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Solving the correspondence problem within the Ternus display: The differential-activation theory

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Abstract. The Ternus display produces a bistable illusion of motion: at very short interstimulus intervals (ISIs; < 30 ms) observers perceive element motion while at longer ISIs (> 30 ms) observers perceive group motion. In experiment 1, however, we find that, when the Ternus display's ISI contains an occluding box, group motion is mostly eliminated. These results do not fit the predictions made by the short-range/long-range two-process theory [Braddick and Adlard, 1978, in *Visual Psychophysics and Psychology* (New York: Academic Press)]. We propose that the differential-activation theory (Gilroy et al, 2001 *Perception & Psychophysics* **63** 847 – 861) accounts for our results. We then extend the differential-activation theory as an explanatory mechanism for the Ternus display in experiment 2 by selectively placing an occluder over the first, second, or third Ternus display element. As predicted by the differential-activation theory, the occlusion of the far-left element produced a normal distribution of group motion increasing with ISI, while the occlusion of the other two elements produced an illusion of occluded elements remaining stationary throughout the display. Furthermore, as predicted by the differential-activation theory, each moving element was assigned to its nearest neighbour, producing, in the case of second and third element occlusion, a novel Ternus display motion illusion where only two out of three elements are perceived as moving.

1 Introduction

Apparent motion refers to visual phenomena in which a series of static stimuli presented in rapid succession are perceived as a single moving stimulus. The Ternus display, originally demonstrated by Josef Ternus in 1926, is a classic example of an ambiguous apparent-motion display—one in which an identical sequence of stimuli can produce two different illusions of motion. It consists of multiple, usually identical, elements arranged in a linear or tangential formation. Typically, there are three successive frames (figures 1a – 1c): the elements first appear for a nominal period (frame one), and then disappear for a variable interstimulus interval (ISI; frame two). Finally, the objects re-appear (frame three) and are in every way identical to the initial frame, except that the far-left element is no longer present and is replaced by an identical element on the far right.

Ternus (1926) found that the presentation of these three frames creates an apparent-motion illusion in which every object is seen to move simultaneously to the right. Pantle and Picciano (1976), however, showed that another perception is possible: by varying the duration of the ISI, the authors found that with ISIs greater than 30 ms observers notice Ternus's reported shifting of all elements to the right (termed 'group motion'; see figure 1d), but that at ISIs less than 30 ms, subjects only perceive the motion of the far-left element to the opposite end while the other elements remain stationary ('element motion'; see figure 1e). In other words, as the duration of the ISI increases from 0 ms onward, the percentage of trials during which group motion is perceived increases, with ISIs of around 30 – 50 ms forming a 'bistable' perception, where both group- and element-motion illusions are equally likely to be perceived. A recent review of the phenomenon by Petersik and Rice (2006) notes that even after 80 years, the

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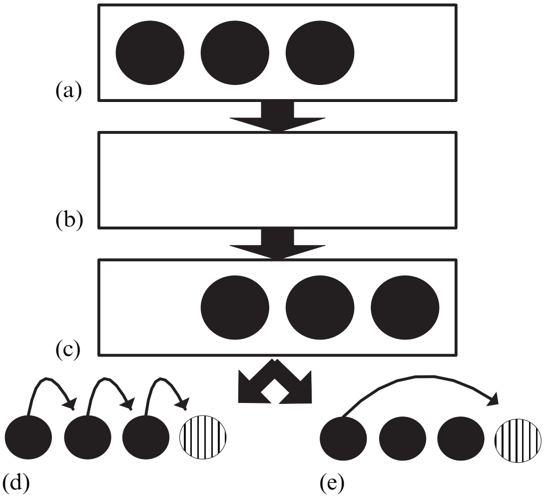


Figure 1. The standard Ternus display: (a) The first frame, where two or more elements appear; (b) the ISI; (c) the third frame, where the elements re-appear shifted to the right; (d) group motion, where every element moves to the right; (e) element motion, where the leftmost element moves while the centre elements remain stationary.

simple and highly replicable Ternus display continues to entice researchers because of its resistance to a parsimonious account explaining the two illusions of apparent motion.

One possible reason why the two competing motion illusions exist may be because of the multiple ways the visual system solves the correspondence problem within the Ternus display. The correspondence problem refers to the question how elements across successive frames are judged to be identical. Within the Ternus display, the importance is clear: if the correspondence problem is solved such that the leftmost element in the first frame is paired with the rightmost element in the third frame, element motion should result. On the other hand, if the leftmost element in frame one is paired with the leftmost element in frame three, group motion should arise. For example, Kramer and Yantis (1997) investigated a Ternus display consisting of two non-identical elements (eg a square and a circle) and found that if the shape of the elements suggests the movement of only one element (ie if the disappearing and re-appearing elements match in identity), the effect of ISI on group motion is largely, but not entirely, reduced. In other words, if the visual system can resolve the correspondence problem by matching element identity, then it will use the temporal variable to a lesser degree. Nevertheless, the question how the correspondence problem is solved in the Ternus display when the elements are identical remains unanswered.

The most prominent explanation of the mechanism of the Ternus display came from Braddick and Adlard in 1978. These authors argued that the key to element motion is the perception of central ('overlapping') elements being stationary. If this is the case, the correspondence problem can only be solved by matching the two non-stationary elements (the far-left element in frame one, and the far-right element in frame three), thus enabling the perception of element motion. The authors further argued that the visual system possesses two separate motion systems: low-level 'short-range' processes, which occur early in visual processing, and 'long-range' processes, which occur later in visual processing. On the basis of extensive research with random-dot kinematograms (RDKs), Braddick and Adlard argued that the short-range processes have a spatial limit of 15 min of visual angle and a temporal limit of about 50 – 100 ms (Braddick 1974). With their limited spatial range, short-range processes cannot track the movement of the elements across to the right side, and, instead, signal 'non-motion' of the overlapping elements. This leaves the long-range process to interpret the leftmost element as the moving one and create the illusion of element motion.

At longer ISIs, however, the short-range detectors reach their temporal limit and do not send any signals to the long-range processes, which, in turn, create the illusion of group motion—their 'natural' preference.

Later research has shown that the illusory motions produced by the Ternus display are more complex than initially thought, as slight modifications to the display highly affected which type of motion was perceived. For example, Alais and Lorenceau (2002) demonstrated that using horizontally oriented, as opposed to vertically oriented, Gabor patches as Ternus display elements increases the percept of group motion, probably by forming an association field ("a facilitative contour interaction"—page 1005) between the elements. This is also in line with Kramer and Yantis (1997), as well as He and Ooi (1999), who both showed that the perceptual grouping of Ternus display increases reported group motion. Other factors including adaptation (Petersik and Pantle 1979), object size (Breitmeyer and Ritter 1986), contrast configuration (Ma Wyatt et al 2001), and dichotic viewing (Pantle and Picciano 1976; but also see Ritter and Breitmeyer 1989) have all been shown to influence the motion illusions. It is important to note that none of these studies explicitly disprove Braddick and Adlard's theory. In fact, several authors, such as Alais and Lorenceau, and Petersik and Pantle, specifically claim that their findings fit within an extension of the two-process account.

This is not to say, however, that Braddick and Adlard's (1978) theory on the Ternus display has gone unchallenged. Scott-Samuel and Hess (2001) used a Ternus display with elements having sinusoidal modulations of 180° and found that the percept of element motion can be almost entirely eliminated across all ISIs. This finding was used as an argument that the long-range processes, sometimes argued to be feature-trackers, are the ones tracking the motion of middle elements and therefore are the only ones responsible for the Ternus display. In other words, Scott-Samuel and Hess suggest that short-range processes do not play a role in the motion illusions elicited by the Ternus display.

A more recent challenge to Braddick and Adlard's (1978) theory came from Dodd et al (2005). While they initially attempted to completely remove element motion by physically connecting the elements, they found the pattern of responses across ISIs unchanged. Subjects reported that during element motion the overlapping element rotated on the Z-plane, thereby acting as a pivot to allow the connected leftmost element to come to its other side. The authors argued that this finding is incompatible with Braddick and Adlard's theory, since the rotating motion of the middle element is seen at the same time as element motion.

The most pointed criticism of the two-process distinction, however, came from Cavanagh and Mather (1989) and Cavanagh (1991), who, through various experiments, challenged the two-process properties suggested by Braddick and Adlard (1978) and Braddick (1974). For example, Braddick (1974) used RDKs to report that the maximum displacement detected by short-range processes is around 15 min of arc. However, Cavanagh et al (1985) found that this value can greatly change depending on the size of the RDK elements. Furthermore, Cavanagh (1991) argued that the bistability of the Ternus display is not a sufficient justification for the need of a two-process theory, since other bistable displays do not require it (however, for criticisms, see Petersik 1991; Petersik and Rice 2006).

In this study we sought to further test the short- and long-range account of the Ternus display. Specifically, although there have been several studies examining the elimination of the element motion, there have been almost no challenges to Braddick and Adlard's (1978) idea of how group motion arises. According to Braddick and Adlard, group motion is a 'natural' response of the long-range detectors and occurs when the short-range detectors fail to fire owing to the lack of a motion signal associated with the middle elements. This occurs predominantly at high ISIs because the temporal limit of the short-range processes expires at around 50 ms of exposure (Braddick 1974). Therefore, just as element motion should be impossible to eliminate at short ISIs because short-range processes always signal non-motion of middle elements, it should also be impossible to eliminate group motion at high ISIs because the short-range processes have expired and, in their absence, group motion should always be perceived. To determine if group motion is always perceived at long ISIs, we conducted two experiments with visual occluders used to alter the perception of the elements in a Ternus display.

2 Experiment 1

For the display in our first experiment, we used a normal Ternus display with the exception that, during the ISI, the elements were covered with a rectangle that matched their colour and luminance. This created a display in which the elements never formally disappeared because they occluded behind the rectangle. If the two-process model of Braddick and Adlard (1978) is correct, then short-range processes should be active only within their temporal limit. After this point, group motion should be seen, regardless of the presence of the occluder. In other words, the occluding box should have no effect on the overall distribution of illusory motion within the Ternus display. If, however, element motion is perceived at higher ISIs, a challenge would be mounted to the two-process theory.

2.1 *Method*

2.1.1 *Subjects.* Twenty-one University of Toronto undergraduate students participated in exchange for course credit and were naive to the purpose of the experiment. All subjects had self-reported normal or corrected-to-normal vision. They were randomly placed in one of two conditions: normal Ternus display or occluded Ternus display.

2.1.2 *Apparatus and procedure.* The experimental program was administered on a Pentium 4 PC with a VGA monitor set to an 85 Hz refresh rate. The experiment was conducted in a dimly lit room. Subjects were placed 44 cm away from the screen and had their head and chin secured in place with a chin-rest. Their responses were recorded on a standard PC keyboard with the keys 'z' and '/' used to signal that element or group motion was seen, respectively. All stimuli were grey on a black background. The luminance of the Ternus display elements and the occluder was 16.5 cd m^{-2}.

Subjects in both conditions first received a series of 20 examples demonstrating group and element motion in a normal Ternus display with ISIs of 0 and 108 ms. Afterwards, participants had a chance to practice making responses in the classic Ternus display until they reported they were comfortable with the procedure. If the subject could not differentiate between the two motions (ie if there was no effect of ISI) their data were eliminated from the experiment.

Each trial consisted of three parts (see figure 2). In the first display, two filled grey circles, each subtending 1 deg, appeared in the centre of the screen; they were separated by 1 deg. This frame stayed on the screen for 500 ms. There were two types of second displays, in which the ISI was presented: in a normal condition this was a blank frame, while in the occluder condition there was a box spanning from the top corner of the left element to the bottom of the right; the box was the same colour and luminance as the elements. In the third frame, the elements reappeared with the left circle removed and replaced by a new element located 1 deg to the right of the centre circle. Therefore, the right element in the first frame switched from being the rightmost element to being the leftmost one.

After the re-appearance of the elements the subjects were asked what kind of motion they had perceived. After the response was detected, or if no response was recorded in 2000 ms, the trial automatically ended and a new one began. After every 100 trials subjects were allowed to have a self-paced break.

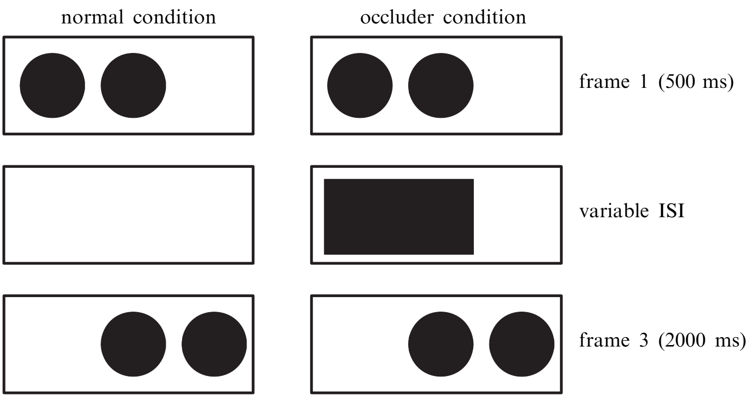


Figure 2. The design of experiment 1. After the first frame, which is identical in both conditions, the ISI is either a blank screen ('normal condition') or an occluding box that matches the luminance of the two elements ('occluder condition'). Both conditions are followed by the identical frame three.

2.2 *Design*

Each of the two conditions (normal and occluded) consisted of 400 trials. In both conditions 10 delays were used for the span of the ISIs. Because the occluder could not be displayed at the ISI of 0 ms, but we did not want to have a different number of trials per ISI per condition, the exact delays of the two conditions slightly differ, with 9 of the 10 ISIs being identical. The delays for the normal-Ternus condition were (0, 12, 24, 36, 48, 60, 72, 84, 96, and 108 ms), and for the occluder-Ternus condition were (12, 24, 36, 48, 60, 72, 84, 96, 108, and 120 ms). Within both conditions, all 10 delays were randomly distributed throughout the session and were equally likely to appear on any given trial.

2.3 *Results*

One subject did not meet the normal-Ternus display criterion (there was no effect of ISI on the responses) and was removed from all further data analysis, leaving the total number of participants at twenty. Figure 3 shows the percentage of group motion for the 10 ISIs. As expected, the normal-condition group showed a typical Ternus display distribution of element/group motion reported, with element motion mostly present at the lowest ISIs, group motion at the highest ISIs, and the crossover/bistable point at around 40 ms. The presence of the occluder greatly reduced the percept of group motion across all ISIs: the highest percentage of group motion in the occluder-condition was 33.7% at the ISI of 60 ms.

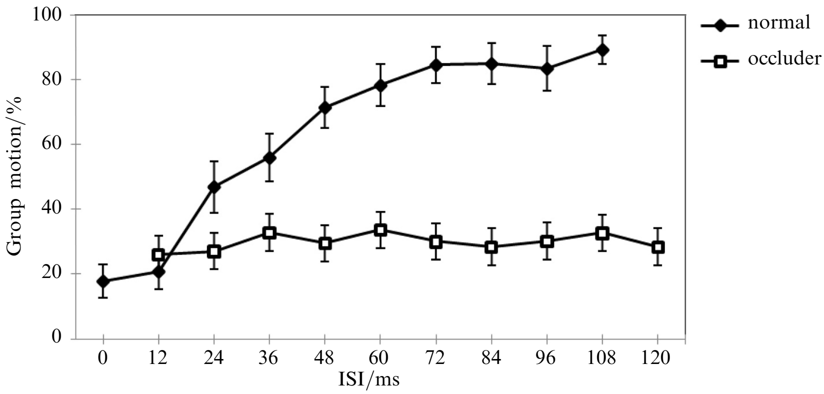


Figure 3. The results of experiment 1; the x-axis represents the ISI and the y-axis the average percentage of group motion reported. Error bars represent ±1 SEM.

To confirm the effect of condition on the percepts across ISIs, we ran a 2 (condition: normal, occluder) $\times$ 9 (overlapping ISI: 12 ms – 108 ms) ANOVA. The results showed a significant main effect of condition ($F_{1,18} = 26.88$, $p < 0.001$) and a significant main effect of ISI ($F_{8,144} = 24.57$, $p < 0.001$). As can be seen in figure 3, these main effects were qualified by a significant interaction between ISI and condition ($F_{8,144} = 18.88$, $p < 0.001$). In addition, the one-way ANOVA of ISI in the occluder condition showed no effect of ISI ($F_{8,72} < 1$). Therefore, these results show that the presence of the occluder removes the percept of group motion from the Ternus display, regardless of the ISI.

2.4 *Discussion*

The results in our first experiment contradict the two-process apparent motion theory as proposed by Braddick and Adlard (1978). By using a visual occluder to 'hide' the display elements, we found predominantly element motion at all ISIs, a difficult feat under the specifications set for the short-range processes. Although the theory could undergo revision (eg have long-range processes responsible for both motion percepts), the present problem is another in a growing list (cf Cavanagh and Mather 1989). Thus, we conclude that it is more useful to move away from the two-process theory and examine other options to account for the apparent motions of the Ternus display [for an additional discussion on the role of two-process theories in the Ternus display, see Petersik and Rice (2006)].

One such option is Gilroy et al's (2001) differential-activation theory, which claims that the correspondence problem can be solved at the level of retinal motion detectors. The authors argue for a relationship between the frequency of motion detectors firing and the luminance contrast between the apparent motion element and its background across several motion frames (see also Hock et al 1997). Specifically, their theory predicts that, if the difference in luminance between successive frames is high, the activation threshold for the retinal motion detectors is likely to be reached, thereby signalling motion of the on-screen element. Importantly, Gilroy et al suggest that, once the motion detectors fire, the visual system resolves the correspondence problem by assigning each moving element in one frame to its nearest neighbour in the following one (Burt and Sperling 1981; Dawson 1991).

The differential-activation hypothesis has not yet been explicitly tested as an account of the Ternus display apparent motion. It seems, however, that the theory and the display are well-suited for each other, as the duration of the ISI can affect whether or not motion detectors will fire for each individual element by increasing or decreasing the amount of luminance change across the three frames. In other words, for the spatial location of each element, there is a temporal summation of luminance differences across the three frames; this difference is pronounced by the contrast of luminance between the background and the element itself. Therefore, if this temporal summation of contrast (TSC) is sufficiently high, the element in that spatial location is perceived to move, while, if the TSC is low, the element is perceived to remain stationary. Thus, at short ISIs, the brevity of the second frame prevents the TSC from being high enough to activate the motion detectors for the overlapping elements, and they are perceived as remaining stationary. The leftmost element, on the other hand, experiences a high TSC owing to its disappearance in frame three and is, therefore, seen to move to its nearest neighbour (which, owing to the stationary status of overlapping elements, ends up being the rightmost element in frame three). At longer ISIs, the contrast summation is high for all elements, which are subsequently seen to move to their nearest neighbours, thus producing group motion.

Within the framework of our first experiment, the differential-activation hypothesis explains (albeit a posteriori) our findings well. Since the occluder effectively sets the TSC to 0 for the central element across all three frames, the overlapping element is always perceived as stationary. The position of the left element, on the other hand, experiences a change of luminance (and, therefore, TSC) at frame three, and is perceived to move. The combination of the two produces a strong percept of element motion once the occluder is introduced, even at long ISIs. In other words, according to the differential-activation hypothesis, the occluder overrides the effect of ISI by altering the TSC.

3 Experiment 2

The differential-activation theory leads to the following predictions. First, any item whose luminance does not change across frames is perceived as stationary. This was also found by Ramachandran et al (1986) who suggested that "the presence or absence of occluders *gates* the strength of the motion signal" (page 1749). It was also suggested by Dawson et al (1994), who found that matching luminance for overlapping elements resulted in increased element motion. Second, the Ternus display is driven by the relative activation of motion detectors responding (or not responding) to each element. On the basis of this information, the visual system analyses which elements have remained stationary and which have moved. Further, by using the nearest-neighbour principle, the visual system creates a motion illusion across the overall display (cf Dawson 1991). This also implies that the motion perception does not occur until all three frames are perceived, a notion consistent with the experiments by Ogmen et al (2006), who suggest that the first frame of the Ternus display is kept inside of visual short-term memory until the third frame, after which the two are integrated into a coherent motion illusion. The outcome of these predictions is that any manipulation of the activation of the motion detectors will determine which motion is perceived, and that one such factor is the TSC. While in classic Ternus display experiments the TSC is manipulation via ISIs, other motion-detector manipulations, such as fatiguing, may alter which kind of motion is perceived in the Ternus display (see section 4).

In order to further our predictions, in the second experiment we used a Ternus display with three elements (named A, B, and C; see figure 4) in four different conditions: the ISI frame could consist of a normal, blank screen (normal condition; NO), only the leftmost element occluded (AO), only the middle element occluded (BO), or only the rightmost element occluded (CO). The normal condition should produce a regular Ternus display curve. Furthermore, if our interpretation of the differential activation hypothesis is correct, then condition AO should also produce a normal pattern of element and group motion because the occlusion of the leftmost element (A) still produces a TSC greater than 0 across the entire display, since the element is no longer present at frame three.

The key conditions are BO (where element B is occluded) and CO (where element C is occluded). Here, the differential-activation hypothesis predicts that new motion illusions should be formed, with the occluded element perceived as stationary, and the other two moving to their nearest neighbour. In the BO condition, element A should pair up with element C, while element C should pair with element D (B-stationary 2-element motion; see third column of figure 4). In the CO condition, element A should pair with B, while B should pair with D (C-stationary 2-element motion; see fourth column of figure 4). Within the three-element Ternus display literature, we do not know of any experiments that have demonstrated the exclusive motion of two of the three elements (as opposed to one in element motion and three in group motion). Therefore, the idea behind the second experiment is to see if the presence of occluders at specific spatial locations can override and replace the typical perceived motion of the Ternus display without occluders.

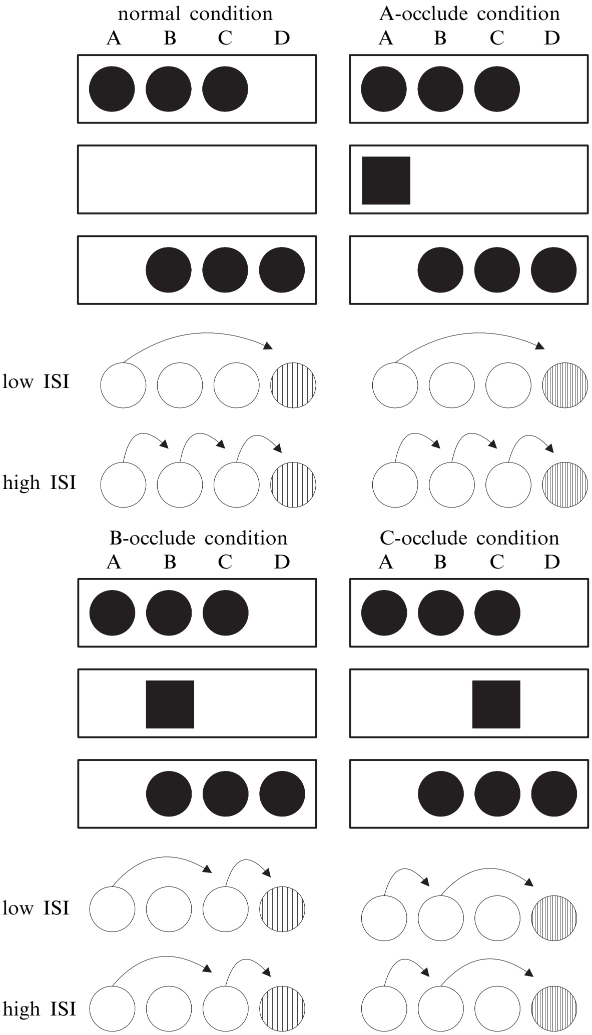


Figure 4. The experimental design of experiment 2; for ease of reference, we have named each one of our elements, with elements A, B, and C being present in frame one, and elements B, C, and D in frame three. The experiment has four possible conditions, each of which is illustrated here.

3.1 *Method*

3.1.1 *Subjects.* Ten University of Toronto undergraduate students participated in exchange for monetary compensation and were naive to the purpose of the experiment. All subjects had self-reported normal or corrected-to-normal vision. We used a repeated-measures design with subjects being in all four conditions during a single block.

3.1.2 *Apparatus and procedure.* The computer and room setup matched those of experiment 1. All stimuli were white on a black background. The luminance of the Ternus display element and the occluder was 70.5 cd m^{-2}.

Each trial began with the three circular elements, each subtending 1 deg and separated by 1 deg appearing for 500 ms. The second frame, the ISI, was randomly chosen by the computer program and could be one of four possibilities: in the no-occluder condition the ISI was a blank screen; in the AO condition the ISI was a white box that covered the entire element A; in the BO condition the ISI was a white box that covered the entire element B; in the CO condition the ISI was a white box that covered the entire element C. All occluder boxes stretched from the top corner to the bottom corner of the given element; all other elements were left covered by the blank screen. The length of the ISI was randomly selected and matched one of six possible delays (see below). The ISI was followed by a third frame which consisted of the same three elements as the first frame, but each shifted 1 deg to the right. The third frame stayed on the screen for 800 ms.

Subsequently, the three elements all disappeared and two schematic drawings appeared. The schematic drawings illustrated the three circular elements from the first frame and had a fourth element, a white outline of a circle, 1 deg to the right of the rightmost circle (ie in the position of element D). The circles were connected with lines; the subjects were instructed that the schematic drawing illustrated a potential motion illusion and that lines represented movement paths. On any given trial, subjects had a choice between two schematic drawings, one appearing on the left and the other on the right. Their choice was determined by the ISI displayed. During the NO condition the subjects could choose between schematic drawings of the group and element motion. During AO conditions the subjects could also choose between group and element motions. During BO conditions the subjects could choose between element motion (at low ISIs), group motion (at high ISIs), or the predicted B-stationary 2-element motion (at all ISIs). During CO conditions the subjects could choose between element motion (at low ISIs), group motion (at high ISIs) or the predicted C-stationary 2-element motion (at all ISIs). The side on which each schematic drawing appeared was randomised. The subjects were instructed that, should their perception match the left schematic drawing, they should press 'z' on the keyboard; on the other hand, should their perception match the right schematic drawing, they should press '/'. Finally, the subjects were instructed that, in the case where neither side matched their perceived motion, no key should be pressed. The trial automatically ended if no key was selected within 5000 ms.

It is important to note that in the BO and CO conditions, the subjects did not always have the same two choices: at low ISIs, they could only select between element motion and the predicted motion; at high ISIs, they could only select between group motion and the predicted motion. This was done for three reasons. First, as shown in the first experiment and numerous other studies, when identical stimuli are used, group motion is not found at short ISIs and element motion is not found at long ISIs. Second, the purpose of the experiment is to determine whether the occluder manipulation will have an effect on the normal distribution of Ternus display responses (element motion at low ISIs, group motion at high ISIs). As such, the strongest method is the comparison between typical Ternus responses and the new pattern of responses predicted by the differential-activation model. Third, as a control, subjects were instructed not to press any key if neither option matched their perception. Finally, if subjects had a bias against non-responding, and neither of the available options matched what they perceived, their responses should always be around 50%. As will be seen shortly, this was not the case.

Subjects first received a series of 20 examples demonstrating group and element motion in a normal Ternus display. Afterwards, they had a chance to practice making responses in the normal condition until they reported they were comfortable with the procedure. If the subjects did not demonstrate that they could differentiate between the two motions (eg if there was no effect of ISI) their data were eliminated from the experiment.

3.2 *Design*

We used six ISI delays: 12, 24, 36, 48, 60, and 72 ms. For our purposes, we classified the delays 12, 24, and 36 ms as 'low ISI', and the delays 48, 60, and 72 ms as 'high ISI'. Each ISI appeared 120 times, 30 times in each of four conditions. Therefore, in total 720 trials were displayed. Subjects were given a rest every 120 trials. Within each testing block, each of the 6 ISIs was equally likely to occur. Furthermore, subjects were equally likely to see any one of the four conditions.

3.3 *Results*

Four subjects were eliminated from the analysis, three because they did not meet the normal Ternus display criterion, and one because more than 50% of trials were not responded to; this left six participants for our data analysis. For all other subjects, $< 1\%$ of all trials were not responded to, suggesting that on every trial all subjects saw one of the two schematic options.

We first separated our data into two groups depending on what the given response choices were. First, the percentage of element motion reported was compared in the conditions NO and AO across all six ISIs. The results are shown in figure 5a, and a 2 (condition: NO, AO) $\times$ 6 (ISI: 12 – 72 ms) repeated-measures ANOVA confirmed no significant main effect of condition ($F_{1,5} = 5.245$, $p > 0.07$) but a significant main effect of ISI ($F_{5,25} = 7269.9$, $p < 0.001$). The interaction failed to reach significance ($F_{5,25} = 1.256$, $p > 0.3$). These results confirm the prediction that occluding the far-left element (AO) creates a normal Ternus display, with element motion at the shortest ISIs and group motion at the longest.

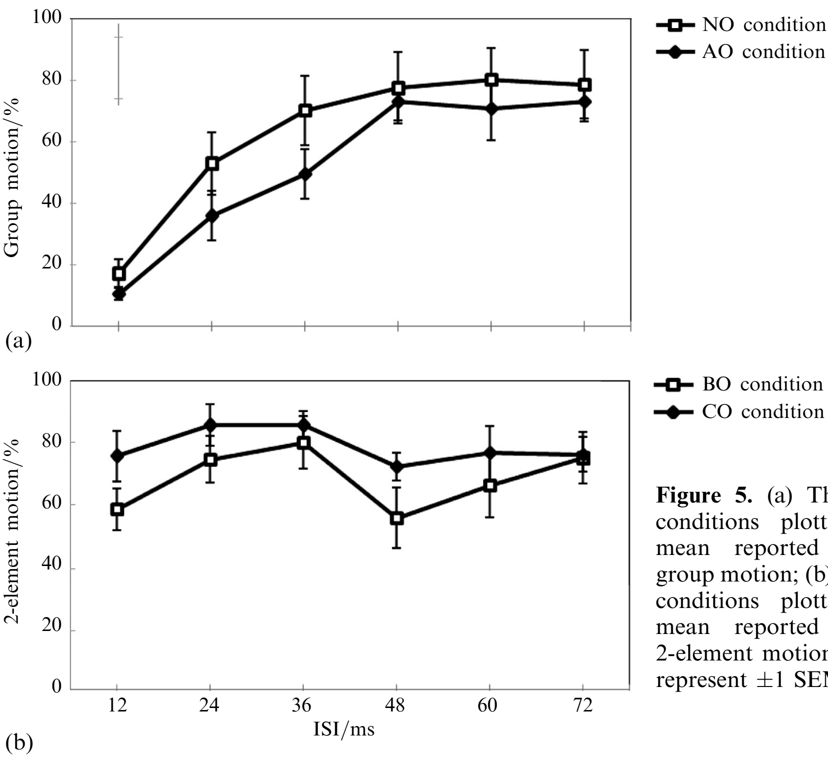


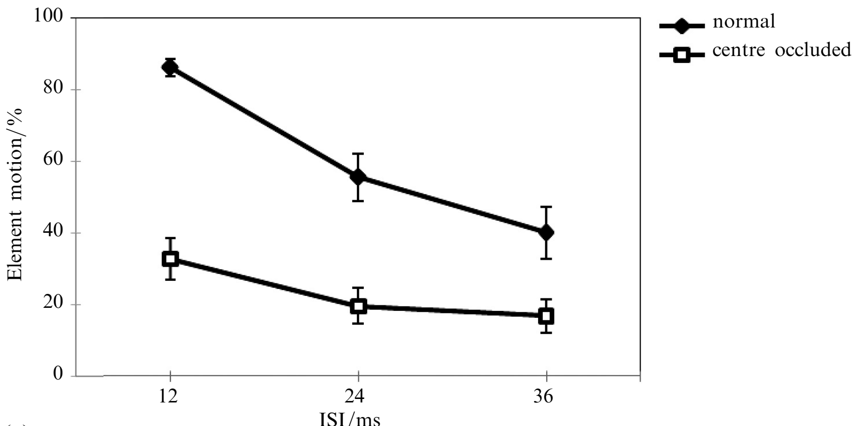
Figure 5. (a) The NO and CO conditions plotted against the mean reported percentage of group motion; (b) the BO and CO conditions plotted against the mean reported percentage of 2-element motion. The error bars represent ± 1 SEM.

We then compared the percentage of reported 2-element motion in the BO and CO conditions across all ISIs. The results are shown in figure 5b and suggest that there was no difference between the two conditions. A 2 (condition: BO, CO) $\times$ 6 (ISI: 12 – 72 ms) repeated-measures ANOVA yielded no significant main effect of condition ($F_{1,5} = 3.747$, $p > 0.1$), a significant main effect of ISI ($F_{5,25} = 4.203$, $p < 0.01$), and a non-significant condition $\times$ ISI interaction ($F_{5,25} = 1.554$, $p > 0.2$). Therefore the two occluders had an equivalent effect on subjects' reported percentage of 2-element motion. Although the main effect of ISI was not expected, it may be due to the occluder's inability to entirely reduce element motion at the lowest ISIs, since both overlapping elements may be seen as stationary owing to a low TSC: one owing to the occluder effect, and the other owing to a low ISI. The important finding, however, is that when either of the overlapping elements is occluded, observers consistently reported 2-element motion.

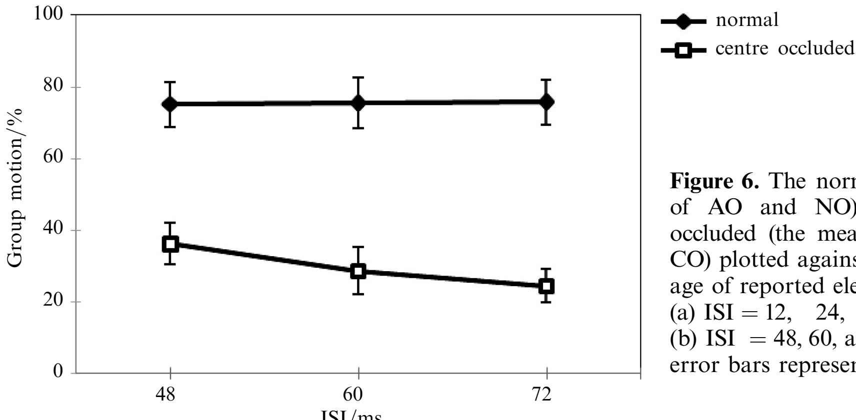
To find out if the BO and CO conditions were indeed successful in reducing the overall percentage of reported element and group motion, we administered two additional tests. First, the NO and AO conditions were averaged, yielding a NO/AO ('normal') values across all six ISIs; the BO and CO conditions were also averaged, yielding a BO/CO ('centre-occluded') values across all six ISIs. Because the BO and CO conditions had a choice of element motion only at the first three ISIs, and group motion only at the last three ISIs, the two analyses were run separately. In both cases, the normal values were compared to the centre-occluded ones.

The low-ISI results compared the percentage of reported element motion in the normal and centre-occluded groups. The results shown in figure 6a suggest a large difference, with the centre-occluded groups having reduced element motion. A 2 (type: normal, centre-occluded) × 3 (low ISI: 12, 24, 36 ms) repeated-measures ANOVA found a significant main effect of type ($F_{1,11} = 40.371$, $p < 0.0001$), a significant main effect of ISI ($F_{2,22} = 55.705$, $p < 0.0001$), and a significant type × ISI interaction ($F_{2,22} = 9.249$, $p < 0.001$).

The high-ISI results compared the percentage of reported group motion in the normal and centre-occluded groups. The results in figure 6b show a similar trend as in the low ISI condition; a 2 (type: normal, centre occluded) × 3 (high ISI: 48, 60, 72 ms) repeated-measures ANOVA found a significant main effect of type ($F_{1,11} = 24.003$, $p < 0.001$),



(a)



(b)

Figure 6. The normal (the mean of AO and NO) and centre-occluded (the mean of BO and CO) plotted against the percentage of reported element motion. (a) ISI = 12, 24, and 36 ms; (b) ISI = 48, 60, and 72 ms. The error bars represent ±1 SEM.

a non-significant main effect of ISI ($F_{2,22} = 2.784$, $p > 0.8$), and a non-significant type × ISI interaction ($F_{2,22} = 2.368$, $p > 0.1$). These results confirm that the conditions BO and CO largely eliminated the normal Ternus display illusions in place of the 2-element motion.

3.4 *Discussion*

The results from experiment 2 confirm our predictions: by itself, occlusion does not change the Ternus display, as shown by condition AO. Instead, the placing of occluders over the overlapping elements, those for whom the luminance does not change in frame three, produces a new illusion of two elements moving, with the occluded element perceived as stationary. In addition, as predicted, when movement is perceived, each element pairs off with its nearest neighbour in the subsequent frame. Participants' average responses were over 50% on all ISIs in both the BO and CO condition, indicating that our manipulation in the BO and CO conditions did change the apparent-motion illusions of the Ternus display.

These findings are consistent with the differential-activation theory. Specifically, the occlusion of element A, owing to the contrast change in frame three, creates a TSC > 0, while the occlusion of elements B and C creates a TSC ≈ 0. Under these conditions, A is perceived to move, while B and C are seen as stationary. Additionally, as Gilroy et al (2001) suggest, the motion of elements is followed by the visual system's solution to the correspondence problem via the nearest-neighbour principle. Furthermore, by using these predictions we have shown a new motion illusion that can occur within the Ternus display where only two out of three elements move. Therefore, the differential-activation theory has good predictive power in the Ternus display.

4 General discussion

Two experiments were conducted to better understand the apparent motion that is perceived in the Ternus display. In experiment 1, the occluder box effectively eliminated the effect of ISI and created a near-complete element motion illusion, a finding that cannot be accounted for by the two-process model of Braddick and Adlard (1978). To test an alternative explanation for the Ternus display, experiment 2 contained four conditions in which subjects reported new apparent-motion perceptions that are in line with the differential-activation hypothesis. Here we found that the overlapping occluded elements appear to remain stationary, while the remaining elements appear to move to their nearest neighbour from the previous frame. These findings are consistent with the differential-activation solution to the correspondence problem. Therefore, on the basis of these findings, we conclude that the apparent motion of the Ternus display is driven by two competing ways in which the visual system can solve the correspondence problem.

In its essence the model proposed is very simple. Apparent motion occurs when elements across successive frames are judged to be identical. The visual system prefers to match these elements through a nearest-neighbour principle (Burt and Sperling 1981; Dawson 1991). But this matching of elements should only occur if an element is seen to disappear and a new element is seen to appear. The TSC variable, therefore, becomes useful as the measure of whether or not an element has moved and, therefore, activated a motion detector. Essentially, if the TSC in each of the element's spatial positions is high, the element will be perceived as moving and will be matched to its nearest neighbour. If the summation of contrast is low, however, the element will be perceived as stationary. Within the Ternus display framework, at short ISIs the temporal summation of contrast is low for the overlapping elements, causing them to appear stationary (element motion). At longer ISIs, however, the TSC is high and the motion of all elements is perceived (group motion).

The present model is not exclusive to all Ternus display models proposed in the past, and it may easily be included into some of them. For example, the model of Grossberg and Rudd (1989) proposes a Gaussian filter that is centred on the middle of the three elements display and has a certain width, which interacts with ISIs. If the width is sufficiently large, it follows the middle point of the elements across all three frames and produces group motion. If the ISIs are low, however, the Gaussian filter does not move across the frames, and matches the overlapping elements as identical and, therefore, stationary. This model's explanation of our findings may be that the sudden onset of an occluder re-centres the Gaussian filter on the occluded element and, as in the case of low ISIs, forces the perception of the occluded/centred element as stationary. Inclusion into their model of the differential-activation hypothesis suggests that the Gaussian filter is constantly re-adjusted by the spatial changes in luminance.

Our findings also fit well with the model of Dawson (1991; Dawson et al 1994), who proposed a large parallel network of constraints, which includes the nearest-neighbour principle and a polarity-matching principle. To demonstrate the importance of the latter, Dawson et al (1994) created a Ternus display in which elements varied in contrast and, across the three frames, overlapping elements would either match or differ in contrast. Their results showed that changes in overlapping element contrast between frame one and frame three produced group motion, while maintenance of overlapping element contrast between frames one and three produced element motion. These findings fit well with the present paper, and can be interpreted as showing that a change in contrast across three frames results in a perception of motion, which is then resolved with other constraints, including the nearest-neighbour principle. Our study, therefore, furthers Dawson's model by demonstrating how the Ternus display can be modified if polarity matching occurs through the ISI itself.

Our framework also suggests explanations for previous findings in the Ternus display literature. For example, Petersik and Pantle (1979) found adaptation effects within the Ternus display, so that prolonged exposure to one type of motion (eg group) subsequently reduced the chance of its perception, especially within the range of ISIs that produce bistable perceptions. Although the authors relate the results back to a two-process theory, they are also parsimonious with the present theory, since the prolonged exposure to group motion may desensitise/fatigue the motion detectors, raise their TSC threshold, and, subsequently, make them less prone to firing, resulting in increased element motion. On the other hand, prolonged exposure to element motion may lower the TSC threshold of motion detectors and make them more likely to fire, creating increased group motion. Importantly, the differential-activation hypothesis suggests that any modification to the TSC will subsequently affect the distribution between the two Ternus-display motion illusions.

Finally, the differential-activation hypothesis can also account for why intermediate ISIs would produce bistability. Under such circumstances, the ISI can sometimes create a high enough TSC to create the signal for the motion of centre elements, but owing to various factors that include motion detector desensitisation, it may not be able to do so on every trial. For example, if the preceding few trials have all been perceived as group motion, a heightened activation threshold may not permit the motion detectors to fire for group motion during the bistable trials. Under this view, the bistability of the Ternus display occurs at the point where the TSC's temporal summation is just around the activation threshold of the motion detectors. This holds important ramifications for future research as, when presented with intermediate ISIs, it is important to consider which motions were registered by the system beforehand, as they may push the bistability in the opposite direction.

Although the differential-activation hypothesis provides a good account for perceived motion in the Ternus display, several factors surrounding the hypothesis remain unexplored. For example, as noted in the introduction, a host of recent Ternus-display findings have found that perceptual grouping affects the Ternus display. How this may interact with the differential-activation hypothesis remains uncertain. Kramer and Rudd (1999) have found that object identity may override the effects of ISI and produce constant element or group motion. In line with the present framework, it is possible that a change of object identity may, nevertheless, produce a change in luminance and, thus, in the TSC. Another possibility is that the visual system only resorts to using the TSC variable if no other cues for solving the correspondence problem are available.

Overall, the two experiments presented in this paper have shown that the Braddick and Adlard's two-process theory does not fully account for the competing motion illusions of the Ternus display. Instead, Gilroy et al's (2001) solution to the correspondence problem itself, combined easily with the model of Dawson (1991), can be integrated within the Ternus display. This not only accounts for the existing data, but also has very promising predictive power for future studies.

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