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Vision Research 43 (2003) 1951–1960

Vision Research

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Fusion of competing features is not serial

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Received 7 April 2001; received in revised form 11 September 2002

Abstract

How features of an object are bound into a unique percept is one of the puzzling problems in the cognitive and neuro-sciences. In order to investigate the spatio-temporal mechanisms of feature binding, we serially present *two* verniers with opposite offset directions for very short durations. Only *one* vernier is perceived with its offset dominated by the vernier presented second. This dominance reverses if the two verniers are followed by masking gratings, i.e. the *first* presented vernier dominates performance. Therefore, feature fusion can neither be explained completely by spatially local mechanisms nor by the temporal order of appearance of elements.

1. Introduction

In the mammalian brain, individual features, such as color and motion, are processed partly in parallel. This parallel information processing requires a mechanism to bind these features into a coherent percept. The nature of this mechanism is a hotly debated subject. Two major psychophysical paradigms to investigate feature binding can be distinguished: mis-binding of features and feature fusion. Mis-binding occurs, for example, with illusory conjunctions. Under heavy attentional load features of one object can be bound to a nearby object (e.g. Treisman, 1998). Feature fusion occurs when elements, presented in rapid succession, are collapsed to one single object and their respective features are fused. For example, a green disc followed immediately by a red disc leads to the percept of a yellow disc (Efron, 1967).

In order to investigate the temporal aspects of feature fusion, we use the feature inheritance and the shine-through effects. In both effects, a vernier stimulus is followed by a grating consisting of *straight* verniers. In the case of feature inheritance the grating comprises five elements. Subjects focus attention on one of the edges of this grating. We call this the *preferred edge*. Surprisingly, at this preferred edge subjects perceive an illusory offset whereas the preceding vernier remains largely invisible (see Fig. 1; Herzog & Koch, 2001). Since the vernier is presented at the center of the grating observers, mislocalize the vernier offset, i.e. the feature "vernier offset" is mis-bound. Vernier offset discrimination occurs only at the *preferred* edge. Properties of the grating outside this focus of attention do not play a major role for performance (Herzog & Koch, 2001). To explain mislocalization we hypothesized that neural activity spreads within cortex from the (topographical) stimulus representations into the focus of attention. Feature inheritance reveals temporal dynamics. For example, performance improves if an inter-stimulus interval (ISI) is inserted between the vernier and the grating (Herzog & Koch, 2001).

Shine-through occurs when the grating is composed of more than seven elements. In this case, the vernier is rendered visible and appears to shine-through the grating (see Fig. 1; Herzog, Fahle, & Koch, 2001). Subjectively, the shine-through element looks wider, brighter, and sometimes even longer than the vernier really is. In the shine-through condition, subjects focus attention on the center of the grating. Performance in the shine-through effect is superior to that in the feature inheritance conditions. For example, most trained observers perceive shine-through with a vernier presentation time as low as 10 or 20 ms while experience of feature inheritance requires at least display times of 20–50 ms.

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doi:10.1016/S0042-6989(03)00278-5

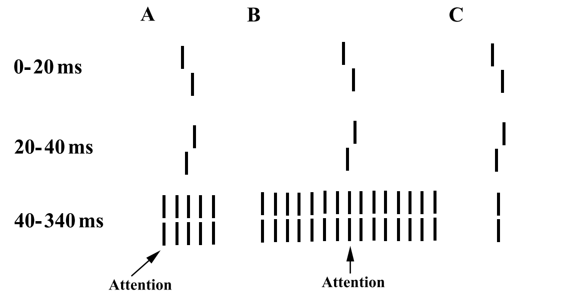

Fig. 1. In most experiments, two sequentially presented verniers precede gratings comprising 5 or 25 elements or a single aligned vernier (A, B, and C, respectively). The two preceding verniers are offset in opposite directions, e.g. if the first vernier is offset to the left, the second one is offset to the right (vernier and anti-vernier). Presentation time and spatial properties of both verniers, other than offset direction, are identical. (A) Feature inheritance. Subjects focus attention on the preferred edge where they perceive an illusory offset. The foregoing verniers remain largely invisible, i.e. naive observers are not aware of the generation of the illusory offset. (B) In the shine-through condition a grating comprising 25 elements follows after the verniers (only 15 elements are shown due to space considerations). Observers perceive a *single* shine-through element looking wider, brighter, sometimes even longer, and superimposed on the grating. Attention is focused on this element, that is at the center of the grating. Contrary to the figure, most observers require different stimulus presentation times in the feature inheritance and shine-through conditions. (C) Verniers precede a single straight vernier.

Using feature inheritance and shine-through, we show that strictly local mechanisms are not sufficient to explain feature processing. Moreover, we will show that visual information processing in our paradigm is not serial, i.e. elements of a visual display are not processed in the order of appearance. For example, if the two verniers follow each other, the second vernier contributes more strongly to feature fusion. If, however, these two verniers are followed by a grating the first element dominates feature fusion.

2. General materials and methods

2.1. General paradigm

Stimuli were displayed on an analog monitor (Tektronix 608 or on a HP 1334 A) controlled by a Power Macintosh computer via fast 16 bit D/A converters (1 MHz pixel rate). Vertical verniers were presented without mask or preceded either a single aligned vernier or gratings comprising 5 or 25 vertical verniers without offset. The segments of both the verniers and the grating elements were 600″ long and separated by a vertical gap of 60″. Hence, length of verniers or grating elements was 1260″ altogether. Verniers were presented at the center of the screen where the mask was centered, too (see Fig. 1). Gratings were displayed for 300 ms. The spacing between elements was 200″ and the refresh rate was 100 Hz.

Subjects observed the stimuli from a distance of 1.2 or 2 m in a room dimly illuminated by a background light (around 0.5 lx). Luminance of stimuli was around 80 cd/m^2. Before stimulus presentation began, a fixation dot was presented at the middle of the screen and four markers were shown at the corners of the monitor.

2.2. Observers

Most of our data were obtained from paid Caltech graduate students, from two of the authors, and from a lab technician. All observers had normal or corrected-to-normal visual acuity and were aged between 21 and 50 yr. After observers signed a consent form, acuity was determined by means of the Freiburger visual acuity test (Bach, 1995). To participate in the experiments subjects had to reach a value of 1.0 (corresponding to a visual acuity of 20/20) in this test in at least one eye. Only highly experienced observers participated in the experiments.

2.3. Conditions

After the first vernier usually a second, anti-offset vernier followed, i.e. a vernier presented for the same duration as the first vernier but with its offset direction opposite to the first vernier. This vernier is called the *anti-vernier*. With offset size we refer to the absolute value of offset size, i.e. irrespective of offset direction.

After these two verniers a single straight vernier could follow or else gratings composed of 5 or 25 elements. The gratings consisted of verniers with the same spatial parameters as the preceding verniers but were not offset. The presentation time and offset size of the vernier(s) were chosen individually for each observer and each condition. Special attention was given to reduce presentation time as far as possible without abolishing shine-through or feature inheritance.

As mentioned in the introduction, feature inheritance conditions (five element grating) usually require longer presentation times of the preceding vernier than shine-through conditions (25 element grating) to reach comparable performance. For trained subjects, required vernier durations range from 20 to 60 ms in feature inheritance and from 10 to 30 ms in shine-through if only one vernier precedes the grating (Herzog & Koch, 2001).

In the feature inheritance condition subjects were asked to look to their preferred edge. Most observers tend to do this without being prompted. The task was to discriminate the illusory offset direction perceived at the preferred edge and to indicate its direction by pressing the corresponding one of two push-buttons in a binary forced choice paradigm. The verniers remained largely invisible and there was only one illusory vernier offset perceived that fused the offset of both preceding verniers. In the shine-through condition observers were asked to base their discrimination on the offset of the shine-through element that also combines the offsets of both preceding verniers. If a single straight vernier followed the two preceding verniers only one vernier was perceived, i.e. all three verniers were fused.

Duration of verniers and offset size were adjusted for each of our well trained observer individually. A display time of 20 or 30 ms was sufficient to perceive shine-through and of 20–40 ms to perceive feature inheritance. A duration of 20 ms was also used for a single straight vernier. Offset sizes ranged from about 60″ to 120″ in feature inheritance, from 15″ to 80″ in shine-through, and from 12″ to 15″ for a single straight vernier.

2.4. Strategies

In conditions in which a vernier precedes its anti-vernier performance is always presented as the percentage of correct responses consistent with the *first* offset vernier. Thus, if performance is below 50% in such a condition, performance is dominated by the anti-vernier. Performance above 50% indicates dominance of the first vernier. No error feedback was given.

Each condition was measured twice for every subject. Conditions were randomized across subjects. The order of measurements in the second run was opposite to that of the first run to compensate at least partially for learning effects. Experiments were run in blocks of 80 presentations. To prevent excessive tiring of the observers, no session lasted longer than 20 blocks or exceeded 2 h.

3. Experiments

3.1. Unmasked verniers

In this experiment we determine how vernier offsets are fused when a vernier is followed by an anti-vernier or by a straight vernier.

Methods. A vernier was presented for a short time

1. alone (V);
2. followed by the anti-vernier (V–AV);
3. followed by the anti-vernier and a straight vernier lasting for 300 ms (V–AV–G);
4. followed by a straight vernier lasting for the same duration as the first vernier (V–N); and
5. followed by a straight vernier lasting for 300 ms (V–G).

'N' indicates that the vernier had neutral offset whereas 'G' indicates that the duration of the neural vernier was 300 ms, i.e. as long as the durations of the gratings in the following experiments. In this experiment, the vernier and the anti-vernier had the same offset size. Three subjects, who participated in this experiment, participated also in one of the following experiments. We chose the same presentation time of the first vernier in this first and in the following experiments. For other subjects a display time of 30 ms was used. Offset sizes were chosen for each subject to yield performance near 75% correct responses for the presentation of a single vernier (V).

In a second condition, we presented the vernier only followed by the anti-vernier and varied the offset size of both verniers simultaneously.

Results and discussion. Performance is close to 75% correct responses when a vernier is presented alone as it was intended (see Methods). However, performance deteriorates to a level below 50% correct responses when the anti-vernier follows the first vernier (Fig. 2, condition V–AV). This result indicates that the anti-vernier, that is the stimulus presented second, dominates performance (Figs. 2 and 3). No dominance of either the first or the anti-vernier occurs if the verniers are followed by a straight vernier for 300 ms (V–AV–G). A straight vernier, presented for a short time (V–N), can express the offset of the preceding vernier stronger. Performance

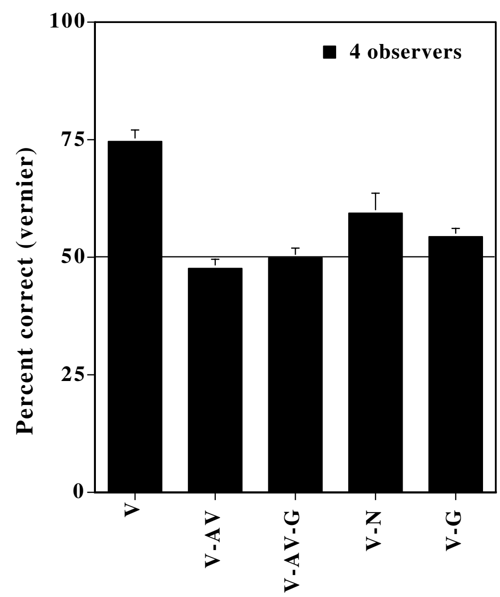

Fig. 2. The five conditions of experiment 3.1: (1) a vernier was presented alone (V); (2) a vernier was followed by the anti-vernier (V–AV); (3) a vernier was presented followed by the anti-vernier, followed by a straight vernier lasting for 300 ms (V–AV–G); (4) a vernier was followed by a vernier without offset for the same duration as the vernier (V–N); (5) a vernier was followed by a vernier without offset lasting for 300 ms (V–G). In the V–AV condition performance is below 50% correct responses. A straight vernier, presented for a long time following the vernier and the anti-vernier yields performance around 50% correct responses (V–AV–G). An aligned vernier, presented for a short time after a vernier (V–N), can inherit the offset of a single foregoing vernier. If presentation time of this straight vernier increases (V–G), performance decreases to little above 50% correct responses. Mean values and standard errors are shown.

in both conditions is weaker compared to when the vernier is presented alone.

If the vernier is followed only by the anti-vernier, dominance of the anti-vernier increases with increasing offset of both verniers (Fig. 3). For all offset sizes larger than 20″ performance is significantly below 50% (one sample t-tests $p = 0.1101, 0.02, 0.0033, < 0.0001, 0.0134$ for offset sizes of 20″, 40″, 60″, 80″, 100″).

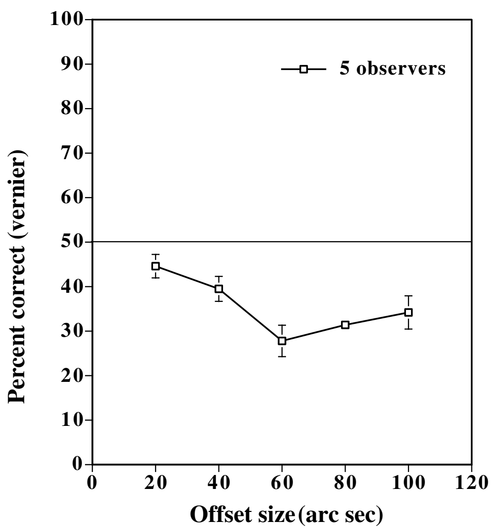

Fig. 3. Presentation of a vernier followed only by an anti-vernier. The spatial offset of both the vernier and the anti-vernier was varied by the same degree, i.e. vernier and anti-vernier have always the same (absolute) offset size. Performance above 50% indicates dominance of the first vernier, below 50% dominance of the anti-vernier. Dominance of the anti-vernier increases if the offset of both verniers increases up to around offset sizes of 60″.

3.2. Feature inheritance

In the last experiment 3.1, we found that when the vernier and the anti-vernier were serially presented the anti-vernier dominated. This result might be explained by a local integration mechanism that gives more weight to the stimulus presented most recently. The following experiments, investigating feature inheritance, address this issue.

3.2.1. Effects of temporal order in feature inheritance

Methods. One or two verniers preceded a grating composed of five aligned verniers. The foregoing elements were displayed sequentially at the center of the screen where also the middle element of the grating appeared (see Fig. 4). Presentation time and offset size of the verniers were adjusted for each observer individually. We aimed to reduce presentation time as much as possible.

In the experiments the first vernier could be

1. followed by the anti-vernier (V–AV);
2. followed by the grating after an inter-stimulus-interval of the same duration as the vernier (V–ISI);
3. followed by a straight vernier of the same duration as the vernier (V–N); or
4. preceded by the same straight vernier (N–V).

After these elements or the ISI, the grating followed immediately. Subjects were asked to focus attention on their preferred edge at which they perceived one unique, illusory offset. All observers who participated in this experiment had participated in other experiments re-

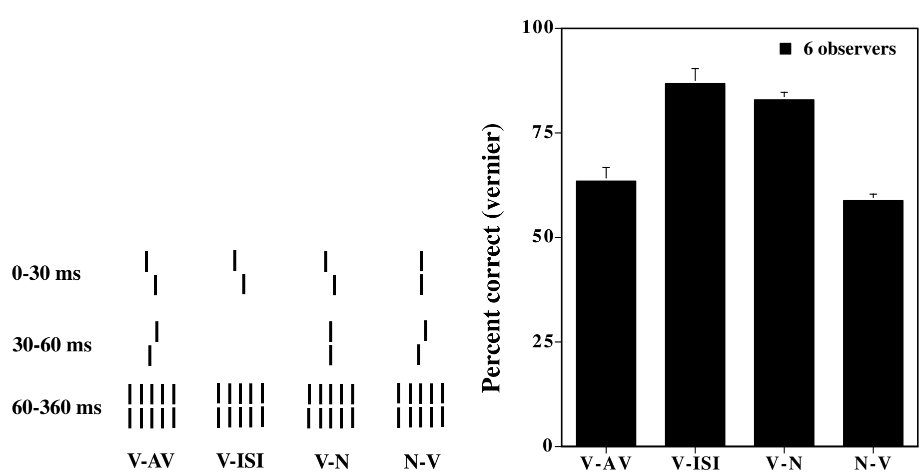

Fig. 4. Effects of temporal order in the *feature inheritance* condition. A vernier was followed by the anti-vernier (V–AV); followed by a blank period with a duration equal to the presentation time of the anti-vernier (V–ISI); followed by a vernier without offset (V–N), or was preceded by a vernier without offset (N–V). In all cases a grating comprising five aligned verniers followed the preceding elements (see also Fig. 1A). In the condition V–AV the vernier dominates the anti-vernier, i.e. performance is above 50% correct responses determined according to the first vernier. However, the anti-vernier reduces performance, as may be seen by comparing the V–AV condition to either the V–ISI or V–N condition. Temporal order effects are also seen if a straight vernier precedes or follows the offset vernier. Performance in the N–V condition is significantly lower than in the V–N case.

garding feature inheritance before. In these experiments, we showed that observers perceived the illusory vernier offset only at the attended edge (see Herzog & Koch, 2001).

Results and discussion. If vernier and anti-vernier are followed by a five element grating the first vernier always dominates, i.e. performance is above 50% correct responses (one sample t-test: $p = 0.0039$). The grating exerts a strong influence on the two preceding verniers favoring the first vernier (see Fig. 4). Still, the anti-vernier contributes to performance since performance in the condition V–AV is significantly deteriorated relative to the V–ISI condition (paired t-test: $p = 0.0015$).

Effects of temporal order are also found with straight verniers. If one of these elements *precedes* the offset vernier performance is significantly lower than if this elements *follows* the vernier (paired t-test: $p = 0.0001$).

3.2.2. Feature inheritance and spatial parameters: varying the offset of the anti-vernier

Offset discrimination of the first vernier is superior if a straight rather than an anti-vernier follows the first one. In this experiment, we quantify this phenomenon.

Methods. The vernier was followed by the anti-vernier. Immediately afterwards a grating containing five elements followed (see Figs. 1A and 4). We, first, determined the offset size x for which around 65% correct responses occurred if the offset size of the two verniers had the same absolute value. This offset size x was kept constant for the first vernier throughout the following experiment in which the offset size of the anti-vernier was varied in fractions of x. Duration was identical for both verniers.

For each observer, we reduced display times to the lowest possible value for which feature inheritance occurred. The three subjects looked towards their preferred edge (two to the left, and one to the right edge of the grating).

The first author and two naive subjects participated. One of the naive subjects knew that illusory features were perceived but not about the two vernier regime. The other naive subject was not informed that the grating elements were aligned and that the perceived offset was illusory. The results are comparable across the three subjects. The three observers received a vernier presentation time of 20, 30, and 40 ms respectively. Gratings appeared after 40, 60, and 80 ms, respectively.

Results and discussion. Performance is best if the anti-vernier is straight, i.e. offset size 0.0 (see Fig. 5; see also condition V–N of Fig. 4). Performance drops almost linearly from this point to a performance close to 50% correct responses for an offset of the anti-vernier of $2x$ (see Fig. 5). The integration of the offsets of the two verniers seems to be a linear process in which the offset size of the anti-vernier must be twice as large to cancel the offset of the first vernier.

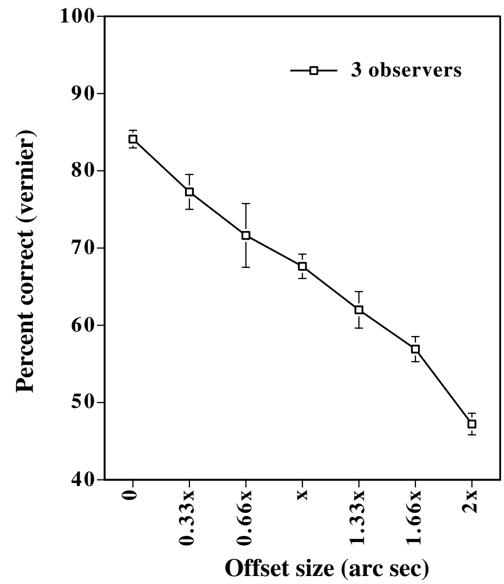

Fig. 5. In the feature inheritance condition, we determined the offset size x for which around 65% of the responses were correct relative to the first vernier if both verniers had the *same* offset size (x) but *opposite* offset direction. In the following, the offset of the first vernier was kept constant at x while the offset of the anti-vernier was varied. Performance drops almost linearly from the condition in which the "anti-vernier" was straight ("0") to about 50% correct responses if the offset size of the anti-vernier was $2x$. This result shows that the anti-offset of the anti-vernier must be twice as large as the offset of the first vernier to cancel its dominance.

3.2.3. Feature inheritance and spatial parameters: varying the offsets of both verniers

In the last experiment only the offset size of the anti-vernier was varied. In this experiment, we investigate the quantitative effects when the offset sizes of both verniers change simultaneously. We will show that feature fusion is a monotonic process revealing almost linear characteristics as in the last experiment.

Methods. The same three observers who participated in the last experiment continued in this one. Both verniers had always the same offset size. As offsets sizes, we used the same fractions of x employed for the anti-vernier in the last experiment. Subjects looked to their preferred edge.

Results and discussion. Performance for all conditions never falls below 50% correct responses. This means that always more or less strongly the first vernier dominates performance (see Fig. 6). This result holds for every observer and for every offset size. Performance increases monotonically with increasing offset size ranging from about 50.7% correct responses for the smallest offset size to about 74.9% for an offset size of $2x''$. It seems that feature fusion reveals some linear characteristics—the larger the offsets, the more the first vernier dominates perception.

Some observers experienced apparent motion in some conditions of this experiment. Also, as is often the case

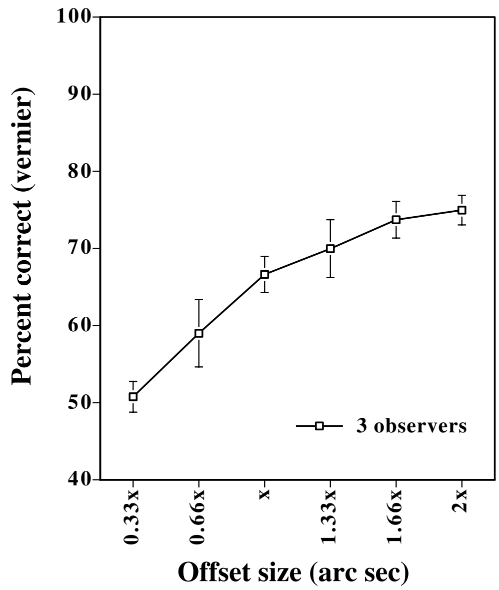

Fig. 6. In experiment 3.2.3, vernier and anti-vernier had identical but variable offset sizes of opposite direction. We used as offset size the same fractions of x as in the preceding experiment. For small offset sizes performance is close to 50% correct responses. For increasing offset sizes performance clearly favors the first vernier.

in feature inheritance, some large response bias effects were observed. This bias usually is in favor of the offset in the direction of the preferred edge. For example, if an observer looks to the left edge performance for left offset verniers is superior than for right offsets.

3.3. Shine-through

In the next set of experiments, we investigate feature fusion in the shine-through effect. Shine-through occurs when the number of elements in the grating is larger than seven. In the following experiments, a 25 element grating is used. This 25 element grating contains the five element grating, used in the feature inheritance experiments in which the first vernier dominates. In shine-through, the verniers are visible as one unique shine-through element at the center of the grating. Here, the question arises whether the anti-vernier dominates as in the unmasked condition in which the vernier is followed only by the anti-vernier, or whether a reversal of dominance occurs as in feature inheritance, i.e. a reversal of dominance between the first and second vernier, when a mask is added.

3.3.1. Effects of temporal order in shine-through

Methods. As in experiment 3.2.1 on feature inheritance, the first vernier could be

1. followed by the anti-vernier (V–AV);
2. followed by a grating after an ISI of the same duration as the display time of the first vernier (V–ISI);
3. followed by a straight vernier (V–N); or
4. preceded by a straight vernier (N–V).

For each subject, we used the shortest presentation time possible for shine-through. For most subjects this turned out to be 20 ms.

Offset size was chosen to yield performance clearly in favor of the first vernier in the condition V–AV. Presentation times for all elements, V, AV, N, and ISI, are the same across all conditions.

Results and discussion. As in the analogous experiment regarding feature inheritance, performance is best if the vernier is followed by an ISI (of the same length) as the preceding vernier. Presenting a straight, vernier instead of the ISI reduces performance slightly (see Fig. 7). Presenting a straight vernier before the offset vernier (N–V) reduces performance even more. Worst performance occurs when the vernier is followed by its anti-vernier (V–AV). Performance significantly deteriorates compared to the V–ISI condition (paired t-test: $p = 0.0059$). An offset vernier preceding a straight element (V–N) yields significantly better performance than vice versa (N–V; paired t-test: 0.0398). Though a shine-

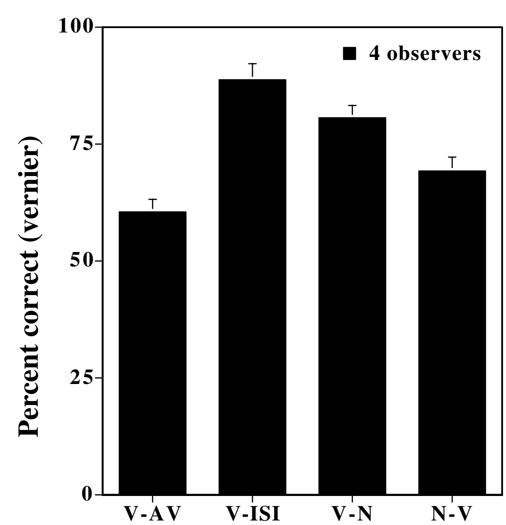

Fig. 7. We used four conditions to investigate the effects of temporal order in the *shine-through* effect (see Fig. 4 for very similar effects in the feature inheritance condition). (1) A vernier followed by the anti-vernier and a grating with 25 elements (V–AV); (2) a vernier, followed by an ISI of the same duration as the vernier, followed by a grating with 25 elements (V–ISI); (3) an offset vernier followed by an aligned vernier, followed by a grating with 25 elements (V–N); and (4) an aligned vernier followed by an offset vernier followed by a grating comprising 25 elements (N–V). Offset, anti-offset, and straight verniers had the same spatio-temporal properties except for offset size and/or direction. Performance is lowest in the V–AV case and best in the V–ISI condition. In every condition performance is above 50%, indicating that the vernier determines performance. Effects of temporal order are also found in the conditions in which straight verniers precede or follow an offset vernier. A straight vernier presented before an offset vernier (N–V) yields lower offset discrimination than vice versa (V–N).

through element is clearly visible to all observers in all conditions, neither the anti-vernier dominates nor offsets cancel each other as in the condition in which these verniers are presented without the grating or followed by a single straight vernier, respectively—even though the straight vernier is contained in the 25 element grating (see Fig. 2).

3.3.2. Spatial parameters in shine-through: varying offset size of the anti-vernier

This experiment is the analogue to the feature inheritance experiment described in Section 3.2.2, in which the offset size of the anti-vernier was varied. The offset size of the first vernier was constant throughout the whole experiment in order to investigate for which offset sizes, if at all, the anti-vernier dominates performance.

Methods. For each subject individually, we determined the offset size x of both the vernier and the anti-vernier for which 65% correct responses to the first vernier occurred in the shine-through condition (vernier and anti-vernier have same offset size). In the following, this offset size was kept constant whereas the offset size of the anti-vernier varied as a fraction of x: $0'', 0.25x'', 0.5x'', 0.75x'', x'', 1.25x'', 1.5x'', 1.75x'', 2x''$. In the shine-through conditions, we used a finer spacing of offsets than in the feature inheritance condition because, as will be seen in this and the following experiment, performance varies over a larger scale. Presentation time was 20 ms for one observer and 30 ms for the other two subjects. The grating followed immediately after the vernier.

Subjects, except for the first author, were not informed about the procedure. The task was to discriminate offset direction using the central shine-through element to which subjects attended.

Results and discussion. Performance drops almost linearly with increasing offset size of the anti-vernier (see Fig. 8). An offset size twice as large as that of the foregoing vernier is needed to bring performance down to near 50% correct responses. One observer scored slightly below 50% correct responses in this condition. In all other conditions performance is always superior to 50% correct responses. Even for large offsets of the anti-vernier, the first vernier dominates performance.

3.3.3. Spatial parameters in shine-through: varying the offsets of both verniers

In this experiment we investigate feature fusion quantitatively for variable offset sizes of *both* verniers as in experiment 3.2.3.

Methods. The same three observers who participated in the last experiment participated in this one. Set up and task were identical. In the first condition only one vernier preceded the grating. In the second condition, vernier and anti-vernier were presented. Spatial parameters of the vernier were the same except for offset direction. The same fractions of x were used as in the last experiment.

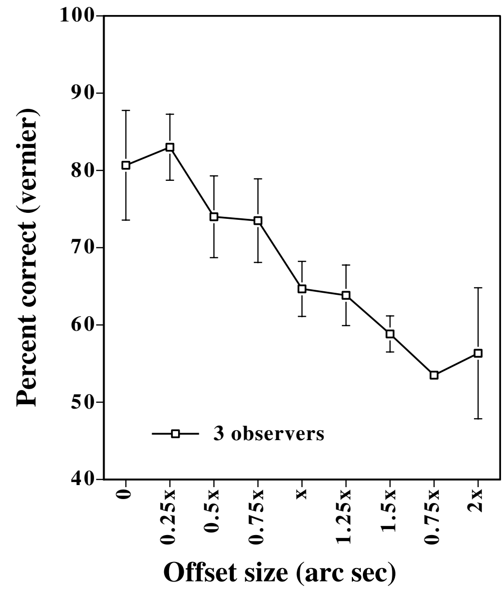

Fig. 8. In an experiment analogous to experiment 3.2.2 (feature inheritance, see Fig. 5), we varied the offset of the anti-vernier. The offset size for the first vernier was constant at x, for which performance was around 65% if both verniers had the same offset size. This value x was kept constant over the experiment for the first vernier, while the offset size of the anti-vernier was varied. As in the analogous experiment regarding feature inheritance, the first vernier dominates most strongly if the "anti-vernier" is straight decreasing to close to 50% correct responses if the offset size of this element is twice as large as that of the first vernier.

Results and discussion. As in the experiments regarding feature inheritance, the first vernier always determines performance (see Fig. 9). The percentage of correct responses, dominated by the offset of the first vernier, increases with the offset size of both verniers. The larger the offset of the first vernier the better performance is. Therefore, as in feature inheritance, the element presented first dominates performance. However, the anti-vernier also contributes to performance down-shifting results relative to the condition in which only one element precedes the grating. Apart from floor and ceiling effects, performance seems almost linearly shifted. Slopes of regression lines are quite similar: 4.47 for the one-vernier condition ($r^2 = 0.92$) and 4.82 for the two-verniers condition ($r^2 = 0.97$). Therefore, the preceding vernier does not completely suppress the second one but both verniers contribute to an almost linear computation giving the first vernier a higher weight.

4. General discussion

4.1. Effects of temporal order

If a vernier is followed by its anti-vernier the anti-vernier dominates performance (Fig. 3). If, however,

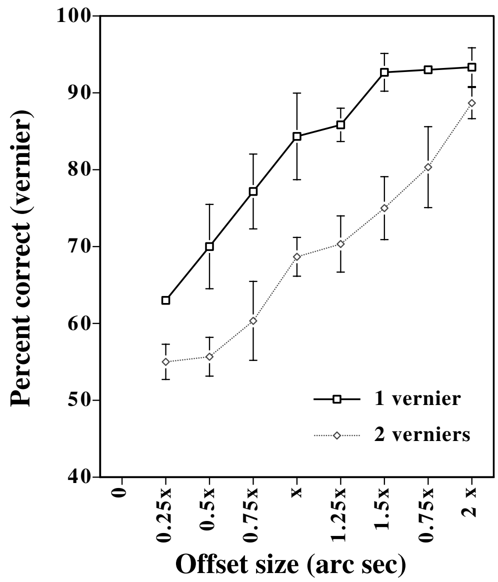

Fig. 9. Dominance of first vernier in *shine-through* with (two verniers) and without (one vernier) following anti-vernier (see Fig. 6 for a similar effect in feature inheritance). For every observer an offset size x was chosen to yield a performance level around 65% correct responses if offset sizes were the same for both verniers. The other offset sizes used were multiples of a fourth of x. In the first condition, only one preceding vernier was displayed. The grating followed immediately (one vernier). In the second condition the first vernier was followed by the anti-vernier and the grating. Both verniers had the same offset size (two verniers). In both conditions an almost linear increase in performance is found which reaches a ceiling effect for an offset size of $1.5x''$ if only one vernier is presented. In the second condition the offset of the first vernier dominates over the offset of the anti-vernier for all values, i.e. performance is always above 50% correct responses. This result holds not only for the mean but for all observers individually (per block of 80 presentations). Discarding ceiling effects, computation and averaging of vernier offsets seem to be almost linear.

gratings composed of 5 or 25 elements are presented, the first vernier dominates (Figs. 4 and 7). Therefore, perceptual dominance can be reversed depending on the temporal order of elements. This reversal of dominance shows that stimuli are not processed independently in the sequence of appearance, i.e. one after the other. If vernier and anti-vernier are followed by a single aligned vernier, presented for 300 ms, performance is around 50% correct responses suggesting cancellation of offsets (Fig. 2, V–AV–G).

Effects depend not only on the temporal order of elements but also on the spatial layout of the subsequent grating. These masking gratings consist of either 1, 5, or 25 elements, each one being a superset of the preceding version. Hence, the spatio-temporal layout in the center of the grating is identical in these three conditions but results differ. Moreover, in the unmasked condition, the single aligned vernier condition, and the shine-through condition, performance is based on a unique element at the center of the grating where the fused vernier offsets are perceived. However, performance differs qualitatively in these three conditions. Clearly, effects cannot be explained by spatially local processing solely. Therefore, the temporal order *and* the spatial layout of the mask determine the fused offset changing from dominance of the anti-vernier, to offset cancellation, and dominance of the first vernier.

The reversal of dominance shows that visual information processing is not determined exclusively by the temporal order in the presentation of stimuli. The reversal of dominance reveals complex temporal mechanisms that may be in operation during the very first neural processing epoch (e.g. Keysers, Xiao, Foeldiak, & Perret, 2001; Sugase, Yamane, Ueno, & Kawano, 1999; Van Rullen, Gautrais, Delorme, & Thorpe, 1998; Thorpe, Fize, & Marlot, 1996; Tovee, Rolls, Treves, & Bellis, 1993).

Dominance of the first vernier in the feature inheritance and shine-through conditions cannot be attributed to a fast (unconscious) priming effect, as found in paradigms using masked congruent and incongruent prime stimuli, since dominance of the first vernier should also be present in the unmasked condition (Klotz & Neumann, 1999; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003).

4.2. Unique percepts

Because of the rapid presentation, vernier and anti-vernier are fused to one perceived vernier expressing the weighted sum of the offsets of both verniers. Naive observers in neither condition realize that *two* verniers are presented sequentially.

The perception of the fused offsets depends on the spatial layout of the following mask. For example, vernier and anti-vernier are perceived as one centrally visible shine-through element when a 25 element grating follows. For a 5 element grating, the fused vernier and anti-vernier offset is rendered visible at the edges of the grating (future inheritance). Therefore, in this condition fused offsets are, in addition, mis-localized. Still, the first vernier dominates in both condition.

For a five element grating vernier and anti-vernier offsets are fused but rendered visible at the edges of the grating (feature inheritance). Therefore, in this condition fused offsets are mis-localized but still the *first* vernier dominates.

In feature inheritance and shine-through fusing the features seems to be a linear process dominated by the *first* vernier—at least within the range of offsets tested, and discarding floor and ceiling effects.

Results of the conditions—single vernier, 5, and 25 element masking grating—cannot be compared directly because presentation times and offset sizes used differ widely, being smallest for a single masking element following after vernier and anti-vernier and largest for a grating consisting of five elements. Still, qualitative results are very similar in feature inheritance (five element grating) and shine-through conditions (25 element grating), while mechanisms might differ since visibility of the verniers and the focus of attention differ.

In *feature inheritance* the fused features are mis-bound. Mis-binding is experienced in several other phenomena such as in illusory conjunctions in which, for example, a red letter '*X*' may appear as blue if neighboring a blue letter and if attention is distracted (Treisman, 1998). Feature mis-binding in our terminology occurs also with masked stimuli in which the mask does not spatially cover the target (Enns, 2002; Wilson & Johnson, 1985; Stewart & Purcell, 1970; Werner, 1935). In crowded displays, the orientation of a number of Gabor patches can be averaged yielding one perceived orientation (Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). The feature inheritance paradigm allows us to study mis-binding in great spatio-temporal detail. In feature inheritance, features seem to migrate from the location of vernier stimulus presentation to the preferred edge. Performance improves when a blank period follows the vernier indicating a process of feature spread in time (see Herzog & Koch, 2001). The dominance of the first vernier may arise because its offset reaches the preferred edge before the anti-vernier does (see Herzog & Koch, 2001).

In *unmasked* conditions the anti-vernier dominates performance. Dominance of the anti-vernier might be explained by a prolonged afterimage favoring the anti-offset. A following mask terminates this persistence as the anti-vernier may mask the persistence of the first vernier (for another explanation, see next section "Masking").

It remains an open question whether the anti-vernier modulates neuronal response to the "stronger" first vernier, thereby increasing the signal to noise ratio, or if there is a neural competition between vernier and anti-vernier yielding more often a percept dominated by the first vernier.

4.3. Masking

In backward masking, two elements presented one after the other can interfere strongly with each other (e.g. Bachmann, 1994; Breitmeyer, 1984). The reversal of dominance and the effects of temporal order might be explained as follows on the basis of masking models. In the "unmasked" condition, the anti-vernier dominates since backward masking exerted by this stimulus is stronger than forward masking exerted by the first vernier. In the conditions with the additional grating masks, the anti-vernier suffers from both backward and forward masking from the mask and the first vernier, respectively. The first vernier, on the other hand, is only backward masked and therefore dominates. However, the effects of the spatial layout are not easily explained with most masking models since these models are usually based on spatially *locally* restricted interactions. The effects of the extension of the mask on the other hand, yielding feature inheritance or shine-through, can only explained by more *global* spatial aspects of the mask (see also Herzog & Fahle, 2001; Herzog & Koch, 2001).

Bachmann (1994) proposed that masking does not result from local energy competition but from a lack of conscious resources available. According to this view, a visual stimulus is processed in two loops. Fast signaling is achieved in visual routing from the retina to different cortical areas. A slower processing occurs in the thalamo-cortical loop which is thought to trigger conscious resources. After a signal has reached the thalamus, unspecific conscious resources are provided to the appropriate cortical sites which support visual processing. Cortical signaling of the first stimulus is, however, so fast that for short display times the thalamic signal arrives late and processing of the stimulus presented second is supported, rather than of the first. As a consequence, perception and performance are dominated by this stimulus. Since this model, as many others, processes stimuli strictly depending on the order of presentation, it cannot explain why dominance reverses between the first and second stimulus if a mask follows. In our paradigm, vernier offsets cannot be consciously resolved by the observers. Therefore, it might be that the fusion of vernier and anti-vernier is accomplished before conscious resources are allocated at all, and therefore, Bachmann's theory might simply not apply for this fusion mechanism.

If two masks sequentially follow a target, performance can be better than if only one mask follows (e.g. Robinson, 1966; Dember & Purcell, 1967; Dember, Schwartz, & Kocak, 1978; Breitmeyer, Rudd, & Dunn, 1981; Tenkink & Werner, 1981; Briscoe, Dember, & Warm, 1983; Tenkink, 1983; Francis, 1997). The second mask somehow neutralizes the first one. Analogously, in our paradigm, introducing a second, anti-offset vernier deteriorates performance. If a third stimulus, an extended grating, follows after the verniers discrimination of the first vernier improves. However, the anti-vernier is fused with the vernier rather than simply masking it. Offsets of both verniers are taken into account for the decision. In this sense, in our experiments two targets are followed by a mask rather than the first vernier by two masking elements.

4.4. Summary

Feature fusion is not a purely local process. Dominance reversals show that stimuli are not simply processed in the sequence of appearance. Features can be detached from their objects, migrate, and be bound to different elements. Feature inheritance and shine-through allow to determine these various kinds of feature integration processes in great detail.

Acknowledgements

M. Herzog was supported by a fellowship from the Deutsche Forschungsgemeinschaft (Forschungsstipendium) and by the SFB 517 "Neurocognition" of the Deutsche Forschungsgemeinschaft (DFG). C. Koch received funding from the Keck Foundation, NIMH and the NSF-sponsored Engineering Research Center at Caltech. Sven Heinrich's and Marc Repnow's help in setting up the equipment and maintaining the computers was invaluable. We like to thank Bruno Breitmeyer and Talis Bachmann for very useful discussions.

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