

Seeing properties of an invisible object: Feature inheritance and shine-through

Michael H. Herzog^{*†‡} and Christof Koch^{*}

^{*}Computation and Neural Systems Program, California Institute of Technology, 139-74, Pasadena, CA 91125; and [†]Section of Human Neurobiology, University of Bremen, Argonnenstrasse 3, D28211 Bremen, Germany

Communicated by George Sperling, University of California Irvine, Irvine, CA, January 30, 2001 (received for review March 15, 2000)

We characterize a class of spatio-temporal illusions with two complementary properties. Firstly, if a vernier stimulus is flashed for a short time on a monitor and is followed immediately by a grating, the latter can express features of the vernier, such as its offset, its orientation, or its motion (feature inheritance). Yet the vernier stimulus itself remains perceptually invisible. Secondly, the vernier can be rendered visible by presenting gratings with a larger number of elements (shine-through). Under these conditions, subjects perceive two independent "objects" each carrying their own features. Transition between these two domains can be effected by subtle changes in the spatio-temporal layout of the grating. This should allow psychophysicists and electrophysiologists to investigate feature binding in a precise and quantitative manner.

The mammalian visual system is organized in terms of a multitude of visual areas that operate in parallel. This raises the problem of feature integration (1). If, for example, motion is represented in one cortical area and color in another, how is a colored moving object encoded? And how can one such object with one combination of properties be distinguished from another object with a different combination of features? Here we describe an illusion with two complementary effects that illuminates feature integration over small spatio-temporal dimensions.

In the basic "vernier" paradigm of our effect, the first stimulus is a pair of vertical bars, one of which is offset in the horizontal direction from the other by a small amount. For trained observers, the vernier is flashed at fixation for 20–50 ms on an analog monitor (Fig. 1*A*). It is followed immediately—at the same location—by a grating consisting of a number of vertical, aligned double-bars that are left on for 300 ms. Twenty-six of thirty subjects report that the grating is offset, with its offset direction given by the offset direction of the vernier that is perceptually invisible because of short display time.

In the "orientation" paradigm, the two vertical bars of the vernier are tilted either clock- or counterclockwise (Fig. 1*B*). Under these conditions, subjects report that the grating has a slant in the same direction as the preceding vernier.

In the "motion" paradigm, the vernier consists of a double-bar that is flashed for, say, 20 ms at five consecutive locations (for a total of 100 ms; Fig. 1*C*). Subjects perceive the grating to flash on, one bar at a time, in the direction determined by the invisible motion of the vernier elements, but to disappear simultaneously.

Both naive and trained psychophysical observers profess surprise when told about the vernier and report not having perceived anything different from real orientations, offsets, or motion. More than one feature of the vernier can be induced. For example, an aligned grating, having all elements displayed at the same time, is perceived as a moving grating comprising offset verniers—if single offset verniers moving in apparent motion were flashed before (that is, combining Fig. 1*A* and *C*). For the remainder of our study, we restrict ourselves to the vernier paradigm.

Methods

Vernier stimuli appeared on an analog monitor (Tektronix 608, Tektronix 606, or HP 1333 A), controlled by a Macintosh

computer via fast 16 bit D/A converters (1 MHz pixel rate). Vernier stimuli or oriented double-bars were 21' (arc min) long. Spacing between grating elements was 200–250'' (arc sec). Subjects observed the stimuli from a distance of 1.2 or 2 m in a room illuminated dimly by a background light. The luminance of the stimuli was around 80 cd/m².

All subjects had normal or corrected-to-normal acuity and ranged from being totally naive to the purpose of the experiment to subjects familiar with the entire set-up. We first determined the appropriate displacement size for each observer by measuring his or her threshold for a vertical vernier followed by a grating lasting for 300 ms by using the adaptive staircase procedure PEST (2).

In feature inheritance, vernier duration times of 90 ms and longer are often needed for naive subjects to reach a threshold of 75% correct responses if vernier offset sizes are around 140'' or if elements are tilted by 7°. However, interindividual differences are very large. For some observers, a strong and vivid percept occurs from the very beginning, whereas for others, even after extensive training, percepts as well as performance are weak. After a period of training comprising between 300 and 1,500 trials, most observers reach (asymptotic) values of 60–120'' for verniers and 2–4° for orientation at display times of verniers of 20–50 ms. Again, large differences in the time course of improvement are found between subjects.

In feature inheritance (that is, gratings with five and less elements), subjects were asked to indicate the induced direction of offset of the grating (perceived at one of the outer elements of the grating) by pressing either one of two push-buttons. If this response matched the true vernier offset direction, a correct response was recorded. In shine-through (that is, gratings with more than seven elements), subjects judged the offset of the illusory shine-through element. Shine-through is perceived more easily than feature inheritance and requires far less training.

Experimental Details for Fig. 2. The offset size of the element at the nonpreferred edge and the vernier offset were chosen independently for each subject individually to allow interference effects between the conditions Pref 2 and Non-Pref. Performance is quantified in terms of the percentage of trials in which the offset of the grating indicated by the subjects in a binary task corresponds to the direction of offset of the invisible vernier. The upper curve in *C* corresponds to a blank interstimulus interval of the same duration as the vernier (either 20 or 30 ms) being introduced between vernier and grating, whereas the lower curve had none, as in all of our other experiments.

Experimental Details for Fig. 3. One parameter controls the offset of the vernier in the illusory condition and a second parameter is used to determine the offset of the grating in the real

[‡]To whom reprint requests should be addressed at: Section of Human Neurobiology, Argonnenstrasse 3, 28211 Bremen, Germany. E-mail: mherzog@uni-bremen.de.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

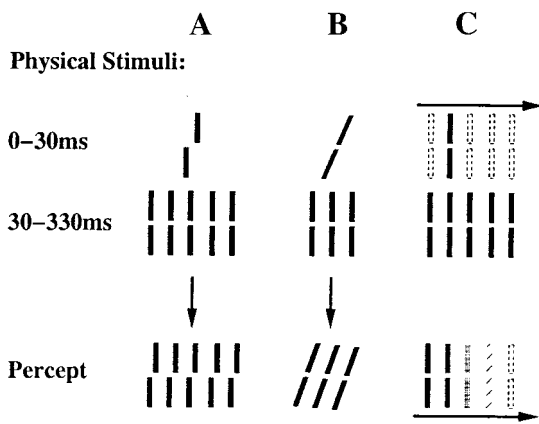


Fig. 1. Three examples for inheritance of features. (A) The flashed vernier stimulus, two lines of the same orientation slightly offset from each other, are followed by a grating, comprising five elements without offset. Twenty-six of thirty subjects perceive a grating with an illusory offset. Task instruction is not necessary for inheritance of features to occur. (B) A clockwise tilted double-bar followed by a grating, comprising three straight elements, results in the percept of a clockwise tilted grating. (C) In the onset delay task, a double-bar is flashed at five consecutive locations for a short time (each 10–30 ms) and followed by a grating comprising five lines all displayed simultaneously at the locations where the double-bar had appeared before. Observers perceive a grating in which the elements are drawn one after the other in the direction of the double-bar moving in apparent motion.

condition. Both parameters are chosen to yield equivalent percepts. To prevent subjects from judging the genesis of stimuli by comparing offset sizes, three different values for each of the two parameters were used. Moreover, it should be noted that we do not claim that in a binary task regarding existence vs. nonexistence of the vernier the sensitivity index d' is zero.

Experimental Details for Fig. 4B. We reduced presentation time of the preceding vernier compared with the conditions in which observers perform feature inheritance (e.g., Figs. 2 and 4C) because practicing shine-through causes a relative rapid increase in the temporal sensitivity of subjects. These times stabilized at 20 ms for four observers and at 40 ms for the remaining subject. Longer presentation times yielded ceiling effects, rendering the vernier visible in the gap condition.

Results

Features Travel into the Focus of Attention. If a grating with five elements follows the vernier, almost all subjects focus attention on one of the edges of the grating. In a quantitative study, none of our 30 observers reported focusing on the middle double-bar (at the location where the vernier was flashed).

However, do these statements reflect reality? The results of the experiments shown in Fig. 2A and B indicate that observers indeed attend to only one of the outer elements, called the preferred edge. Moreover, subjects do not take information outside the focus of attention into account because performance (expressed as percentage of responses that correctly determined the direction of offset of the preceding vernier) does not depend strongly on whether or not a real offset is introduced at the nonpreferred edge (compare Pref 1 with Pref 2 in Fig. 2B). Switching attention to the nonpreferred edge of the grating—where a real offset always opposite to the offset of the vernier has been introduced—reduces the percentage of correct responses to about 15%. Because this result is below chance performance (50%), it implies that observers base their discriminations on the outer element of the grating whose offset is in the direction opposite to that of the vernier.

Varying the position of the vernier in relation to the grating strongly influences performance: the closer the vernier is presented to the focus of attention, the better the discrimination performance of inherited offsets (Fig. 2C). Providing a blank interstimulus interval (ISI) yields superior performance than if the grating immediately follows the grating, although verniers in both conditions were displayed for the same amount of time. Taken together, information about offsets has to “travel” from the center into the focus of attention. This process depends on the spatial (vernier location) and temporal (ISI) parameters of presentation.

Perceptual Equivalence. As shown above, one or more features can be inherited from an invisible object present at an earlier time. It is invisible in the phenomenological sense: our observers verbally report not having “seen” any vernier.

But is feature inheritance really unconscious in the sense that observers are unaware of the *genesis* of their percepts? To answer this question we presented randomly either an offset vernier followed by a grating with nonoffset elements (as in the experiments above), or a vernier with no offset followed by a grating with real offsets about 6–10 times smaller than the offsets of the foregoing vernier. As is evident in Fig. 3, subjects can discriminate the offset, whether real or illusory, yet are at chance level if asked to discriminate between the two conditions. In other words, both stimuli “look” the same. Or, put differently, they are metamers.

We do not claim that subjects are in principle unable, after sufficiently long training, to discover some aspect of the stimulus (such as overall intensity) that allows them to distinguish between illusory and real offsets (although we have not been able to do so). Rather, we claim that phenomenally, the conscious perception of the real offset of the grating is similar to the perception of offset induced by the invisible vernier.

Shine-Through. If, instead of a grating of five elements, a grating comprising nine or more double-bars follows the spatially offset vernier, most of our subjects report seeing a vernier superimposed onto the grating. This vernier appears to be wider and brighter than the original vernier or the grating elements (Fig. 4A). “Shine-through” is also evident in a strong increase of performance (Fig. 4B).

The number of elements constituting the grating is crucial. Gratings with less than seven elements allow feature inheritance but not shine-through. The reverse situation occurs for gratings comprising more than seven elements: if the grating is spatially too extended, shine-through occurs (Fig. 4C; for seven elements interindividual differences are found).

Simple spatial or temporal manipulations of the extended array of elements can eliminate shine-through. For instance, removing one double-bar on each side of the central five elements—creating a gap—renders the vernier once more invisible, while leading to inheritance of its offset to the central five elements of the grating (Fig. 4B and D). Tilting the outside double-bars by 5° with respect to the central bars causes a strong deterioration of performance (data not shown).

Manipulating temporal parameters interferes with shine-through as well. Flashing the outside 2 × 9 double-bars of a 23-element array 10 ms later than the central five double-bars results in a diminishing of shine-through and a significant deterioration of performance (Fig. 5).

If, as in the “gap condition,” the grating is perceived not as unitary but as three segmented objects, the central one might inherit some of its property from the preceding vernier. Therefore, with our paradigm we can investigate the transition from an invisible to a visible state in a quantitative manner. Our current hypothesis is that image segmentation cues play an important role in whether the vernier remains invisible and its features are

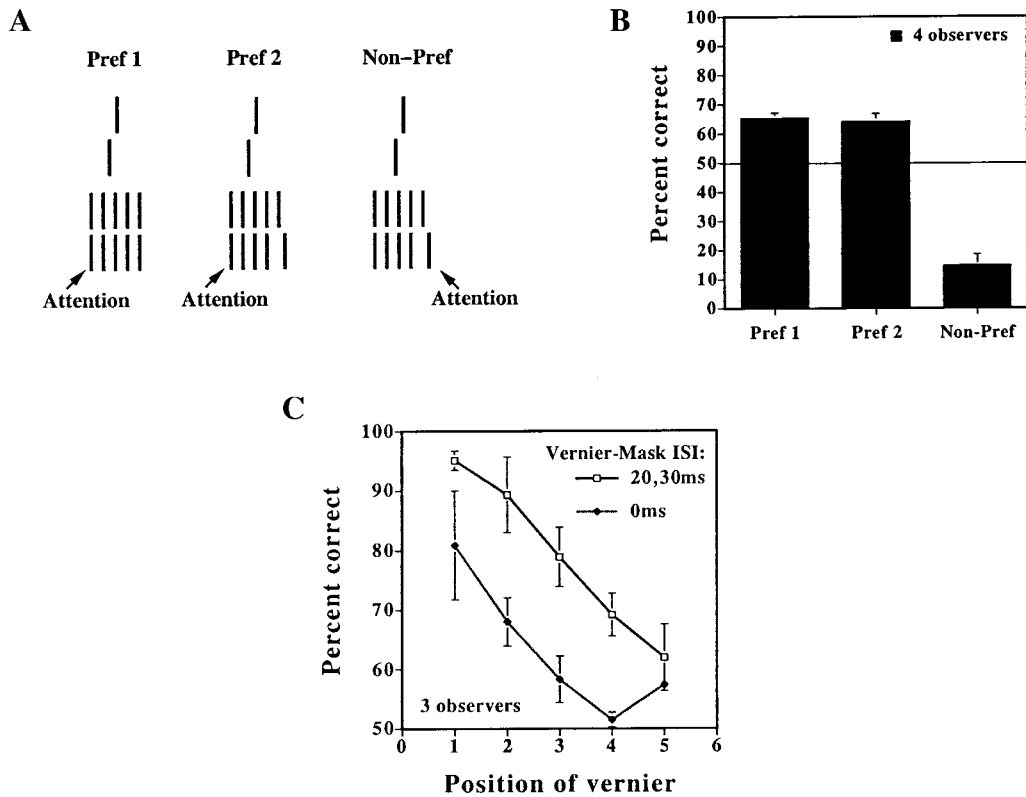


Fig. 2. Features are mislocalized and "travel" into the focus of attention. (A) Most subjects claim to focus on one of the two outside edges of the grating to judge the direction of induced offset (preferred edge). To test this statement, we displayed a vernier followed by a grating in three conditions. In the first condition (Pref 1), the vernier is followed by a grating having only straight elements. Subjects attend to their preferred edge. In the second condition (Pref 2), the grating comprises four elements without offset plus an additional double-bar carrying an offset with offset direction *opposite* to the vernier. This element is located opposite the subject's preferred edge. Observers attend to their preferred edge. In the third condition (Non-Pref) the same stimuli were used as in the condition before (that is, outer element offset in opposite direction than vernier). However, subjects were instructed to switch attention to their nonpreferred edge. (B) Focusing on the preferred location hardly changes the amount of correct responses determined according to the *foregoing vernier* independent of whether (Pref 1) or not (Pref 2) the grating comprised an element with a real offset. However, focusing on the opposite location, where the offset element is displayed, leads to a very significant reduction of correct responses. This indicates that the offset element of the *grating* determines decision (Non-Pref). (C) To investigate feature inheritance in a more quantitative fashion, the vernier was presented at the five positions of the grating having five straight elements. Position 1 indicates the preferred location, position 5 the opposite location. Percentage of correct responses drops monotonically and almost linearly from its maximum if the vernier is presented close to the preferred, attended edge to almost chance level at the nonpreferred edge of the grating. C also shows the dependence of performance on interstimulus (ISI) time between vernier and grating (for two observers, 30 ms; for the other one, 20 ms).

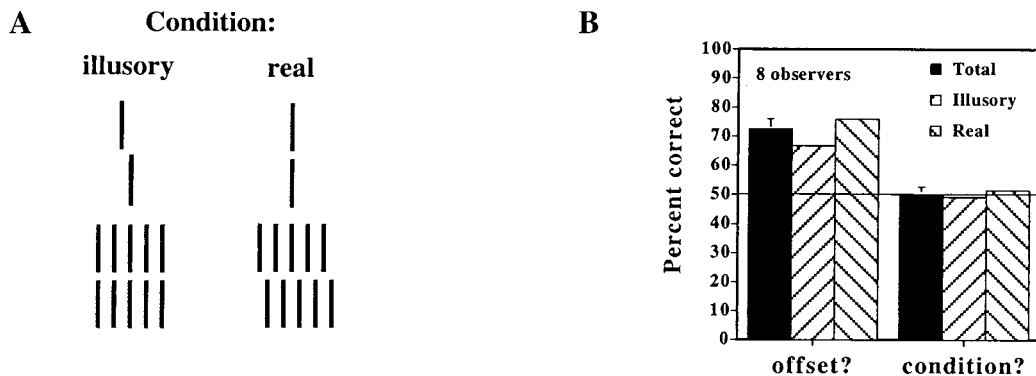


Fig. 3. Inheritance is unconscious. (A) Randomly, either an offset vernier (offset to the left or right) followed by a grating with straight elements (Condition: illusory) or a vernier having no offset followed by a grating with real offsets (to the left or right), which were about a factor of 6–10 smaller than the vernier, were displayed (Condition: real). (B) In the first part of the experiment, subjects were not informed about the set-up and had to perform offset discrimination as usual. Observers perform well on both the illusory and the real condition (offset?). Afterward, they were asked whether they had noticed any difference in the stimulus generation, and reported that they had not. In the second part of the experiment, the whole paradigm was explained to them by revealing the spatio-temporal layout. Subsequently, the task was changed and subjects were instructed to ignore offsets but to judge whether the grating offsets were illusory (that is, induced by the vernier) or real (condition?). Observers were unable to discriminate between the two. We conclude that subjective reports and an objective measure of perceptual equivalence correspond very well. An analogous experiment was conducted employing the orientation discrimination task (Fig. 1B). Because results are similar, the data are combined in the above figure.

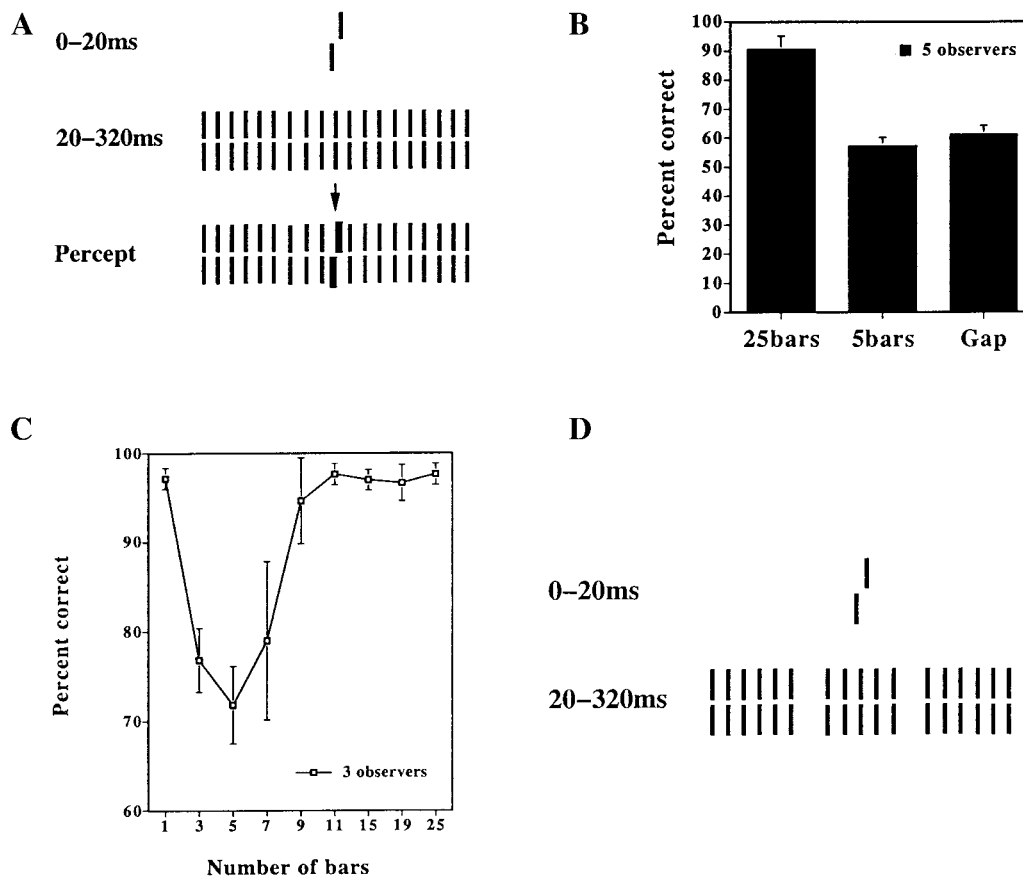


Fig. 4. Contextual effects. (A) Gratings with more than seven elements render the vernier and its features visible, a phenomenon we call “shine-through.” The shine-through element appears superimposed on the grating: it is brighter, wider than the grating elements, and offset in the direction of the vernier. (B) This visibility leads to an increase in performance: a grating comprising 25 elements yields a better performance than a grating comprising five double-bars (for the sake of clarity, only 19 of 25 double-bars are shown in A). (C) Varying the number of elements of the grating results in feature inheritance for small numbers of elements (3–5) and shine-through for more than seven elements. To avoid floor effects, presentation times of 40 ms were used for the vernier, yielding good feature inheritance. If only one element follows the vernier, apparent motion is perceived and, therefore, performance improved. (D) Subtle changes in the layout, such as leaving out two double-bars, render the vernier invisible (see Gap in B). This leads to a significant reduction in performance.

bound to those of the grating, or whether the vernier becomes visible and fails to bequeath its features to the grating.

Discussion

To summarize, we here describe a class of visual illusions with two complementary properties. Firstly, the orientation, offset, or motion of a briefly flashed vernier that is not visible to the observer can determine the corresponding properties of the following grating (feature inheritance). If, secondly, the grating comprises more than seven elements, the vernier becomes visible (shine-through). This effect can be abolished by subtle manipulations of the peripheral parts of the grating. In particular, spatial cues that lead to segregation of the grating into three parts eliminate shine-through. Therefore, depending on the spatio-temporal layout of the grating, the offset of the preceding vernier can be *seen* bound to a single object, the grating, or belonging to the shine-through element in which case two objects are perceived: the grating and the vernier.

Our “inheritance illusion” is but one instance of a larger set of visual phenomena in which stimuli or their associated properties that are not consciously perceived in normal subjects have some measurable effect on performance (3–8). In our paradigm, objective behavioral performance and subjective percept correlate very well. If the vernier is rendered visible (shine-through), performance is superior compared with the situation if the

vernier remains invisible (yet influences the properties of the grating) and performance is inferior.

Feature inheritance appears to be under the control of visual attention, whereas, as preliminary experiments show, shine-through does not. Interestingly, Ramachandran and Cobb (9) found that a disk, effectively masked by metacontrast, can become visible if another visible disk is added to the stimulus *and* if attention is paid to both of them. A similar result was reported by Werner (10). He demonstrated, moreover, that in stroboscopic succession a disk may be rendered invisible by a following annulus. If the disk contains spokes these can be attributed to the ring while the disk remains invisible. Banks and White (11) have shown that grouping can enhance performance in a letter discrimination task. Weisstein and Harris (12) found that the detection of a line can be enhanced by contextual elements depending on depth cues. Performance can be even better than if the line is presented alone (13). Verghese and Stone (14) found that speed discrimination depends on the spatial layout of stimuli, in particular with respect to the extent of the target(s).

Suzuki and Cavanagh (15) demonstrated that if a line is briefly flashed, followed by a circle, an ellipse is perceived, elongated in the *orthogonal* direction of the axis of the line (suggesting an interpretation in terms of an after-effect). Surprisingly, an ellipse is perceived even if line and circle do not spatially overlap. Because of this, the authors favor the inferior temporal cortex as

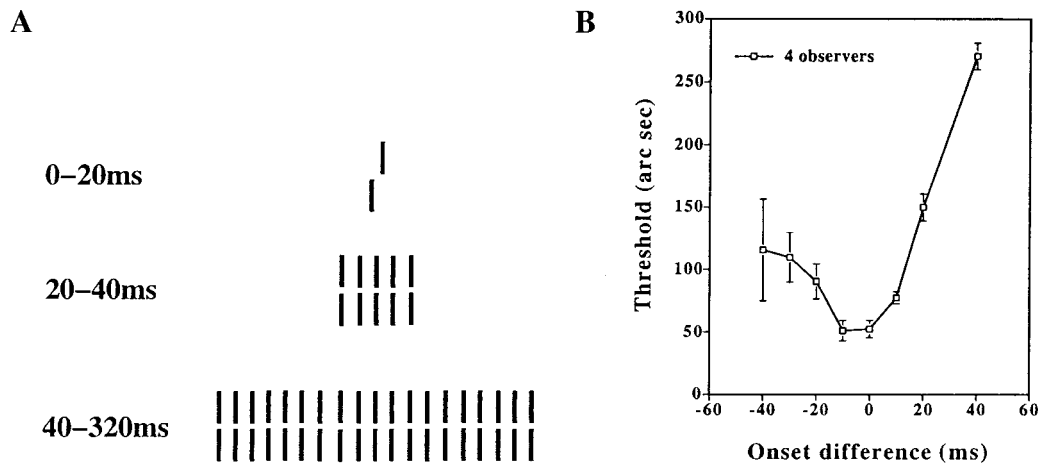


Fig. 5. An example of how shine-through depends on the temporal layout of the grating is shown. The results are determined in terms of thresholds (i.e., the spatial offset of the preceding vernier for which 75% correct responses are reached). (A) Elements in the center of the grating were displayed earlier (as in this example) or later than outer elements. Actual gratings comprise 23 elements. (B) Even if the outer 2×9 double-bars are presented only 10 ms later than the central five elements, a significant deterioration of performance is found. Depending on temporal onset difference, shine-through can be completely eliminated. Negative onset differences mean the outer elements appear *before* the central five elements; positive onset differences mean the outer elements appear *after* the central five elements. Simultaneous presentation occurs for zero onset difference.

the site of integration, given the large size of the associated receptive fields. In our case, small changes in the layout of the grating cause dramatic changes in the associated percept. In particular, shine-through occurs when the grating exceeds about 0.5° , implicating neurons in the primary visual cortex (V1) and their nonclassical receptive fields (16).

Our findings contribute to the topic of masking phenomena in that they show that masking cannot solely be explained by theories focusing on local features (17, 18). Shine-through and its abolishment by segmentation demonstrates that contextual effects play a powerful role. It might be possible that an inheritance-like effect could be found in repetition blindness (19).

Finally, our findings relate to illusory conjunctions and feature migration (20–22). As in these phenomena, features of one object are incorrectly bound to another. One crucial difference to illusory conjunctions is that the first stimulus (the vernier) need not be visible for feature binding to occur and that feature inheritance depends on the spatio-temporal layout of the grating (e.g., Fig. 4).

Feature inheritance and shine-through might be considered as two states of feature binding (23). In feature inheritance only one

object, the grating, is perceived and features in a small spatio-temporal window are *bound* to it. In shine-through two independent entities are perceived, but only the shine-through element *binds* the offset (the grating does not). Any neuronal explanation of this illusion has to account for the fact that the information pertaining to the vernier offset is present under both feature inheritance and shine-through conditions. Because of the simple and metric nature of our stimuli, they might lend themselves to studying these different states of feature binding in the awake behaving monkey (24–28).

We thank Landi Parish for help in the experiments and Steffen Egner, Manfred Fahle, Gabriel Kreiman, and Geraint Rees for comments on the manuscript. Two anonymous referees provided very useful references. Mike Walsh's expertise was invaluable in providing the oscilloscopes. Anne Lilje helped maintain and fix the computers. We also thank all of our subjects, some of whom patiently spent a very long time in front of the screen. M.H. was supported by a fellowship from the Deutsche Forschungsgemeinschaft (DFG) and by the SFB 517 "Neurocognition" of the DFG. C.K. received funding from the Keck Foundation, the National Institutes of Mental Health, and the National Science Foundation.

1. Wolfe, J. M. & Cave, K. R. (1999) *Neuron* **24**, 11–17.
2. Taylor, M. M. & Creelman, C. D. (1967) *J. Acoust. Soc. Am.* **41**, 782–787.
3. Blake, R. & Fox, R. (1974) *Nature (London)* **249**, 488–490.
4. He, S., Cavanagh, P. & Intriligator, J. (1996) *Nature (London)* **382**, 334–337.
5. Bar, M. & Biederman, I. (1998) *Psychol. Sci.* **9**, 464–469.
6. Reingold, E. M. & Merikle, P. M. (1988) *Percept. Psychophys.* **44**, 563–575.
7. Moore, C. M. & Egeth, H. (1997) *Percept. Psychophys.* **23**, 339–352.
8. Marcel, A. J. (1983) *Cognit. Psychol.* **15**, 197–237.
9. Ramachandran, V. S. & Cobb, S. (1995) *Nature (London)* **373**, 66–68.
10. Werner, H. (1935) *Am. J. Psychol.* 40–64.
11. Banks, W. P. & White, H. (1984) *Percept. Psychophys.* **36**, 285–295.
12. Weisstein, N. & Harris, C. S. (1974) *Science* **186**, 752–755.
13. Williams, A. & Weisstein, N. (1978) *Mem. Cognit.* **6**, 85–90.
14. Verghese, P. & Stone, L. S. (1997) *Vision Res.* **37**, 397–406.
15. Suzuki, S. & Cavanagh, P. (1998) *J. Exp. Psychol. Hum. Percept. Perform.* **24**, 1315–1341.
16. Snodderly, D. M. & Gur, M. (1995) *J. Neurophysiol.* **74**, 2100–2125.
17. Breitmeyer, B. G. (1984) *Visual Masking: An Integrative Approach* Oxford Psychology Series, No 4. (Clarendon, Oxford).
18. Bachman, T. (1994) *Psychophysiology of Visual Masking*. (Nova Science, Commack, NY).
19. Kanwisher, N., Yin, C. & Wojciklik, E. (1999) in *Fleeting Memories*, ed. Coltheart, V. (MIT Press, Cambridge, MA), pp. 119–150.
20. Wolford, G. & Shum, K. H. (1980) *Percept. Psychophys.* **27**, 409–420.
21. Treisman, A. & Schmidt, H. (1982) *Cognit. Psychol.* **14**, 107–141.
22. Butler, B. E., Mewhort, D. H. & Browse, R. A. (1991) *Percept. Psychophys.* **49**, 91–99.
23. Roskies, A. L. (1999) *Neuron* **24**, 7–9.
24. Macknik, S. L. & Livingstone, M. S. (1998) *Nat. Neurosci.* **8**, 144–149.
25. Schiller, P. M. (1968) *Vision Res.* **8**, 4040–4055.
26. Rolls, E. T. & Tovee, M. J. (1994) *Proc. R. Soc. London B* **257**, 9–15.
27. Thompson, K. G. & Schall, J. D. (1999) *Nat. Neurosci.* **2**, 283–288.
28. Das, A. & Gilbert, C. D. (1999) *Nature (London)* **399**, 655–661.