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Spatial versus temporal grouping in a modified Ternus display

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Abstract

The Ternus display can induce a percept of 'element motion' or 'group motion'. Conventionally, this has been attributed to two different motion processes, with different spatial and temporal ranges. In contrast, recent studies have emphasised spatial and temporal grouping principles as underlying the apparent motion percepts in the Ternus display. The present study explored effects of spatial and temporal grouping on the apparent motion percept in a novel Ternus display of oriented Gabor elements with no inter-frame interval. Each frame of this stimulus could be further divided into 'sub-frames', and the orientation of the carriers was changed across these sub-frames. In four experiments transitions were found between the motion percepts with changes in orientation across time (Experiment 1) and space (Experiment 2), and with a temporal offset in the orientation change of the outer element (Experiment 3) to the extent that group motion was not perceived even with large orientation changes over time that previously led to group motion (Experiment 4). Collectively, these results indicate that while spatial properties have an influence in determining the percept of the Ternus display, temporal properties also have a strong influence, and can override spatial grouping. However, these temporal effects cannot be attributed to spatio-temporal limits of low-level motion processes. Some aspects of the observed spatial grouping effects can be accounted for in terms of a modified association field, which may occur through connectivity of orientation selective units in V1. The temporal effects observed are considered in terms of temporal integration, the transitional value at a temporal offset of 40 ms being remarkably similar to psychophysical and neurophysiological estimates of the peak temporal impulse response. These temporal responses could be detected at a higher level in the system, providing a basis for apparent motion perception.

Keywords: Ternus; Apparent motion; Orientation; Lateral interaction; Temporal coding

1. Introduction

An enduring concept in understanding apparent motion perception is the distinction drawn between 'low-level' and 'high-level' motion processing (Braddick, 1980; Dawson, 1991; Watanabe, 1998). The 'low-level' process is thought to be pre-attentive and based upon dedicated motion sensors, while the 'high-level' process is possibly attention-based and senses motion via an analysis of spatial form. Evidence exists that these processes may occur at different cortical levels (Claeys, Lindsey, Schutter, & Orban, 2003; Liu, Slotnick, & Yantis, 2004; Muckli et al., 2002; Zhou et al., 2003). One stimulus that has been often used as evidence for two such processes is the Ternus display (1926, 1938).

This display consists of three collinear elements, displaced from one presentation to the next, such that the second and third elements of the first frame become the first and second elements of the second frame (Fig. 1). This manipulation poses a motion correspondence problem, as there is more than one possible way in which elements can be matched across frames. In fact, this ambiguous displacement generally evokes one of two different percepts: in 'element' motion the central elements are perceived as static, while the outer element appears to skip back and forth over the central elements; in 'group' motion, all the elements are perceived to move in unison from one frame to the next, and the identity of the central elements changes

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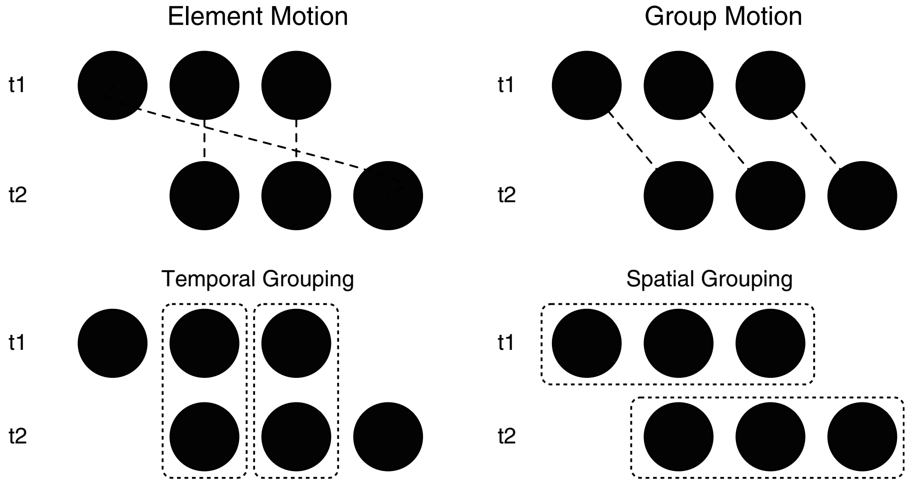

Fig. 1. In the classical Ternus display, a group of dots are spatially displaced on alternate frames (t1 and t2). With no inter-frame interval between frames the percept is of the outer element 'skipping' over the static central elements, this is known as 'element motion' (upper left figure); with an inter-frame interval longer than ~40 ms, the apparent motion is perceived for the group of elements as a whole, this is known as 'group motion' (upper right figure). Element motion can be attributed to the central elements being grouped across time, leaving the outer element ungrouped and free to move independently (lower left figure). Group motion can be attributed to all the elements being grouped spatially, making the central elements non-identical on each frame, and resulting in all the elements moving as a whole.

across frames (Fig. 1). We used a novel variation of the stimulus in which the display consists of frames of oriented Gabors, further divided into 'sub-frames'. With this stimulus we focused on manipulations of spatial and temporal properties that can selectively favour one motion percept over another.

The great majority of previous studies have relied on varying the inter-frame interval (IFI) between successive frames of the Ternus display: Generally, longer IFIs resulted in more frequent reports of group motion, with a transition between the element and group motion percepts (i.e. at the 50% point of the psychophysical function where reports of element/group motion are equally likely) at an IFI around 40 ms (Pantle & Petersik, 1980; Pantle & Picciano, 1976; Petersik & Pantle, 1979). Other manipulations can also influence the motion percept, such as: frame duration (Petersik & Pantle, 1979); adaptation to group or element motion (Petersik & Pantle, 1979); varying contrast (Petersik & Pantle, 1979); perturbing the location of elements (Pantle & Petersik, 1980).

Initially, the reliance of the motion percept on the IFI led to accounts of the phenomenon in terms of mechanisms with different spatial and temporal limits (Braddick, 1980; Pantle & Petersik, 1980; Petersik & Pantle, 1979). By one account (Petersik & Pantle, 1979) the transitions observed between two perceptual behaviours reflected the 'short-range' and 'long-range' motion processes (Braddick, 1974): the short-range process operating within a temporally and spatially limited range drove the element motion percept, considered as a cross-correlation of luminance over time (the two stimulus frames), while the long-range process (operating beyond the temporal and spatial span of early short-range processing) underpinned the group motion percept via an analysis of form. One flaw in this account is that element motion is known to occur for displacements (of the outer element) much larger than the spatial limit of 'short-range' processing (Petersik, Pufahl, & Krasnoff, 1983). An alternative account of the phenomenon that retained the short/long-range distinction proposed that (for low IFIs) short-range processing signalled the 'non-motion' of the inner elements, while long-range processing was responsible for the motion of the outer element (Braddick & Adlard, 1978; Petersik, 1984). While this modified argument retained the short-/long-range distinction, it was suggested that at a fundamental level it confounded a description of the stimulus with underlying perceptual processes and that a distinction between 'first-order' and 'second-order' motion might be more appropriate (Cavanagh & Mather, 1989), but it is not entirely clear how these distinctions can account for the transition in percept in the Ternus display (Cavanagh, 1991; Petersik, 1991). Furthermore, it has been argued that while the short-/long-range distinction may be valid, the percept of the Ternus display might be driven only by the long-range or 'feature-tracking' process (Scott-Samuel & Hess, 2001). Clearly, there has been little consensus on what form a short-/long-range account of the Ternus display should take, or even if it is appropriate (for a more detailed discussion of these different accounts see Petersik & Rice, 2006). There is, however, another approach to accounting for the Ternus phenomenon that does not appeal to different motion processes.

More recently, the perceptual transitions of the Ternus display have been found to depend upon perceptual grouping principles (He & Ooi, 1999; Kramer & Yantis, 1997; Ma-Wyatt, Clifford, & Wenderoth, 2005). However, the influence of grouping factors is not easily explained by the short-/long-range account. Kramer and Yantis (1997) examined the effects of 'spatial grouping' (similarity and proximity within a single frame of the display) and 'temporal grouping' (similarity and proximity across frames of the display). They found that the similarity of elements, and their spatial context, could bias perception towards group or element motion. Configurations that encouraged grouping of all elements within frames (e.g. where all elements have the same shape) resulted in more group motion, while those that 'anchored' the internal elements in place and encouraged grouping across frames (e.g. where additional elements were placed above and below the inner but not the outer elements) resulted in more element motion percepts Similarly, grouping by contrast, similarity (Ma-Wyatt et al., 2005) and stereoscopic depth, surfaces or occlusion (He & Ooi, 1999), influenced the motion percept. These studies of contextual effects suggest the Ternus display may not simply tapping into two different motion processes with different spatio-temporal ranges. Rather, the transition from element to group motion in the Ternus display could be understood in terms of a competition between spatial and temporal grouping (Kramer & Yantis, 1997; Ma-Wyatt et al., 2005) or 'within-frame' and 'across-frame' grouping (He & Ooi, 1999): spatial grouping results in group motion, and temporal grouping results in element motion. This argument therefore places processing of form (i.e. perceptually organising the stimulus into meaningful groups) before the motion analysis.

What are the mechanisms of the spatial and temporal grouping in the Ternus display? Alais and Lorenceau (2002) addressed this question, measuring perceptual transitions as a function of IFI in Ternus displays composed of Gabor patches with parallel or collinearly aligned carriers, and looked for transition points between percepts of group and element motion. They found that spatially continuous internal element structure (collinear Gabors) biased the percept towards group motion (within-frame grouping), shifting the function across the dimension of IFI. This effect of co-linearity of elements suggests a mechanism of contour integration, similar to that demonstrated by 'path-finding' experiments (Field, Hayes, & Hess, 1993). Indeed, they found that within-frame grouping at a fixed IFI could be disrupted by perturbing the co-linearity by inter-element separation, orientation jitter, and phase differences, all leading to increased element motion. Finally, they demonstrated that the contour-linking effect held for a circular configuration of Ternus elements, but was attenuated at increased eccentricity, concurring with previous evidence that contour linking is strongest in central vision (Hess & Dakin, 1997). Alais and Lorenceau explained their results in terms of an 'association field' that links elements of similar orientation, suggesting a basis for the Ternus effect in early spatial visual processing. This approach effectively applied a model that was developed to account for spatial processing to an apparent motion phenomenon. However, the findings only assessed the effect of orientation on spatial grouping, it remained unclear what effects orientation have on temporal grouping, and while the association-field model accounted for the effect of orientation found for the Ternus display of Gabor stimulus elements, it was not clear how generalisable the model was to other stimulus configurations. The present study further explores the effects of orientation, on both spatial and temporal grouping, on apparent motion perception in the Ternus display, to further elucidate the mechanisms that underlie the behaviour.

The basic manipulation of the present study is similar to that used previously by Scott-Samuel and Hess (2001). They varied the orientation (about vertical) of sinusoidal luminance modulations of static noise elements across frames of their Ternus display. They found that with a 0 ms IFI, increasing the orientation difference across frames elicited a transition from element to group motion. This is another example of spatial influences on the apparent motion percept in the Ternus display. However, as the transition angle found by Scott-Samuel and Hess (2001) was larger than previously reported spatial vision thresholds, they concluded that the Ternus display does not rely upon spatial vision, but a purely long-range motion or 'feature-tracking' process that signals motion when it identifies that something in the scene has changed. This argument therefore does not consider any processes of perceptual organization as an underlying factor, and is not entirely consistent with the findings of Alais and Lorenceau (2002) who found that processes of spatial vision are important in the Ternus display, at least for one composed of oriented Gabor elements. Here, we combine the basic manipulation of Scott-Samuel and Hess (2001) and of Alais and Lorenceau (2002) in an attempt to provide further insight into the mechanisms underlying the apparent motion perception in the Ternus display, specifically focusing on manipulations of carrier orientation that influence perceptual grouping, i.e. spatial and temporal grouping.

2. General methods

The stimulus was a modified Ternus display in which the elements were Gabor patches of with a fixed carrier spatial frequency and envelope size. Alais and Lorenceau (2002) compared the effects of two carrier orientations, parallel and collinear, as a function of IFI. In contrast to this and to most previous studies of the Ternus phenomenon, we used a 0 ms IFI, following Scott-Samuel and Hess (2001). Therefore, the effects observed are not indirect modulations of transitions over IFI: any transitions between group and element motion percepts observed here are solely a result of spatial and temporal manipulations that are independent of IFI. The spatial aspect of the stimulus varied was the orientation of the Gabor carrier, and this was varied not only across time, but also over space. In addition to this, a temporal manipulation was introduced, which was an offset in change in orientation between elements. These manipulations are clarified below.

In addition, the changes in orientation were relative to either vertical (equivalent to the Alais and Lorenceau parallel condition), or horizontal (equivalent to the Alais and Lorenceau collinear condition). Thus, comparing the effects of changes in orientation across frames in the horizontal and vertical conditions permits an assessment of whether any spatial grouping effects that could be attributed to an association-field modulate the orientation effect. A unique aspect of the stimulus is that each frame of the display was further divided into 'sub-frames', which served to dissociate the changes in orientation with changes in element location.

By varying the number of sub-frames it was possible to assess if changes in orientation or the timing of changes in element location were the determining factor in transitions between motion percepts.

Stimuli were generated in MATLAB running on MacOSX (Powerbook G4) with the PsychToolbox extensions (Brainard, 1997; Pelli, 1997). Stimuli were presented to observers on a Lacie electron22blue monitor at a resolution of 1024 by 768 pixels, and a refresh rate of 100 Hz. Luminances were measured at the centre of the screen (our presentation location) using the Optical OP200-E (Cambridge Research Systems Ltd.) photometer; mean luminance was 22.8 cd/m^2. Stimuli were then gamma corrected during experiments using a lookup table. Experiments were performed in a dark room. Ternus elements were Gabor patches (1 cpd, sd = 0.25 deg, 2 deg centre-to-centre separation), at 50% contrast. The carrier orientation, with respect to the horizontal or vertical axis in different conditions (see Fig. 2), was varied over time in four experiments.

In all experiments the stimuli consisted of two 'stimulus frames' (f1 and f2), that differed in their outer element location. These two stimulus frames were presented in cycles, such the on each trial five stimulus frames were presented in total (f1 → f2 → f1 → f2 → f1). The duration of each of these stimulus frames depended upon the number of 'sub-frames', across which the exact orientation was varied as described below. The duration of a single sub-frame of a stimulus frame in all experiments was 200 ms. In the vertical axis condition, carrier orientation was varied about the vertical axis, and in the horizontal axis condition, carrier orientation was varied about the horizontal axis. The total change in orientation across frames is referred to as the 'orientation difference'. In the example in Fig. 2, carrier orientation is the same across frames. In all experiments, carrier phase was constant for all elements within a trial, and randomised across trials.

In all Experiments, observers were required to indicate on a given trial whether they perceived element or group motion. Psychophysical functions were then derived, ranging between the two percepts. The point of transition between element and group motion (i.e. the point at which observers perceive group or element motion 50% of the time) elicited by changes in orientation over space and time provided estimates of the limits of spatial and temporal grouping by orientation selective mechanisms. Experiment 1 varied the change in orientation of the Gabor carriers over time, revealing the magnitude of orientation differences required to impair temporal grouping and drive the group motion percept. In Experiment 2, the change in orientation across frames was fixed, and the difference in orientation between outer and central elements was further varied. Any effect arising from this manipulation permits a direct comparison between the limits of temporal (Experiment 1) and spatial grouping (Experiment 2) by orientation, and hence an insight into whether the same process is involved in both cases. Experiment 3 varied the temporal offset in the change of orientation between outer and central elements, to assess whether the spatial grouping that results from changes in orientation (Experiment 1) is dependent on common onsets. Finally, Experiment 4 repeated Experiment 1 over the range of temporal offsets used in Experiment 3. Because manipulations of Experiment 1 bias group motion, while those of Experiment 3 bias temporal grouping, Experiment 4 puts these in conflict to assess what grouping principle has a stronger effect in biasing motion percepts.

One experimenter (J.W.) and four naïve observers (J.A.M., M.T., C.L., C.B.) participated in the experiments. All had normal or corrected to normal vision. J.W. completed all experimental conditions in all experiments. J.A.M. and C.L. completed all experimental conditions in Experiments 1, 3 and 4. M.T. and C.B. completed all experimental conditions in Experiments 1 and 2.

3. Experiment 1: Effect of orientation on temporal grouping

This experiment investigated how similar the carrier orientation of elements is required to be across frames for temporal grouping (and thus element motion) to occur. Additionally, effects of the axis of orientation and potential effect of sub-frames were assessed.

3.1. Procedure

The two stimulus frames of each stimulus were presented in cycles, such that on each trial five stimulus frames were presented in total. A number of sub-frame conditions were used, from one sub-frame (s1) through to seven sub-frames (s7). Carrier orientation was changed on alternate sub-frames, through a total orientation difference which varied from 0 deg to 45 deg in 7.5 deg steps. Because each sub-frame was presented for a duration of 200 ms, the total duration that the outer element was located at the left or right position increased with number of sub-frames, as did the number of changes in orientation for all elements. Note that if total stimulus frame duration was important in determining the motion percept for our stimulus, this would predict that more group motion would be perceived with increasing number of sub-frames (Petersik & Pantle, 1979). Fig. 3 (leftward panels) illustrates a total orientation difference of 45 deg, for the horizontal and vertical axis conditions, for one sub-frame. In this case, on successive frames, the orientation flips from 22.5 deg one side side of horizontal/vertical, to 22.5 deg the other side of horizontal/vertical. Fig. 3 (rightward panels) illustrates an orientation difference of 45 deg in the horizontal axis condition for three sub-frames. In this case, on successive sub-frames, the orientation flips from 22.5 deg one side side of horizontal/vertical, to 22.5 deg the other side of horizontal/vertical. This holds for all sub-frame conditions, the orientation flip-flopping by the given angle from sub-frame to sub-frame. In a given experimental session, all possible conditions were randomly interleaved. Observers ran up to 15 sessions to attain 30 trials per data point.

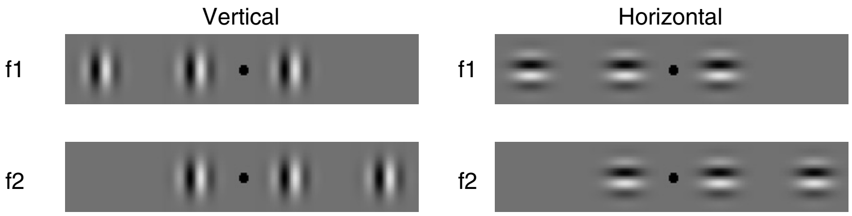

Fig. 2. Stimuli for all experiments consisted of two alternating stimulus frames of 200 ms duration (f1 and f2) that differed in outer element location. Carrier orientation varied with respect to the vertical axis (left figure) or the horizontal axis (right figure) in different conditions.

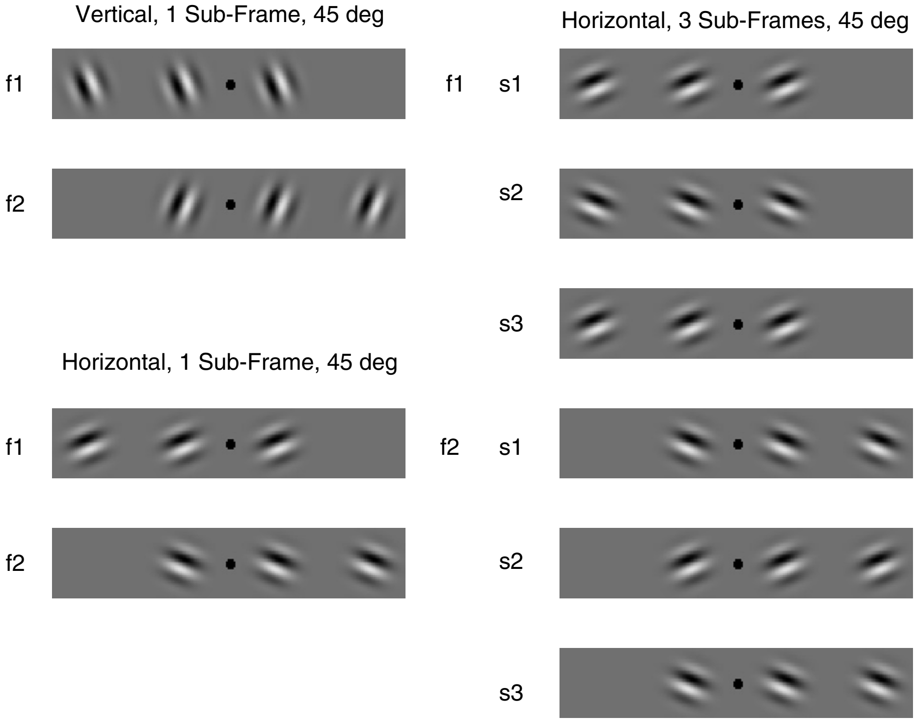

Fig. 3. Stimuli for Experiment 1. The leftward panels contain stimulus frames for the one sub-frame condition, at a total orientation difference of 45 deg (i.e. ±22.5 deg from horizontal or vertical across successive frames) from the vertical (upper) and horizontal axes (lower). The rightward panel contains stimulus frames for the three sub-frame condition (sub-frames labelled s1–s3), again at a total orientation difference of 45 deg (from the horizontal axis).

3.2. Results and discussion

The results for Experiment 1 are shown in Fig. 4. With minimal change in carrier orientation of the Gabor patches, only element motion was perceived and the inner Gabors were seen as static. In contrast, group motion was dominant when the change in orientation across sub-frames was sufficiently large (e.g. from −22.5 deg to +22.5 deg, a total orientation difference of 45 deg, with respect to the axis of orientation). It can be seen that there was a smooth transition between these two extremes, in which there was an increasing frequency of group motion as the orientation difference increased. In this and the following experiments, Weibull functions were fitted through the average[1] data points for each of the different conditions (implemented by the fminsearch fitting routine of MATLAB, over 9999 iterations). It can be seen that the functions for the different sub-frames within each axis of rotation overlap considerably (Fig. 4a and b). Clearly, all functions are shifted to the right for the vertical axis condition compared to the horizontal axis condition. To summarise these data, transitional values were extracted from each function at the 50% group/element level. Ninty-five percent confidence intervals were computed (plotted as error bars) on these transitional values by a bootstrapping procedure.

The average (across sub-frames) transitional orientation differences found here were 15 deg in the horizontal condition, and 23 deg in the vertical condition. From the summary plots (Fig. 4c), it can be seen that group motion was overall more frequent for horizontal axis alignment. This confirms that the effect of co-linearity found by Alais and Lorenceau (2002) at variable IFIs also holds at a 0 ms IFI, and suggests a mechanism of contour linking within frames that biases the perception towards group motion. However, contour linking by collinear elements can only be understood to occur for smaller orientation differences across frames (as the larger the difference the larger the carriers deviate from the axis within a frame), and beyond a point that linking must break down. This leads to the somewhat paradoxical situation that at large orientation differences across frames, there is unlikely to be contour linking by co-linearity within a frame, yet it is precisely at these large orientation differences that group motion is more likely to occur. Thus while a contour linking by co-linearity can clearly facilitate the spatial grouping here, accounting for differences between axis of orientation conditions, it is not necessary for the spatial grouping effect.

In general, transitional values remain constant across sub-frames. This is inconsistent with the prediction that with increasing number of sub-frames, i.e. as the total frame duration is increasing, more group motion will be perceived. Indeed, if anything there is a trend towards less group motion (spatial grouping) with increasing number of sub-frames. This result implies that it is not the total frame

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[1] Following Alais and Lorenceau (2002), as we were not interested in individual biases we averaged the data across the five observers.

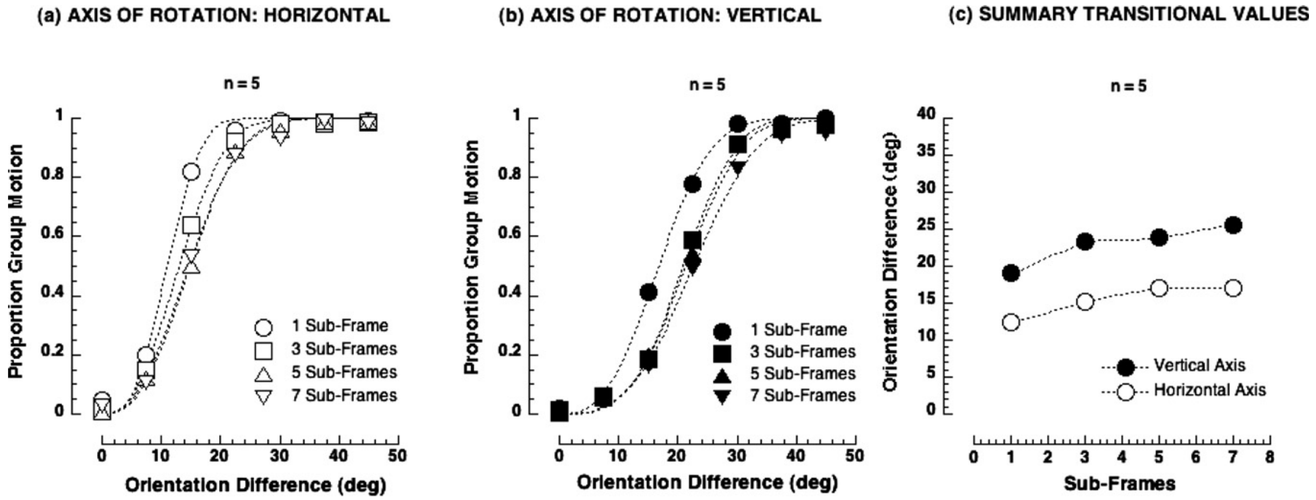


Fig. 4. Results for Experiment 1. These are data averaged over the five observers. (a) Leftward panel is the horizontal axis condition, (b) central panel is the vertical axis condition, (c) rightward panel contains the summary thresholds (error bars not visible). The dotted lines in (a) and (b) are Weibull fits.

duration that is crucial in determining the transition point for these stimuli; rather, it is related to the change in orientation over sub-frames driving the change.

The results indicate that beyond an orientation difference across frames of around 20 deg (depending on number of sub-frames and axis of orientation) temporal grouping cannot occur. This finding rules out two accounts of the temporal grouping, one based on orientation discrimination, the other on orientation selectivity of motion detectors. An orientation discrimination account states that when the change in orientation is below the discriminable difference, no change is detected and elements are grouped temporally; however, when they exceed a discrimination threshold the change is detected and hence provides a signal for group motion. However, orientation discrimination has high acuity—less than 1 deg (Burbeck & Regan, 1983; Caelli, Brettel, Rentschler, & Hilz, 1983)—and therefore does not predict the large transitional values of changes in orientation across frames here. Similarly, an orientation bandwidth account states that temporal grouping occurs due to integration of orientations across frames. Orientation bandwidths for motion selective detectors have previously been estimated by a number of different techniques. Snowden (1992) found that bandwidth varies with both temporal and spatial frequency, and reported a figure of 30 deg at 1 cpd for stimuli over the range 0.5–4 Hz. Our stimuli were very similar, 1 cpd at temporal frequency of 5 Hz, yet the transitional values are lower than the bandwidth reported by Snowden (1992). Other studies either agree well with Snowden's estimate (e.g. Anderson, Burr, & Morrone, 2001; Van den Berg, van de Grind, & van Doorn, 1990), or are even wider (Georgeson & Scott-Samuel, 2000; Scott-Samuel & Hess, 2002). None of these estimates fit particularly well with the average transitional angle of 15–23 deg (dependent upon the axis of orientation) reported here. The transitional orientation differences are similar to the value of around 15 deg found by Scott-Samuel and Hess (2001), who argued that a high-level feature tracking mechanism was responsible for the detection of orientation change leading to the group motion percept. This remains plausible here, although the effect of the axis of orientation points to the influence of a lower-level spatial grouping process. We return to this in further detail in Section 7.

4. Experiment 2: Effect of orientation on spatial grouping

In Experiment 1 there was evidence for some effect of carrier continuity, in that more group motion was perceived in the horizontal condition. However, such continuity of carrier orientation between elements within any frame was not necessary for spatial grouping: group motion occurred in both the vertical axis and horizontal axis conditions, as long as the orientation difference across sub-frames was sufficiently large (to impair temporal grouping). Experiment 2 investigated the effect of carrier orientation within a frame—does the spatial grouping require a common carrier orientation across elements within a frame?

4.1. Procedure

The methods were as for Experiment 1, but here similarity within a given frame was manipulated by rotating the outer element by a further 0–60 deg beyond the orientation difference of the inner elements. This is illustrated in Fig. 5, which shows two stimulus frames for the one sub-frame condition, for both horizontal and vertical axis conditions, and for three sub-frames in the vertical axis condition. In this experiment, the different sub-frame conditions were fully interleaved as in Experiment 1. Again, observers ran 15 sessions to attain 30 trials per data point.

4.2. Results and discussion

Results for Experiment 2 are presented in Fig. 6. With no difference in carrier orientation between the central

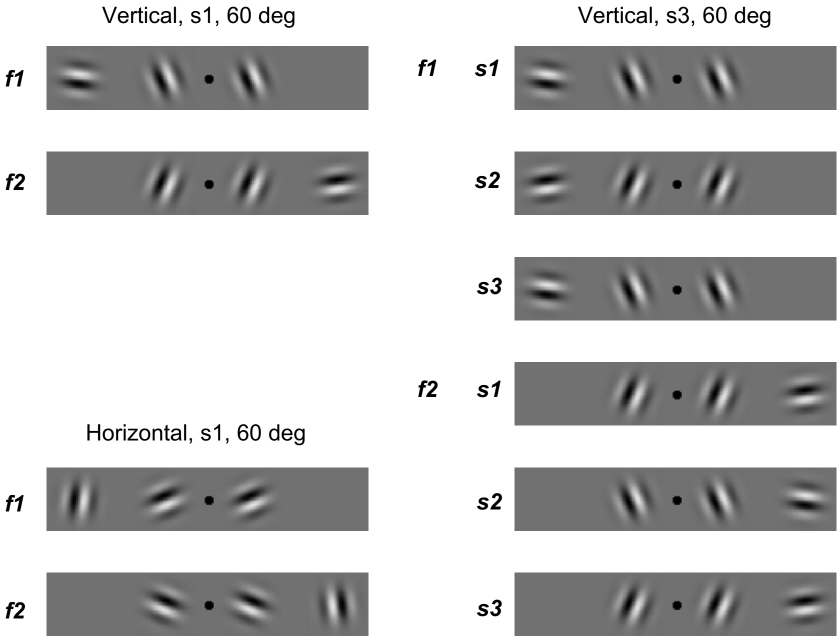


Fig. 5. Example of stimuli for Experiment 2. Here the total orientation difference is fixed at 45 deg (the largest angle of Experiment 1), and the outer element is further rotated (in these examples by 60 deg). This manipulation was repeated for a range of 'angular differences' (the angle of the outer element minus that of the inner element). On the left are frames for the one sub-frame condition, and the right are frames for the three sub-frames condition (sub-frames labelled s1–s3).

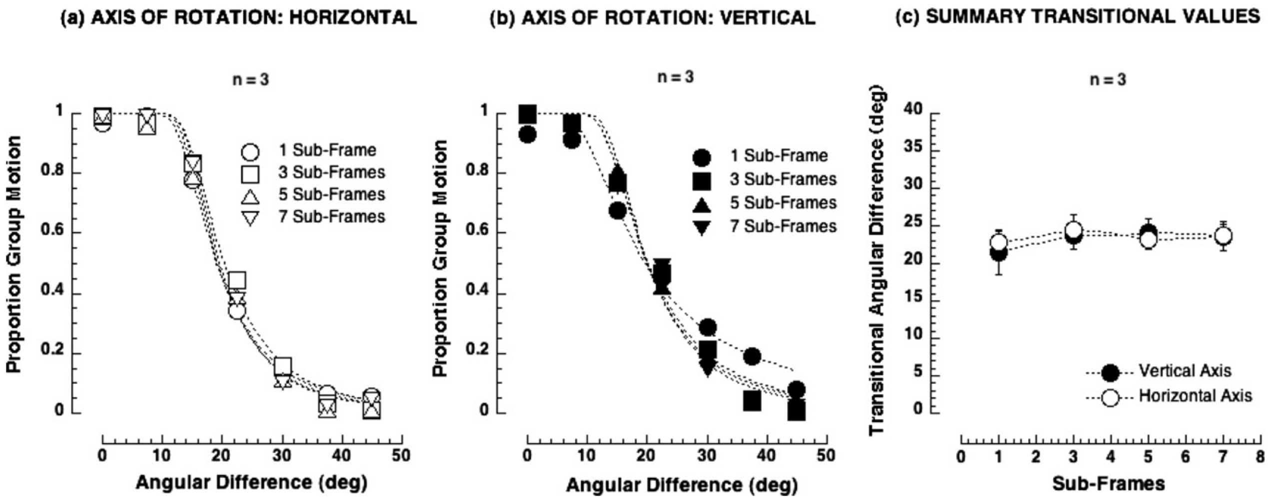


Fig. 6. Results for Experiment 2. These are the average data for the three observers. (a) Leftward panel plots data for the horizontal condition, (b) central panel plots data for the vertical condition, (c) rightward panel plots transitional values for both conditions. The dotted lines in (a) and (b) are Weibull fits.

and outer elements, only group motion was perceived (with an orientation difference across sub-frames that prevents temporal grouping). In contrast, element motion was dominant when there was a sufficiently large orientation difference within a frame (i.e. a 60 deg difference between the central and outer elements), even though the central elements were changing orientation over time in a way that previously impaired temporal grouping (Experiment 1). It can be seen that there is a smooth transition between these two extremes, in which there is a decreasing frequency of group motion as the orientation difference increases. This shows that while spatial grouping will occur when temporal grouping fails (Experiment 1), spatial grouping of oriented Gabor elements requires similarity in orientation. There is little influence of number of sub-frames on the motion percept, again indicating that it is the orientation changes and not the total frame duration that is important in determining the motion percept.

Looking at the summary transitional values (Fig. 6c), the outer element is grouped with the inner elements in a frame for an orientation difference of up to around 25 deg (average across conditions). This indicates that spatial grouping depends on a similar, but not necessarily identical, orientation of the individual elements. Furthermore, the elements need not be collinear for this difference in orientation to cause a switch in the motion percept—there is no effect of the axis of rotation, with horizontal and vertical axis transitional values falling within a similar range—suggesting that a similar process underlies the transition in both the axis conditions.

While the manipulation of Experiment 1 impaired temporal grouping and increased the likelihood of spatial grouping, the manipulation of Experiment 2 impaired spatial grouping and increased the likelihood of temporal grouping. Nevertheless, the average transitional values for the vertical axis condition are identical between Experiments 1 and 2 (23 deg)—this similarity in the thresholds here suggests that a similar process might underlie the grouping of orientation both across space and time. It must be noted, however, that the element motion is occurring despite large differences in orientation between the inner elements, a difference that previously resulted in a breakdown in temporal grouping. Thus while there are very similar effects of grouping by orientation in Experiments 1 and 2, it appears that they are not absolute—here temporal grouping can be forced to occur when spatial grouping is impaired. In Experiment 2 there was not an additional effect of contour linking (there was no difference between axis of rotation conditions), whereas in Experiment 1 horizontal transitional values were lower than vertical transition points. This translates to a difference in transitional values between the horizontal axis condition of Experiment 1 and Experiment 2—an average of 15 deg in Experiment 1 to 23 deg in Experiment 2. This between experiments comparison therefore supports the additional effect of linking for horizontally oriented elements within a frame in Experiment 1.

5. Experiment 3: Effect of temporal offset on spatial grouping

In both Experiment 1 and Experiment 2, spatial grouping occurred when changes in orientation across frames were sufficiently large and when the carrier orientations were similar enough within a frame. In Experiment 2 spatial grouping was found to occur only for elements when the carrier orientation of elements were within a similar range; beyond this range temporal grouping occurs, even with large orientation differences across frames which previously prevented such grouping. In other words temporal grouping can be induced by similar orientation across time, but is not a necessary requirement. Experiment 3 assessed the temporal limit of the spatial grouping by common orientation. The orientation difference across frames was fixed, and the timing at which the changes in orientation between central and outer elements occur was varied.

5.1. Procedure

The methods were as for Experiment 1, except that the total orientation difference was fixed (45 deg). In addition, a temporal offset (Δ) between changes in carrier orientation of central and outer elements was introduced and varied from 0–80 ms, in seven linearly spaced steps (offsets used were 0, 10, 30, 40, 50, 70, and 80 ms). An example of the stimulus is shown in Fig. 7. Each sub-frame was again 200 ms, and within each sub-frame there was an additional frame due to the offset in orientation change between the central and outer elements. The first change in central carrier orientation occurred after 200 ms − Δ. The outer element then changed orientation to come in line with the others after the offset duration (Δ). It can be seen then that the presentation duration for each orientation of the central and outer elements therefore remained 200 ms despite the offset between the central and outer elements. There were three changes in orientation changes for each position of the outer element, equivalent in duration to the three sub-frame condition of Experiment 1.

5.2. Results and discussion

Results for Experiment 3 are presented in Fig. 8. With no difference in temporal offset of orientation change between the central and outer elements, only group motion was perceived. In contrast, element motion was dominant when there was a sufficiently large offset in the change in orientation between the central and outer elements (i.e. an 80 ms difference in offset between the central and outer elements). The data (Fig. 8a and b) show that longer temporal offsets of the change in carrier orientation between the central and outer elements resulted in more element motion. Indeed, there was a sharp transition between frequency of group and element motion percepts in all conditions, except the one sub-frame condition that gave a shallower function, and apart from this condition there is also little effect of the sub-frames, with transitional values remaining largely constant across the conditions. Elements were grouped within a frame when the change in outer element orientation was offset by up to around 40 ms (on average); beyond this value, spatial grouping again failed and gave way to temporal grouping, even though the changes in orientation over time previously impaired such grouping. The summary transitional values are presented in Fig. 8c: there was little difference between the horizontal- (40 ms on average) and vertical-axis (36 ms on average). This shows that the manipulation has the same effect regardless of the relative alignment of the elements. The transition of around 40 ms is within the range of the point of transition usually found with IFI manipulations in Ternus displays yet here the transition occurs without an IFI and occurs at this same value regardless of whether or not the offset occurs during a shift in element position (as demonstrated by the constant effect across sub-frames). The similarity in this value across different studies suggests that there may be a common process underlying the transition, an idea returned to in Section 7.

6. Experiment 4: Temporal grouping versus spatial grouping

Here the manipulations of Experiment 1 and Experiment 3 were combined: Experiment 1 demonstrated that

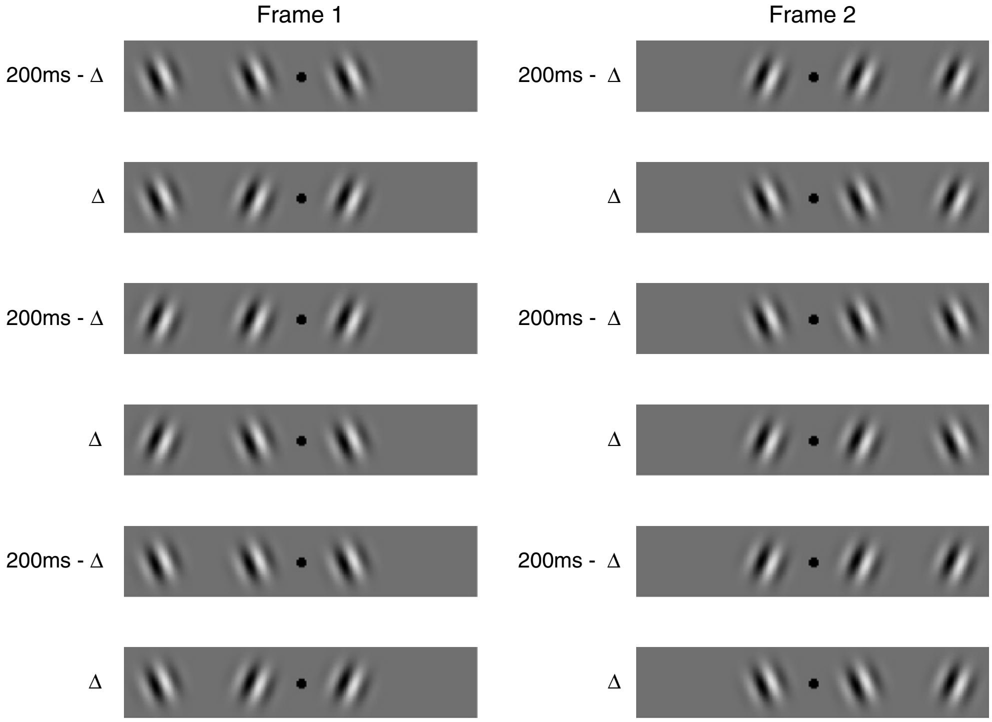


Fig. 7. Example of stimuli for Experiment 3. Here the central elements change orientation on the first sub-frame after 200 ms − Δ, where Δ is the temporal offset for that condition. The outer element then changes orientation after a further Δ ms, for three orientation changes (sub-frames) per stimulus frame (time course of sub-frames runs from top to bottom for each frame in the figure). The temporal offset was varied (range 0–80 ms) to find the transition point from group to element motion.

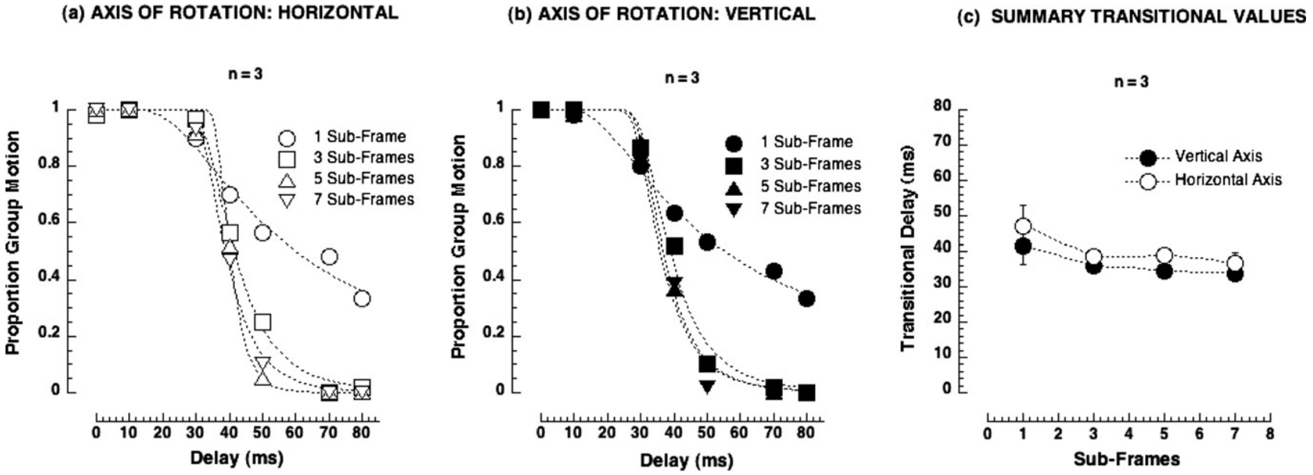


Fig. 8. Results for Experiment 3. These are the average data for the three observers. Leftward panel is the vertical axis condition, central panel is the horizontal axis condition, rightward panel contains the summary thresholds. The dotted lines in (a) and (b) are Weibull fits.

large changes in orientation across frames disrupted temporal grouping, and resulted in group motion. Experiment 3 demonstrated that a temporal offset in the change of orientation between central and outer elements disrupted spatial grouping and facilitated temporal grouping, resulting in element motion. Thus one manipulation biases spatial grouping, and another biases temporal grouping. In this final experiment, the two types of grouping were played off against each other. To this end the magnitude of change in carrier orientation across frames was varied (as in Experiment 1) for a range of temporal offsets in carrier orientation change (as in Experiment 3), so as to assess whether spatial or temporal grouping has the strongest influence.

6.1. Procedure

The methods were as for Experiment 1 except that here, for each temporal offset (Δ, 0–40 ms) of changes in carrier orientation between the outer and central elements, the orientation difference was varied through a larger range of difference than in Experiment 1, from 0 to 90 deg. Rotation angles and temporal offsets were randomly interleaved within a session and observers ran up to 15 sessions across days to attain 30 trials per data point.

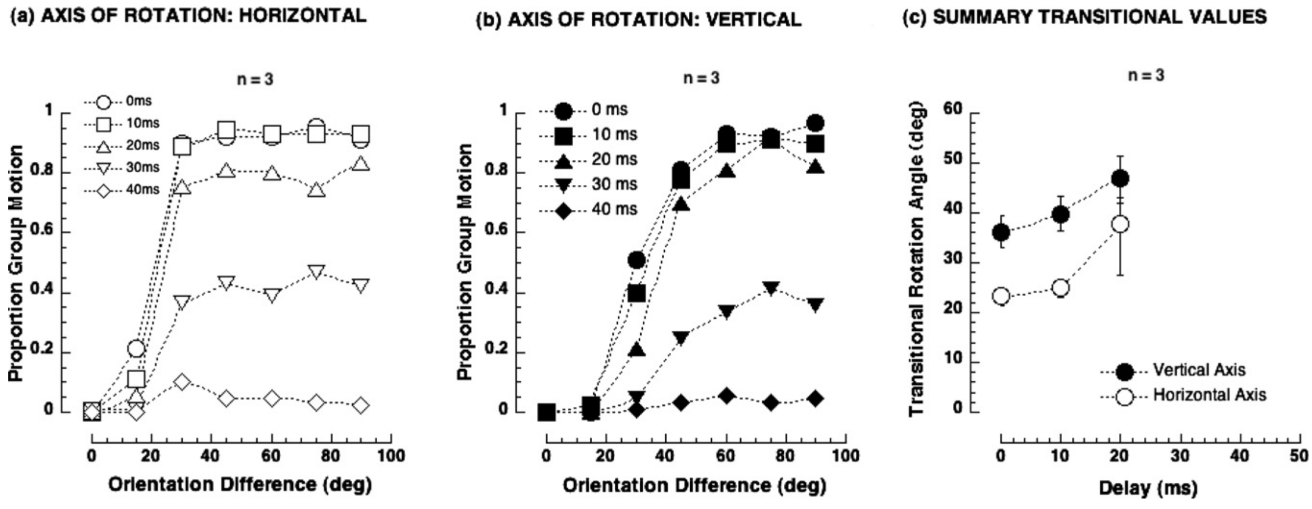
6.2. Results and discussion

The data are shown in Fig. 9a and b. With no difference in temporal offset of orientation change between the central and outer elements, and at low orientation differences, only element motion was perceived; at large orientation differences only group motion was perceived. As before, there was a smooth transition between these extremes. However, when a large temporal offset was introduced (40 ms), element motion was perceived almost exclusively, regardless of the orientation differences across frames. Increasing the temporal offset in carrier orientation change between the outer and central elements resulted in less frequent and eventually no reports of group motion. While the functions for delays up to 20 ms exhibit the transition from element to group motion found in Experiment 1, at 30 ms only some group motion was possible, and by 40 ms only a few reports of group motion remain—the temporal offset scales the functions. This is summarised in Fig. 9c, where transitional orientation differences (where they exist) are taken from Weibull fits to the data. Elements cannot be grouped across space when carrier orientation change is offset by 40 ms, despite large differences in carrier orientation over time.

7. General discussion

The four experiments reported here focused on the effects of spatial and temporal variations on the grouping of a Ternus display of Gabor elements with no IFI, in an attempt to elucidate the nature of the processes underlying the analysis of such displays. The aspects of the stimulus varied were the change in orientation of the carriers over time (Experiment 1), the difference in orientation between outer and central elements (Experiment 2), and the temporal offset in the change of orientation between outer and central elements (Experiments 3 and 4). Experiment 1 showed that observers required an orientation difference of around 25 deg or more across frames to perceive group motion, indicating that it is around these values that temporal grouping fails and spatial grouping dominates. Experiment 2 demonstrated that spatial grouping is disrupted when the change in orientation of the outer element exceeds that of the inner elements by around 25 deg, regardless of axis of rotation. This indicates that disruption of spatial grouping can lead to temporal grouping, even in conditions that previously were not conducive to such grouping (i.e. when there are large orientation differences across frames). Experiment 3 revealed that a temporal offset in the change in orientation of the outer element had the same effect as that of the spatial difference of Experiment 2: when the orientation change was offset by around 40 ms, spatial grouping was disrupted and temporal grouping again occurred. Finally, Experiment 4 found that applying a 40 ms offset to the manipulation of Experiment 1 completely disrupted the effect of orientation difference: the spatial grouping that leads to a group motion percept requires elements to be of similar orientation within a limited temporal window. If this is not the case, temporal grouping occurs even with large differences in orientation across frames, i.e. under conditions that did not previously favour temporal grouping (Experiment 1). In the following sections we consider possible underlying causes of these perceptual behaviours.

Our findings also confirmed the effect of co-linearity of elements found by Alais and Lorenceau (2002): in Experiments 1 and 4 horizontal axis condition transitional values were lower than vertical axis condition transitional values,


(a) AXIS OF ROTATION: HORIZONTAL

(b) AXIS OF ROTATION: VERTICAL

(c) SUMMARY TRANSITIONAL VALUES

Fig. 9. Results for Experiment 4. These are the average data for the three observers. (a) Leftward panel is the vertical axis condition, (b) central panels are the horizontal axis condition, (c) rightward panels are the summary thresholds. The transitional values of the rightward panel are taken from Weibull fits to the data (not shown) where appropriate.

but this effect was not found in Experiments 2 and 3 in which the initial values equated to ceiling performance for both the horizontal and vertical axes in Experiment 1. The effect of axis of orientation indicates that temporal grouping is more sensitive to changes in orientation over time (i.e. temporal grouping is less likely with smaller orientation differences across frames) for horizontally oriented carriers, as opposed to vertically oriented ones.

There was no consistent effect of increasing sub-frames across observers or experiments, with performance remaining largely stable across a sevenfold increase in the number of sub-frames. Increasing sub-frames increases the number of changes in orientation before the outer element is displaced, and therefore this finding indicates that changes in orientation that lead to transitions in perceptual behaviour are not necessarily correlated with changes in the outer element position. This point is worth emphasising, as the behaviour reported here is not a spatiotemporal effect of the kind usually associated with the Ternus display and motion processing in general.

7.1. Spatial (within-frame) grouping

Within-frame grouping (group motion) occurs for angular differences between outer and inner elements within frames of greater than around 25 deg (Experiment 2). The grouping across space within a frame for a horizontal axis of rotation might be accounted for by the orientation bandwidth of the behavioural receptive fields involved in this task. When the elements have similar orientations (i.e. are within the bandwidths of the sensors which signal their presence), an association field (Field et al., 1993) can serve to link the elements, possibly through intra-cortical connectivity in V1 (Chavane et al., 2000; Malach, Amir, Harel, & Grinvald, 1993). Field et al. (1993) found that the detection of contours defined by Gabor elements deteriorated when the elements defining the contour were oriented greater than +/−30 deg off the axis. The present figure is similar to this value, suggesting similar processes are at play in these different tasks. Indeed, recent model estimates (Beaudot & Mullen, 2006) of static orientation bandwidths are of this order (around 19–30 deg), while a range of earlier studies estimate psychophysical orientation bandwidths in the range of 10–20 deg (Blakemore & Nachmias, 1971; Campbell & Kulikowski, 1966; Movshon & Blakemore, 1973; Thomas & Gille, 1979). In addition, effects of co-linearity have previously been demonstrated in motion tasks: the perceived speed of apparent motion sequences of collinear Gabors is faster than that of parallel oriented Gabors (Georges, Series, Fregnac, & Lorenceau, 2002), accounted for by an orientation-dependent 'latency advance' of V1 cell activity (Series, Georges, Lorenceau, & Fregnac, 2002).

However, the association field theory in its original form assumes linking occurs between *collinear* elements limited by common orientation bandwidth. While there was an effect of the horizontal axis of orientation compared to vertical in the present study, it was shown that this was not necessary for spatial grouping to occur, as the effect also occurred for vertical axis (parallel) displays. This is consistent with previous findings that contours defined by orthogonal elements (similar to the horizontal axis/parallel condition here) can be grouped (Bex, Simmers, & Dakin, 2001; Field et al., 1993; Hess, Ledgeway, & Dakin, 2000). To account for such findings, a modified association field theory has been proposed (Ledgeway, Hess, & Giesler, 2005) that permits linking between similar orientations which are not exclusively collinear. This would satisfy both grouping behaviours shown here, providing a unifying account for the effects of stimulus in the present study. It is not clear if this would be able to account for Ternus effects across a wider range of stimuli, which have tended to rely on looking at transitions in perception as a function of time. Moreover, this spatial theory fails to account for the fact that when the elements are most similar in orientation (i.e. at low or zero rotation angles) group motion is not perceived, implying no spatial grouping. Rather, there appears to be a more complex interplay between temporal and spatial grouping that a (modified) association field, being a purely spatial theory, cannot account for.

7.2. Temporal (across-frame) grouping

Grouping by a (modified) association field could provide the basis of the perceived motion elicited by our modified Ternus display. However, as the association field is conventionally thought of in spatial terms, it is not clear how it could account for the effect of grouping across frames (Experiment 1). In this case, all elements within sub-frames had identical orientations, and so within-frame grouping should have led to group motion, yet such motion was only perceived when the change in orientation across frames was greater than around 25 deg. Thus it was the failure of temporal grouping across frames that allowed spatial grouping to proceed. The across-frame grouping could reflect an integration of orientation across time, i.e. an orientation bandwidth with a sufficient temporal window. By this account, grouping across frames (of central elements and hence element motion) occurs when orientations across sub-frames are within the temporal orientation bandwidth of the underlying detectors. As discussed previously, neither the acuity of orientation discrimination nor the orientation bandwidth of early motion detectors fits particularly well with the present results. A static orientation detector with a temporal bandwidth sufficient to integrate across sub-frames may account for the grouping, the estimate of around 23 deg for temporal grouping (Experiment 1) compares very will with the 23 deg estimate for spatial grouping (Experiment 2). As stated above, estimates of static orientation bandwidth have been found from 10 to 30 deg (Beaudot & Mullen, 2006; Blakemore & Nachmias, 1971; Campbell & Kulikowski, 1966; Movshon & Blakemore, 1973; Thomas & Gille, 1979). However, a limitation of this orientation bandwidth account, while appropriate for the present stimuli, lies in its generilisability. It is not clear how such a process could underlie the Ternus effect in general, for that a consideration of other temporal effects is required.

7.3. Temporal cues to grouping

We found a transition in perceptual behaviour from group motion to element motion with temporal offsets in orientation of around 40 ms (averaged across observers and conditions); changes in carrier orientation across frames of up to 90 deg could not reverse this transition. This value of 40 ms is within the range of the critical IFIs reported in the Ternus literature. The key difference between previous estimates and those of the present study is that here the temporal offset is not correlated with the spatial displacement. This implies that the transition from element to group motion reflects a temporal window for spatial grouping. When elements (with similar orientation) are presented within a temporal window of around 40 ms or less with sufficient changes in orientation across frames (about 25 deg), group motion prevails, but when the temporal offset of the outer element exceeds this value the elements are no longer grouped together across time and element motion is perceived, despite the large changes in orientation across frames. This is evidence of a temporal cue outweighing a spatial cue. Previous evidence exists that spatial cues can outweigh temporal cues, derived from performance in figure/ground discrimination tasks (Fahle & Koch, 1995; Kiper, Gegenfurtner, & Movshon, 1996; Leonards, Singer, & Fahle, 1996).

We found that the grouping of Ternus elements across space into a coherent whole does depend on temporal cues. In Experiment 3, the duration between changes of orientation in the central and outer elements was constant, but the degree of correlation between changes in orientation of central and outer elements varied with temporal offset. Psychophysical evidence that the visual system is sensitive to temporal cues has focused on figure-ground discrimination tasks with flickering elements, where figure and ground are presented in different phases, entropies or asynchrony levels (e.g. Lee & Blake, 1999; Leonards et al., 1996; Usher & Donnelly, 1998). It has also been found that temporal correlations can encourage spatial grouping of apertured motion stimuli (Alais, Blake, & Lee, 1998). The correlated changes in orientation in our experiments could have provided a cue to grouping, with the transitional offset of around 40 ms representing the synchrony window; however this value is quite large compared to neural estimates of around 25 ms (Freidman-Hill, Maldonado, & Gray, 2000; Maldonado, Freidman-Hill, & Gray, 2000) . Indeed, temporal correlation theory (von der Malsburg, 1999)—which states that visual features at different spatial locations can be bound together by synchronization of spiking of early visual neurons—is highly contentious (see Adelson & Farid, 1999; Fahle & Koch, 1995; Farid & Adelson, 2001; Kiper et al., 1996; Shadlen & Movshon, 1999). Recent findings argue against temporal synchrony accounts of grouping. Dakin and Bex (2002) demonstrated that while asynchronous presentations improved contour detection, the advantage did not occur when a visual mask was presented that effectively removed stimulus onset/offset transients. Thus it was not the asychrony *per se* providing a grouping advantage, but the transients due to the flickering stimulus presentation. Similarly, Beaudot (2002) found that paths of oriented Gabors could be detected due to stimulus onset asynchronies as small as 13 ms between figure and ground alone, rather than repetitive asynchrony of presentation. These arguments have support from neurophysiological data showing that the offsets of neural responses arrive earlier and are less variable than onset neural responses, and may provide a code to interpret subsequent changes (Bair, Cavanaugh, Smith, & Movshon, 2002).

Remarkably, the 40 ms transition value of the present study does match very closely to estimated peak of temporal impulse response functions of early visual filters. The peak impulse response for spatial vision has been estimated to be 40 ms at 1.5 cpd (Georgeson, 1987), and similar to the 36 ms peak of the sustained model filter response from data of flicker detection in noise (Fredericksen & Hess, 1998). Further, these estimates have support from physiological data (Hawken, Shapley, & Grosof, 1996) that finds the integration time of V1 simple cells to be within a range from 40 to 80 ms. The temporal impulse response may provide reliable (Muller, Metha, Krauskopf, & Lennie, 2001) and behaviourally relevant (Ludwig, Gilchrist, McSorley, & Baddeley, 2005) information for a higher-level decision making system. If we take our transition value as a measure of the peak of the temporal impulse response, temporal integration would be maximal at around 40 ms, and fall off as duration was increased. In the present study, temporal offsets of changes in orientation of up to around 40 ms are tolerated, for which group motion is perceived (indicating grouping of the Gabor elements across space) almost exclusively. Beyond this value, almost no spatial grouping occurs, and element motion is perceived almost exclusively. How would the temporal impulse response underlie this transition? First, we should restate the stimulus manipulation involved here. Elements were presented all at the same orientation for a duration of 200 ms $- \Delta$, after which the central elements changed their orientation while the outer element remained at the previous orientation for an additional time equivalent to the offset. Therefore as offset increases, the time for which elements remain the same decreases. It is possible that elements in different locations in space can be perceptually grouped only if their *onsets* occur within a duration up to the peak of the impulse response, beyond which they become perceptually segregated. The first frame of the stimulus would be present 200 ms $- \Delta$, and could be grouped, but at the subsequent change, sustained filters responding to the inner elements would peak at 40 ms, and if the outer element did not change orientation before the peak of this response, the elements could not be spatially grouped (resulting in group motion).

This account is not especially restricted to the stimulus configuration used here (although the present stimuli match well with the preferences of early visual mechanisms). The transitional values across a range of Ternus studies are quite similar to the estimate of the peak of the impulse response. While in the manipulation of the present study, increasing the temporal offset in displays of changing orientation causes a transition from group (spatial grouping) to element motion (temporal grouping), in previous studies that have manipulated the IFI the element motion (temporal grouping) occurs at small IFIs, and as IFI increases this leads to more group motion (spatial grouping). Thus the temporal offset and IFI manipulations go on opposite directions. As there is no change in onsets between central and outer elements in previous studies, and the frame duration is usually much longer than 40 ms, there is no impediment to spatial grouping (if the temporal impulse response is a key factor). Rather, if the transitional value in previous studies were to reflect a temporal impulse response, it would have to be in terms of the temporal grouping of central elements presented within 40 ms, resulting in element motion. It is possible that the blank IFI (period after the offset of a stimulus frame) is registered as an event in itself, having its own temporal impulse response: at IFIs of less than 40 ms the subsequent stimulus frame could be somehow integrated with this and not regarded as a unique event; in contrast, at IFIs greater than 40 ms, the subsequent stimulus frame might be treated as a new event providing the cue to spatial grouping and group motion. This idea requires further testing to clarify the details, but we note that as the temporal impulse response depends to some extent upon spatial frequency, contrast and second-order stimulus characteristics, manipulating these variables within the current paradigm would provide different predictions and therefore a means to test the generalisability of this idea.

7.4. Overall conclusions

We examined transitions between element and group motion perception in a Ternus display of Gabor elements with no IFI, depending instead on changes in both temporal and spatial properties of the stimulus. Generally, the findings demonstrate that while spatial grouping is an important determinant in the percept of such displays, and can be attributed to a modified 'association-field' that may result from horizontal connectivity within V1, temporal grouping cues are also important in determining the resulting percept and can override spatial grouping cues. The transitional values of these temporal effects, although in the range of transitional values normally reported with IFIs, cannot be attributed to motion mechanisms with a spatio-temporal delay. Rather they are remarkably similar to the estimated temporal impulse response of early visual filters, suggesting this is a crucial factor in low-level grouping, the results of which are detected at a higher level in the system where they can provide a basis for motion perception.

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