informative variant, Bischof and DiLollo (1995) let their target and mask begin simultaneously and varied the offset asynchrony. The psychophysical result is backward masking functions in which the target's visibility never rises with longer offset asynchronies. Using this design, Bischof and DiLollo found evidence that it is the offsets of target and mask, not the onsets or the ISIs, that are critical to determining the visibility of the target. Previous studies had confounded onset and offset asynchronies. Bischof and DiLollo (1995) simulated their result with the lateral inhibitory model; the simulation results closely followed the empirical psychophysical function. The six-layer model also qualitatively simulates this result (Francis, 1997, Fig. 9B).

MONOTONIC MASKING AND CRITERION SHIFTS

It is in modeling other conditions that the performances of the two models diverge. The shift to monotonic masking with decrease in response criterion, discussed above, is an example. Bridgeman (1971) used integration time to simulate a criterion; to reach a high criterion or to do a difficult task such as brightness estimation requires a long period of correlation, while a less difficult task such as simple detection requires a shorter period of correlation, only three iterations in the model. Using the duration of correlation to simulate the criterion, the lateral inhibitory model yields peaks of masking at 60 msec for a high-criterion task and 0 msec for a low-criterion task. The use of duration to simulate a response criterion has recently gained empirical support from Lachter and Durgin (1998), who find that speeded brightness judgments yield monotonic curves while more deliberate judgments yield U-shaped metacontrast, even when both the stimuli and the task remain identical. In the simulation, speeded judgments would have access only to codes with shorter periods of correlation.

Francis does not model this property of metacontrast. Simulating it would require elaboration of the linking hypothesis. Breitmeyer and Ganz (1976; Breitmeyer, 1984) relate the shift of masking peak with criterion to activities of sustained vs transient cells, where sustained-cell activity is assumed to be needed for high-criterion tasks. The publications describe an idea for a model, but the idea has never been instantiated in a mathematical model or a simulation. Francis (1997) also notes that the sustained-transient theory has not been developed in sufficient detail to allow quantitative comparisons with mathematically defined models. We

do not know whether all of the capabilities that Breitmeyer and Ganz describe for their proposed model will appear with a single consistent set of parameters.

VARIATIONS ON METACONTRAST—CONTRASTS

Another condition simulated in both models is an increase in the duration of both target and mask without changing the energy of one relative to the other. Psychophysically, this results in very little change in the shape of masking functions, a result reproduced in Simulation 5 of the lateral inhibition model. The six-layer model follows an ISI law, especially on the trailing flank of the masking function, and masking always ceases 125 msec after target offset (Francis, 1997, Figs 15C, 15D). Another result, difficult to account for intuitively, is that the target reappears if target and mask are flashed in a regularly repeated sequence, even at the optimum SOA for metacontrast. The lateral inhibitory model simulates this condition with a 60-msec SOA (Simulation 7), because standing waves develop in the distributed network that correlate strongly with target-only activity. It is not clear how the six-layer model could simulate this case, as its output comes from neurons that would be continuously activated by both target and mask under these conditions. Boundaries would not have time to decay.

In a variation that only the six-layer model has simulated, stronger masking was found with more contour (Property 6), a variation that could not be simulated in the present one-dimensional instantiation of the lateral inhibitory model. The six-layer model has also been tested in three disinhibition paradigms (Properties 7, 8, and 9). The lateral inhibitory model has been tested only with a target > inner mask > outer mask sequence, with 60 msec between each stimulus (Simulation 8), resulting in no disinhibition. Bridgeman (1978) interpreted this as a failure to find disinhibition, based on data then available, but subsequent work (Breitmeyer, Rudd, & Dunn, 1981) found disinhibition to cease just at the range where the lateral inhibitory model was tested. Breitmeyer *et al.* (1981) also found a small reverse effect, 11% as great as the disinhibition, for a 90-msec inner mask > outer mask SOA. The six-layer model was tested at a variety of inner mask > outer mask SOAs and showed a reverse effect 75% as large as the disinhibition at 60-msec SOA, a range where the psychophysics showed no effect. Though neither model makes strong statements about the exact timing of events, this is a case where the one-layer model and the six-layer model make different predictions. The one-layer model has not been tested under conditions where Breitmeyer *et al.* (1981) found psychophysical disinhibition.

LIMITATIONS AND CONCLUSIONS

Each model can benefit from lessons learned from the other. The six-layer model could be simplified, with fewer layers, because it is now known that only a small part of that model is necessary to simulate metacontrast and related effects. At the same time, the linking hypothesis is so nonlinear that modeling it more explicitly might be informative. The lateral inhibitory model could benefit from more realistic

modeling of some of its components, especially the lateral inhibitory interneurons, which now are simply weighted delay lines.

Some conditions can be handled by neither model. These conditions represent challenges where another step must intervene between the early-vision level of the models and perception or where other unmodeled processes become important. One of these conditions is a change in the strength of metacontrast with practice (Ventura, 1980). It would be possible to “tweak” each of the inhibitory models post-hoc to simulate this property, but no principled physiological reason has yet been identified to justify such a procedure. One of the great strengths of both models is that both their parameters and their connectivities are within ranges specified by known physiology or at least represent the best estimates we have at present.

Another surprising property of metacontrast was discovered by Ramachandran and Cobb (1995): if the target is a member of a group of identical patterns, the group (and with it the single pattern that is surrounded by a mask) is nearly unaffected by masking. If the observer is encouraged to form another top-down gestalt grouping, however, in which the masked pattern is not a part of the group, masking is strong even though the physical layout and timing are exactly the same. Clearly, low-level bottom-up models such as the two compared here cannot deal with such top-down grouping phenomena; metacontrast still has a lot to teach us about perceptual coding.

Both models use a single parameter to indicate visibility of the target under masked or unmasked conditions. But visual objects differ in many dimensions—contrast, brightness, size, location, color, identity, etc. More complete mathematical models of visual perception will have to include many output parameters to map the many distinguishable features and meanings of real objects. Part of the job was done by Grossberg and his colleagues (Francis and Grossberg, 1996a, 1996b; Grossberg and Mignolla, 1985) for the six-layer model and by Ratliff *et al.* (1966) for the one-layer model, but the effort is far from complete.

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