Journal of Experimental Psychology: Human Perception and Performance

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Online First Publication, March 25, 2021. http://dx.doi.org/10.1037/xhp0000843

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ISSN: 0096-1523

https://doi.org/10.1037/xhp0000843

The Effects of Spatial Attention on Temporal Integration Measured With the Ternus Display

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While a large body of evidence has demonstrated the effects of attention on spatial processes, we know much less about attentional effects on the complementary temporal aspects of visual perception. To narrow this knowledge gap, we examined the effects of endogenous attention—the voluntary component of spatial attention—on temporal integration using the Ternus display. In a typical Ternus display, horizontally aligned discs shift by one position across alternating frames that are separated by a varying interframe interval. This display can induce two different motion percepts: all three discs moving together back and forth (group motion), or the two central discs seeming to remain static and the outer disk jumping across them (element motion). Several studies suggest that element motion reflects temporal integration. Thus, we used the rate of element motion percept to measure temporal integration. Attention was manipulated via the degree of certainty regarding the discs' location (Experiment 1), or with central informative arrows (Experiment 2). The pattern of results was similar in both experiments: The participants reported perceiving element motion more often when attention was allocated in advance to the discs' location. These results suggest that attention prolongs the period of time over which information is integrated.

Public Significance Statement

We know quite a lot about how attending a location affects spatial processing; for example, it sharpens our visual acuity. In contrast, we know little about the interplay between attention and temporal processing. This study narrows this knowledge gap by demonstrating that attention prolongs the time period over which information is integrated.

Keywords: Ternus display, endogenous attention, temporal integration

Spatial covert attention refers to preferential processing of information at the selected location without eye movements to that location. A large body of evidence suggests that spatial attention can take at least one of two forms. It can be involuntarily attracted, in a fast reflexive manner, to sudden changes in the visual field (exogenous attention), or it can be relatively slow, allocated voluntarily to a given location according to our goals (endogenous attention; e.g., Jonides, 1981; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Posner, 1980; Yantis, 1996). These two components of attention are activated through different experimental manipulations. Studies of endogenous attention usually inform the participants of the preferential attention allocation strategy using verbal instructions or central-informative cues. The manipulation of exogenous attention typically involves the presentation of peripheral cues that briefly appear near the target prior to its onset, capturing exogenous attention automatically to the target vicinity. Although a host of studies suggest that a strict dichotomous view of attention does not hold true (see Awh et al., 2012 for a review), it has been reliably shown that these two components of attention may affect behavior differently, suggesting they invoke different attentional mechanisms (e.g., Briand, 1998; Hein et al., 2006; Klein, 1994; Yeshurun & Carrasco, 2008).

The importance of attention in human perception is highly recognized. Numerous studies have shown that attending a specific location improves performance on a variety of tasks in the spatial domain (e.g., Carrasco et al., 2002; Gollaet al., 2004; Rashal & Yeshurun, 2014; V. C. Smith et al., 2000; Yeshurun & Carrasco, 1998, 1999; Yeshurun & Rashal, 2010). For instance, spatial attention can aid performance in acuity tasks such as the detection of a small spatial gap with Landolt-squares (e.g., Bonder et al., 2018; Carrasco et al., 2002; Golla et al., 2004; Yeshurun & Carrasco, 1999), as well as hyperacuity tasks like discrimination of offset direction with vernier targets (e.g., Yeshurun & Carrasco, 1999), suggesting that spatial attention enhances spatial resolution. However, despite the growing interest in the effects of attention on the

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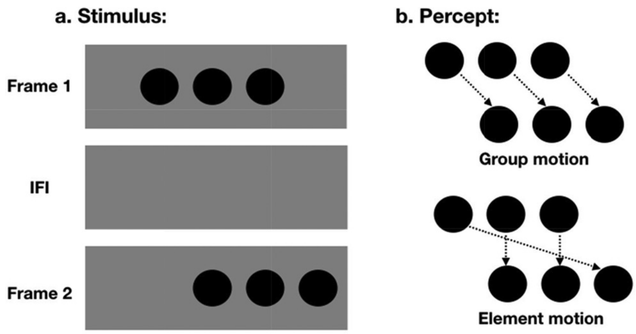
complementary temporal aspect of perception (e.g., Enns et al., 1999; Hein et al., 2006; Rolke et al., 2007, 2008; Sharp et al., 2018; Shore et al., 2001; Yeshurun, 2004; Yeshurun & Levy, 2003; Yeshurun & Marom, 2008), our understanding of these effects remains much more limited. To narrow this knowledge gap, in the current study we examined whether the deployment of spatial endogenous attention to the stimuli location can affect temporal integration, and if so, what is the nature of this effect. Temporal integration refers to processes that integrate information over time to form a coherent percept (e.g., Di Lollo, 1977; Eriksen & Collins, 1968; Wutz et al., 2016). For example, when a green disk immediately follows a red disk, the colors integrate and observers perceive the two discs as one yellow disk (Efron, 1967, 1973; Yund et al., 1983). Temporal integration is supported by visible persistence (i.e., the fact that a visual image remains visible for a short time after the image itself has already vanished), which is thought to be based on the continuous neural activity that persists beyond the input's offset (e.g., Di Lollo, 1977; Visser & Enns, 2001). Prior research provides reasons to assume that spatial attention can affect temporal integration, as several studies demonstrated that spatial attention affects various aspects of temporal processing. For instance, a few studies (Rolke et al., 2008; Yeshurun, 2004; Yeshurun & Levy, 2003) assessed the effect of spatial transient attention on temporal resolution (i.e., the ability to resolve rapid changes in the visual field). These studies measured temporal resolution using the two-flash fusion paradigm. In this paradigm, two flashes of light are presented successively at the same location, and the participants' task is to determine whether they had seen a single flash or two flashes (e.g., Artieda et al., 1992; Reeves, 1996). The ability to detect the temporal gap between the two flashes was worse when a peripheral cue allowed the participants to attend in advance to the flashes' location (Rolke et al., 2008; Yeshurun, 2004; Yeshurun & Levy, 2003). This finding suggests that spatial attention degrades temporal resolution. Hein et al. (2006) examined whether this attentional decrement in performance generalizes to a different temporal discrimination task. They used a temporal order judgment task in which participants had to report the temporal order of two spatially adjacent dots, and found that exogenous attention impairs temporal order discrimination, whereas endogenous attention enhances it. These studies demonstrate that spatial attention can affect temporal processing by focusing on temporal resolution. In the current study, we further examine the effects of spatial attention on temporal integration, which could be viewed as the counterpart of temporal resolution.

Only very few studies have examined the effects of attention on temporal integration. Visser and Enns (2001) manipulated temporal attention using the attentional blink paradigm (e.g., Joseph et al.1997). They have shown that with greater attentional availability temporal integration can occur across longer temporal gaps (but see Rolke et al., 2007). Sharp et al. (2018) examined the effect of spatial attention on temporal integration combining a variant of the missing element task (e.g., Hogben & di Lollo, 1974) with a classic endogenous cuing procedure. In particular, the display was made up of a 4 × 4 matrix of 15 circles (i.e., 1 circle was missing). The matrix was split into two displays presented sequentially and separated by a varying interstimulus interval (ISI). Each display was composed of 7 circles and one half a circle. The task was to report the location of the missing circle, and successful localization of the missing circle required integrating the two displays into a complete matrix. A central cue indicated either the quadrant in which the target would most likely appear or all four quadrants. They found that overall participants were more accurate in the short ISIs, where integration is more likely to occur. Critically, participants' ability to detect the missing circle location was better when they were able to attend in advance to the quadrant in which it appeared, suggesting that spatial endogenous attention prolongs temporal integration. However, the increased accuracy observed when the cue indicated a valid quadrant does not necessarily reflect attentional modulation of perceptual processes. Because the cue was informative, it might have encouraged the participants to adapt higher-level strategies to improve performance. Indeed, attention can operate on postperceptual processes such as decision making, especially when the display includes several stimuli (e.g., Kinchla, 1980). For instance, when the cue indicated a specific quadrant, the participants could choose to ignore all the locations in the nonindicated quadrants, thereby reducing the number of possible locations to 4 instead of 16. Since the cue was valid on most of the trials, this is a helpful strategy that would indeed improve performance. In this case, the effects of attention found in Sharp et al. (2018) would not reflect prolonged integration but rather attentional effects at later stages. Finally, in a previous study, we examined the effect of endogenous attention on feature fusion (i.e., fusion across time of features belonging to different objects). Although we found evidence of increased fusion when stimuli location is attended, that study could not provide unequivocal evidence for attentional prolongation of temporal integration because it did not include a manipulation of the time interval between the two to-be-fused objects. Rather, our findings suggested that attention affects feature fusion via signal enhancement at the encoding stage (Hochmitz et al., 2018).

The goal of the current study was, therefore, to examine whether we can find an attentional prolongation of temporal integration, similar to Sharp et al. (2018), even when using a paradigm that examines temporal integration via measurements of the phenomenological percept rather than measurements of accuracy. That is, even when higher level strategies are deemed futile, because there is no correct or incorrect response, only the report of subjective experience. To that end, we employed the Ternus display, which is an apparent motion display that is perceptually ambiguous (Pikler, 1917; Ternus, 1926). A typical Ternus display consists of two frames separated by a blank interframe interval (IFI), which usually alternate in a cycle. The first frame of the display contains three horizontally aligned equally spaced elements (e.g., discs, squares, bars). In the second frame, the three elements are shifted to the right or to the left by one interelement spacing, such that the two inner elements (of the composite two-frame image) spatially overlap (Figure 1a). The participants' task is typically to report their motion percept. This poses a motion correspondence problem, as there is more than one possible way in which the elements can be matched across the two frames (e.g., Dawson, 1991). Numerous studies (e.g., Breitmeyer & Ritter, 1986b; Dawson et al., 1994; Kramer & Yantis, 1997; Pantle & Petersik, 1980; Pantle & Picciano, 1976; Petersik & Pantle, 1979) suggest that this displacement can give rise to two very different motion percepts, depending on the duration of the IFI (Figure 1b). When the IFI is long, all three elements appear to be moving

Figure 1
An Illustration of the Ternus Display



Note. (a) The display is composed of two alternating frames separated by variable interframe intervals (IFIs), which usually alternate in a cycle. Frame 1 consists of three horizontally aligned black discs, followed by an IFI (a blank screen), followed by Frame 2, in which the three black discs are shifted (relative to those in Frame 1) by one interelement spacing. (b) The two possible motion percepts: With the group motion percept, all three elements appear to move as a group. With the element motion percept, the two inner elements appear static and only the remaining element appears to jump back and forth between the two outer positions.

together as a group, a percept called group motion, whereas when the IFI is short, the two inner elements are perceived as static while the third element jumps back and forth between the outer positions. This latter percept is called element motion.

Several studies suggest that the element motion percept is a result of temporal integration (e.g., Breitmeyer & Ritter, 1986a, 1986b; Gepshtein & Kubovy, 2000; He & Ooi, 1999; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Ma-Wyatt et al., 2005; Wallace & Scott-Samuel, 2007). Elements that are similar in shape and color and appear in rapid succession in the same location are likely to be temporally integrated by the perceptual system into a single unified percept (e.g., Kramer & Yantis, 1997). That is, the elements of the first frame that occupy the overlapping positions are likely to be integrated with elements appearing in those same locations in the second frame, and therefore they seem to remain static. In contrast, motion is perceived between the nonoverlapping elements in the display. Temporal integration in the overlapping positions is particularly likely with short IFIs that allow for close temporal continuity of the elements in the two inner locations. As the IFI increases and the temporal distance between elements of different frames grows, they are less likely to be perceptually integrated, leading to a decrease in the frequency in which element motion is perceived (e.g., Breitmeyer & Ritter, 1986a, 1986b; Casco, 1990). This notion has gained support in several studies. For instance, previous studies have demonstrated that the probability of experiencing element motion at a given IFI was greater when visible persistence increased, for example due to decreased eccentricity, element size, or frame durations (Breitmeyer & Ritter, 1986a, 1986b). Because visible persistence is one of the main factors that mediate temporal integration, these findings support the hypothesis that element motion relies on temporal integration. Moreover, several studies have provided evidence that is consistent with this hypothesis because they show that element motion depends on the degree by which the elements' features support temporal integration. Kramer and Yantis (1997) found that when the elements within a single frame have different shapes while the spatially overlapping elements maintain their shape across frames, participants tend to report perceiving more element motion compared with a condition in which all the elements have the same shape (see also Casco, 1990). Using a two-element Ternus display, Kramer and Rudd (1999) found that when the two elements within a single frame were of different length but the overlapping element was of the same length, element motion predominated. Other studies also found more element motion responses when manipulating across-frame similarity using other features than shape and length, as for example contrast polarity, color, or texture (Dawson et al., 1994; Hein & Moore, 2012; Petersik & Rice, 2008). Additionally, Wallace and Scott-Samuel (2007) investigated the effect of across-frame orientation similarity on the perceived motion in the Ternus display. They used a modified Ternus display that consisted of three oriented Gabor patches. The Gabor orientation was similar within a frame, but it could differ across frames. They found that element motion was predominant with small across-frames orientation differences, but when the difference in orientation across frames was sufficiently large, group motion was perceived more frequently. Because similarity across frames facilitates temporal integration, the results of the aforementioned studies provide convincing evidence that the element motion percept arises from temporal integration. Given the large body of evidence, suggesting that element motion reflects temporal integration, and because the participants in this paradigm only have to report their subjective motion percept (i.e., there is no correct or incorrect answer), the Ternus display seems to be ideal for investigating the effect of spatial attention on temporal integration, while at the same time avoiding attentional effects on higher level strategies employed to optimize performance.

To our knowledge, only two studies exist that examined the effects of attention on the motion percept in the Ternus display. Both studies were not interested in temporal integration in itself. Aydın et al. (2011) examined whether the availability of attentional resources in general affects motion perception using a dual-task paradigm in which attention was oriented away from the Ternus display with a second task. They found more element motion reports in the dual-task condition, that is, with less attentional resources, compared with a single task condition in which attention was fully available for the Ternus display, suggesting that perceiving group motion requires more attentional resources compared with perceiving element motion. Dual-task paradigms, however, do not involve the allocation of spatial attention to a specific location, but rather they involve manipulation of the amount of resources that spread to all possible locations (Ling & Carrasco, 2006). Given this fundamental difference between the dual-task manipulation and direct manipulations of spatial attention, the study by Aydın et al. (2011) does not provide evidence regarding the effect of spatial attention on temporal integration. A second study was done by Stepper et al. (2020). They investigated the influence of endogenous attention on competitive feature biases in the Ternus display that contained simultaneously a group and an element bias (Hein & Schütz, 2019). These competitive displays were contrasted with the classic display, in which all elements had the same color as in the current study. In both display conditions (i.e., competitive vs. classic), endogenous attention was directed using precues to either one individual element or all elements. The authors found that attending an individual element in the competitive display led to more motion percepts in the direction of the bias contained in the element. The authors concluded that the attended element was assigned a higher weight in the correspondence process and therefore biased the percept accordingly in the competitive display. Although this study also examined the way endogenous attention affects the motion percept in the Ternus display, it addresses a very different research question than the current study, and consequently used different attentional manipulations, in which specific elements have to be attended and a distinction between conditions in which the Ternus display is attended versus not attended is not possible.

Unlike previous studies, in the current study we compared the motion percept in the Ternus display when spatial endogenous attention was either allocated to the entire Ternus display or not. This allowed us to compare temporal integration with and without endogenous attention. Specifically, we presented the Ternus display in the periphery and manipulated endogenous attention in two different ways. In Experiment 1, endogenous attention was manipulated by varying the degree of spatial uncertainty regarding the stimuli location, and in Experiment 2 we used central informative arrows to direct endogenous attention to the relevant location. We used a typical Ternus display composed of three frames (Frame 1 followed by Frame 2 followed by Frame 1), each consisting of three horizontally aligned discs. A varying IFI separated the three frames. Participants' task was to report whether they experienced group or element motion. We then compared the proportion of group motion reports across the attentional conditions and IFIs. If spatial endogenous attention indeed prolongs temporal integration, we should get fewer group motion reports (i.e., more element motion reports) in the attended condition, in which the participants could allocate attention in advance to the discs' location, compared to the unattended condition, in which the participants did not know in advance the discs' location.

Experiment 1

This experiment examined whether spatial endogenous attention can affect temporal integration using the Ternus display by varying the degree of spatial uncertainty, a manipulation of endogenous attention that we successfully employed in the past (Hochmitz et al., 2018). In the attended condition, the peripheral location of the three discs was fixed for the entire block. Participants were informed of this location prior to the beginning of the block; this allowed them to allocate attention to the discs' location before their onset. In the unattended condition, the stimuli could appear in one of two possible locations with equal probability, which prevented participants from attending the discs' location in advance.

Method

Participants

Ten students (7 female) from the University of Haifa participated in this experiment (age range: 19–33; $M = 24$, $SD = 5.12$). A power analysis obtained with the Shiny web app (Anderson et al., 2017) for a within-subject ANOVA using an uncertainty and publication bias correction, indicated that the minimum sample size required for the examination of spatial cuing effects at a power >99% with a type I error ($\alpha < .05$) is 9 participants. A similar power analysis indicated that the minimum sample size required for the examination of Cuing × IFI interaction effect at a power >80% with a type I error ($\alpha < .05$) is 10 participants. These analyses confirmed that the current study sample size (Experiment 1: $N = 10$; Experiment 2: $N = 11$) allowed the examination of these effects with sufficient power. The F values, degrees of freedom, and effect sizes used in these analyses were based on Sharp et al. (2018; cuing effect: $F(2, 10) = 13.30$, $\eta_p^2 = .73$; Cuing × ISI interaction: $F(8, 40) = 3.23$, $\eta_p^2 = .39$). Participants were naive to the purpose of the study and had normal vision. The ethics committee of the University of Haifa approved the experiments in this study (031/18 [IRB approval code provided by the University of Haifa ethics committee]), and all of the participants signed an informed consent form. This study adhered to the Declaration of Helsinki.

Stimuli and Apparatus

The stimuli were presented on a 19" monitor of an IBM-compatible PC (1024 × 768 resolution at a refresh rate of 85 Hz), using MATLAB and the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Eye movements were monitored monocularly with an EyeLink 1000 eye tracker (temporal resolution of 1000 Hz; SR Research, Ottawa, Ontario, Canada). A dim background light illuminated the room. The Ternus display used in this study consisted of three frames presented in a single cycle (i.e., Frame1 - Frame 2 – Frame 1). Each frame contained three horizontally aligned black discs with a diameter of 1° each. The discs were separated from each other by 2° (center to center; Figure 1), and were presented on a uniform gray background (24.5 cd/m^2). The three discs in the first frame were shifted randomly to the right or left in the second frame and then shifted back to their initial position in the third frame. All frames included a .3° × .3° black fixation mark (a plus sign) that indicated the center of the screen. The two attentional conditions were as follows: In the attended condition, the display always appeared to the right side of the screen at 5° of eccentricity, whereas in the unattended condition, it could equally likely appear on the right or left side, at 5° of eccentricity.

Procedure

Each trial began with the fixation mark. After 750, ms the first frame was presented for 200 ms followed by a blank screen with the fixation mark only. After a variable IFI (0, 12, 24, 36, 48, 60, or 72 ms), the second frame appeared for another 200 ms, and it was followed by an identical IFI. This second IFI was followed by the third frame presented for 200 ms. IFI duration was selected randomly for each trial, with the constraint that all possible IFIs will be chosen equally often. Participants' task was to indicate whether they perceived element or group motion by pressing one of two keys on the computer keyboard. A speeded response was not required.

The attentional condition was constant within a given block. Altogether, there were eight experimental blocks, equally divided between the two attentional conditions. Each block included 84 trials. The order of the blocks was randomly assigned for each participant, and the participants knew in advance which block they are about to perform. Specifically, a message informing the participants whether this is a "Fixed location" block or a "Changing locations" block was presented on the screen prior to the beginning of the block. The experimental blocks were preceded by a practice session composed of two practice blocks. The first practice block included 20 trials with only the two extreme examples of element and group motion (IFI of 0 and 72 ms). The second practice block included 28 trials identical to those of the experimental blocks.

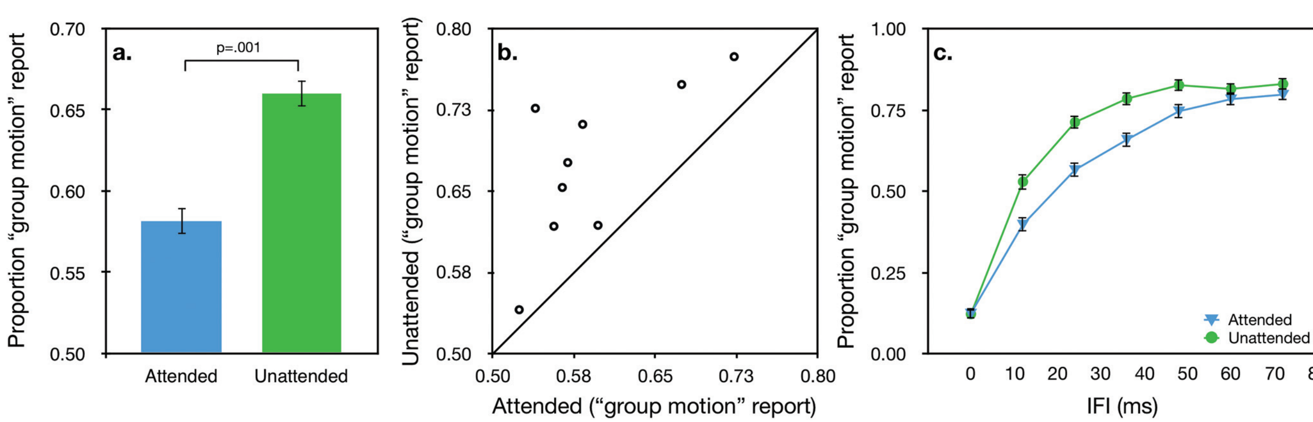
Results and Discussion

Our dependent variable was the proportion of trials in which the observers reported perceiving element motion; however, in the figures we present the results in terms of group motion proportion for better comparison with studies using the Ternus display, which normally present the results this way. A two-way repeated-measures ANOVA (attention × IFI) revealed the typical main effect of IFI ($F(6, 54) = 37.49$, $p = .0001$, $\eta_p^2 = .81$); with short IFIs, element motion was more prevalent, and as the IFI increased, group motion reports increased. This result replicates those of previous studies demonstrating that short IFIs mostly lead to element motion percept while long IFIs lead to group motion percept (e.g., Breitmeyer & Ritter, 1986b; Dawson et al., 1994; Kramer & Yantis, 1997; Pantle & Petersik, 1980; Pantle & Picciano, 1976; Petersik & Pantle, 1979). Most important for the goal of the current study, we found a significant main effect of attention ($F(1, 9) = 21.64$, $p = .001$, $\eta_p^2 = .71$). Specifically, mean element motion reports were higher in the attended condition compared with the unattended condition (Figure 2a), suggesting that when participants were able to attend to the discs' location in advance, they tended to perceive more element motion (i.e., less group motion) than when they could not. Figure 2b illustrates the data points of all the participants for the two attentional conditions. As can be seen in the figure, all data points fall above the equality diagonal, reflecting the fact that for all of our participants the rate of element motion reports was higher in the attended condition compared with the unattended condition.

There was also a significant interaction between IFI and attention ($F(6, 54) = 4.25$, $p = .001$, $\eta_p^2 = .32$). As evident in Figure 2c, with the shortest and longest IFIs there was no effect of attention; the effect of attention emerged with the middle IFIs. This is likely due to the fact that with the shortest and longest IFIs, perception is the least bistable; with these IFIs, participants mainly report perceiving one type of motion and there is not much room for any attentional effect. In contrast, with the middle IFIs, where the percept is most ambiguous, attention is able to affect the final motion percept.

Note that at least on some trials of the unattended condition participants might have shifted their attention to the stimuli location after the Ternus display appeared there and kept it there for the following trial. If this was the case, and given that stimuli location was randomized in the unattended condition, it is possible that at least on some of the trials of the unattended condition, the stimuli were attended. Indeed, previous studies have shown that position repetition can facilitate performance (e.g., Kristjánsson & Campana, 2010; Maljkovic & Nakayama, 1998). To test this possibility, we further analyzed the data of the unattended condition to include a repetition factor, allowing for a comparison between "switch trials" (i.e., trials in which stimuli location switched compared to the previous trial) and "repeated trials" (i.e., trials in which stimuli location was the same as in the previous trial). We performed a two-way repeated-measures ANOVA with repetition and IFI as factors. The typical main effect of IFI was once again significant ($F(6, 54) = 39.33$, $p = .0001$; $\eta_p^2 = .81$). However, we did not find a main effect of repetition ($F(1, 9) = .001$, $p = .98$, $\eta_p^2 = .0001$). This lack of an effect does not preclude the possibility that some of the unattended trials were actually attended due to

Figure 2
Results of Experiment 1



Note. (a) The proportion of group motion reports as a function of the attentional condition. (b) The proportion of group motion reports in the unattended condition as a function of proportion of group motion reports in the attended condition for each participant. (c) The proportion of group motion reports as a function of the attentional condition and the interframe interval (IFI). Error bars correspond to one standard error. See the online article for the color version of this figure.

location repetition, but it suggests that the factor of location repetition did not play a major role in the current experiment.

Overall, the results demonstrate that endogenous attention increased the rate of element motion perception in the Ternus display, suggesting that attention prolonged temporal integration.

Experiment 2

This experiment examined whether similar results will emerge with a more typical manipulation of endogenous attention—central informative arrow cues that indicate the target's most likely location (e.g., Jonides, 1981; Klein & Shore, 2000). The Ternus display employed in this experiment was identical to that of Experiment 1, but it could appear in one of four possible locations. Prior to the appearance of the discs, either an arrow or a cross (×) was presented at the fixation (see Figure 3). The cross was the neutral cue and it did not indicate the discs' location. The arrow pointed to one of the four possible discs' locations, and it could be valid or invalid. In the valid trials (75% of the trials with an arrow), the arrow pointed to the location of the subsequent discs, whereas in the invalid trials (25% of the trials with an arrow), it pointed to one of the other locations. Participants were aware of the predictive nature of the cues. If a similar attentional effect to that found in Experiment 1 will emerge here, this will provide converging evidence to the effect of endogenous attention on the motion percept in the Ternus display in particular and on temporal integration in general.

Method

Participants

Eleven undergraduate students (8 female), from the University of Haifa, participated in this experiment (age range: 19–25, *M* = 21.73 years, *SD* = 2); all were naive to the purpose of the study and had normal vision.

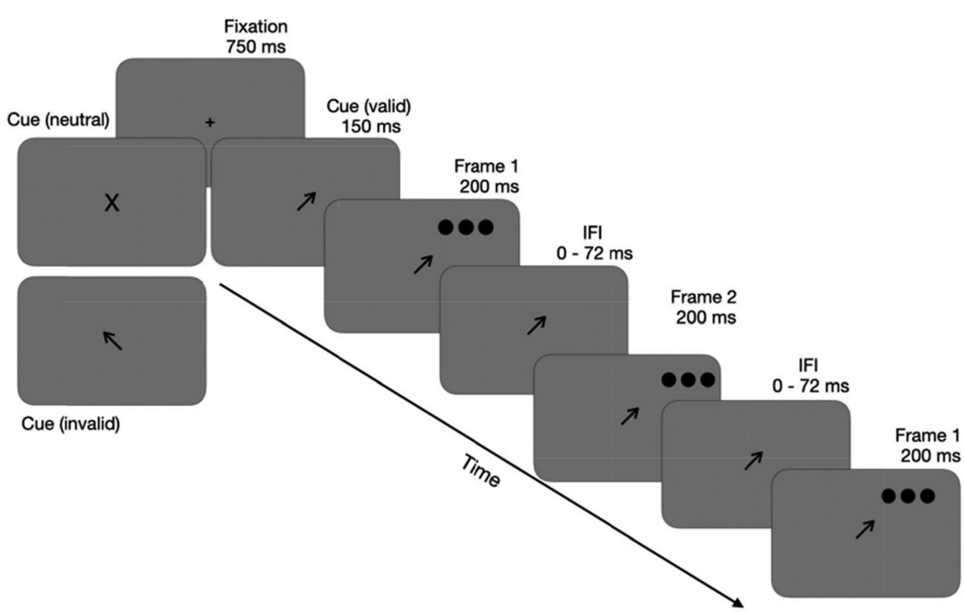
Stimuli, Apparatus, and Procedure

Stimuli apparatus and procedure were similar to that of Experiment 1 except for the following: The discs could appear in one of four possible locations at 5° of eccentricity (upper right/left, bottom right/left). We used central informative cues to manipulate spatial endogenous attention. As in Experiment 1, each trial began with a fixation mark that was presented for 750 ms. Then, a cue appeared for 150 ms. The cue was either a black, 2°-long cross (×), or a black arrow that subtended 2° × .7° × 1° pointing to one of the four possible discs' location (see Figure 3). The cross was the neutral cue, and it did not indicate the discs' location (33% of all trials). The arrow could either correctly indicate the location of the discs, in which case it was valid (75% of the trials with an arrow; 50% of all trials), or it could point to an incorrect location, in which case it was invalid (25% of the trials with an arrow; 17% of all trials). Participants were instructed that the cue usually predicts the discs' correct location and therefore would help them to perform the task. Each participant completed 20 blocks of 42 trials. IFI and cue type were counterbalanced and presented in random order.

Results and Discussion

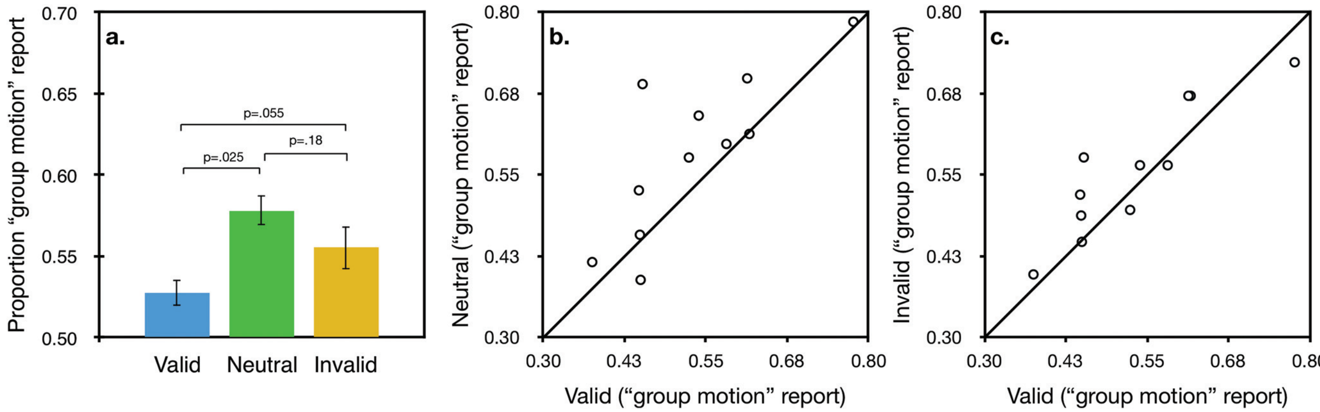
A two-way repeated-measures ANOVA (IFI × cue type) was performed on the element motion report rate (although, as in Experiment 1, the results are presented in the figures in terms of group motion proportion in accordance with most previous studies that used the Ternus display). This analysis revealed a significant main effect of IFI ($F(6, 60) = 34.37$, $p = .0001$; $\eta_p^2 = .77$). Similar

Figure 3
Illustration of the Trial Sequence in Experiment 2



Note. IFI = interframe interval.

Figure 4
Results of Experiment 2



Note. (a) Proportion of group motion reports as a function of the attentional condition. Error bars correspond to one standard error. (b) Proportion of group motion reports in the neutral condition as a function of proportion of group motion reports in the valid condition for each participant. (c) Proportion of group motion reports in the invalid condition as a function of proportion of group motion reports in the valid condition for each participant. See the online article for the color version of this figure.

to Experiment 1, element motion was more prevalent with short IFIs and as the IFI increased, group motion reports increased. Critically, we also found a significant main effect of cue type (F(2, 20) = 4.304, p = .028, η_p^2 =.3; Figure 4a); pairwise comparison indicated that element motion report rate was significantly higher (i.e., lower group motion reports) in the valid condition compared to the neutral condition (t(10) = 2.210, p = .025, dz =.67). The difference between the rate of element motion reports in the valid and invalid conditions as well as the difference between the neutral and invalid conditions did not reach statistical significance (t(10) = 1.75, p = .055, dz = .49; t(10) = 1.44, p = .18, dz = .43, respectively). The interaction was not significant (F $<$ 1). The lack of a significant difference between the neutral (and valid) condition and the invalid condition is not a concern. The invalid condition was included in this experiment to comply with the classic cuing paradigm, but we did not have a specific hypothesis regarding the predominant motion perception in this condition. The cost in performance in the invalid condition is well understood when considering performance measurements such as RT and accuracy, but there is no clear hypothesis regarding the pattern of results when one measures subjective experience, as with the Ternus display. Specifically, there are two main explanations for the poor performance in the invalid condition: The first account refers to the time required for reorienting attention to the stimuli location. When attention is engaged at an invalidly cued location, reorienting it to the correct stimuli location requires first to disengage it from the current focus of attention and then shift it to the correct location (Posner, 1980; Posner, 1988). This process of disengagement is time-consuming and manifests itself in longer RT's in the invalid condition compared with the neutral condition, in which attention is not engaged at a specific location and therefore there is no need for disengagement, only a shift is necessary (with the valid condition even the shift is not needed). Because response time in the Ternus paradigm was not speeded, it is not clear why or how the need to disengage should affect motion perception in a consistent manner (i.e., more/less element motion percepts). Another common account of performance cost in the invalid condition is that the allocation of attention to a location initiates inhibition of processing at the other uncued locations (in addition to the enhancement of processing at the attended location). In the invalid condition, the target appears at one of these inhibited locations, and its processing is therefore impaired (e.g., Cepeda et al., 1998; Posner, 1988). Although it is possible that the processing of the Ternus display was indeed inhibited on invalid trials, it is not clear why should such inhibition leads to consistently more or less group motion percepts. Thus, in this experiment, the invalid condition cannot be easily interpreted.

Importantly, when looking at the individual data (Figures 4b and 4c), it is clear that the difference in element motion report rate between the attended and unattended conditions was present for most of the participants. Thus, the effect of attention on the motion percept in the Ternus display is not restricted to the uncertainty manipulation. This suggests that this attentional effect is robust and is not merely due to the specific attention manipulation. This, in turn, strengthens the hypothesis that endogenous attention can affect temporal integration.

General Discussion

This study examined the effect of covert endogenous attention on temporal integration. We measured temporal integration via the rate of element motion reports generated by the Ternus display. This was based on several studies suggesting that element motion is perceived because the two elements in the positions that overlap across frames are integrated over time into a single event thereby perceived as static (e.g., Breitmeyer & Ritter, 1986a, 1986b; Gepshtein & Kubovy, 2000; He & Ooi, 1999; Kramer & Rudd, 1999; Kramer & Yantis, 1997; Ma-Wyatt et al., 2005; Wallace & Scott-Samuel, 2007). We employed two different attentional manipulations. In Experiment 1, we manipulated endogenous attention by varying the degree of spatial uncertainty (e.g., Hochmitz et al., 2018), while Experiment 2 involved a more typical manipulation of endogenous attention: central informative arrow cues (e.g., Jonides, 1981; Klein & Shore, 2000). Overall, in both experiments, the pattern of element/group motion reports as a function of IFI revealed the typical effect: Element motion reports were more frequent with short IFIs, whereas group motion reports were more frequent with longer IFIs. This result replicates previous studies that varied the IFI between successive frames of the Ternus display (e.g., Breitmeyer & Ritter, 1986b; Dawson et al., 1994; Kramer & Yantis, 1997; Pantle & Petersik, 1980; Pantle & Picciano, 1976; Petersik & Pantle, 1979). Most of the studies reporting this IFI effect involved a foveal presentation of the Ternus display. Only a few studies employed peripheral presentation of the Ternus display (Aydın et al., 2011; Breitmeyer & Ritter, 1986b; Stepper et al., 2020). The results of the current study confirm the finding that spatiotemporal factors influence correspondence processes even in the periphery.

Most important for the goal of this study, the results of both experiments revealed that endogenous attention can affect motion perception in the Ternus display. Specifically, in both experiments, element motion reports were more frequent with attention than without attention. As detailed above, because the perception of element motion depends on information integration across time, this finding suggests that endogenous attention prolongs temporal integration. The fact that the effect of attention occurred with two different attention manipulations suggests that this effect is not merely an artifact of a specific manipulation. Additionally, it might be useful to bear in mind that there was no strict dichotomy between our different attentional conditions. It is possible that the onset of the discs served as an attentional cue, attracting exogenous attention to the discs' location. Considering that exogenous attention is activated fast, and that the display frames were presented for a relatively long duration, it is reasonable to assume that for a part of the time, the Ternus display was processed with attention also in the unattended conditions. This means that the attentional effects found in this study are probably underestimated.

The finding that attention affects the motion percept in the Ternus display adds to the existing literature that demonstrates the role of covert spatial attention in early visual processing. For instance, numerous studies have shown that attention improves early aspects of visual perception such as contrast sensitivity (e.g., Cameron et al., 2002; Carrasco et al., 2000; Dosher & Lu, 2000; Huang & Dobkins, 2005; Lu & Dosher, 1998; Lu & Dosher, 2000; P. L. Smith et al., 2004; Solomon, 2004) and spatial resolution (e.g., Carrasco et al., 2002; Golla et al., 2004; Yeshurun & Carrasco, 1998, 1999). Additionally, previous studies have shown that spatial attention can modulate motion perception (e.g., Dobkins & Bosworth, 2001; Treue & Maunsell, 1996; Yeshurun & Hein, 2011), although there appear to be large variations in the nature of these modulations, partially depending on whether endogenous or exogenous attention is involved, and there is no consensus regarding the nature of the mechanisms underlying these attentional effects (Yeshurun & Hein, 2011). Thus, the findings of the present study underline the critical role played by endogenous attention in early aspects of visual processing. The current study also suggests that different attentional manipulations may be based on very different underlying attentional mechanisms, exerting differential effects on early visual processes. Aydın et al. (2011) found that under limited attentional resources, fewer group motion reports were observed, suggesting that the perception of group motion requires more attentional resources compared with element motion. In contrast, we found that when manipulating endogenous attention, that is, orienting attention to a specific location, less group motion percepts were reported, while more group motion reports were observed when attention was oriented away from the Ternus display. This supports the notion that these two different types of manipulations trigger different attentional mechanisms.

Our results also show that temporal integration is not only influenced by temporal attention, but can also be influenced by spatial attention. In particular, Visser and Enns (2001) found that under limited attentional resources the duration of visible persistence, and therefore the temporal window of integration, is shortened using the attentional blink paradigm. In line with these results, our findings show that endogenously attending to a spatial location can prolong the temporal window of integration. In addition, our results also provide support for Sharp et al.'s (2018) conclusion. Sharp et al. (2018) manipulated endogenous attention and used a variant of the missing dot task. Because the successful localization of the missing element required integrating two sequential displays, their finding implies that endogenous attention can facilitate temporal integration. However, their task involved a correct or incorrect response, and the participants might therefore have been encouraged to apply different strategies in the different attentional conditions in order to maximize performance. Thus, the results found by Sharp et al. (2018) might have reflected attentional effects on high level processing such as response selection. In contrast, our study measured the participants' subjective experience (i.e., there is no correct or incorrect response), and therefore the participants had no reason to adopt different higher-level strategies for the different attentional conditions. Our results clearly suggest that spatial endogenous attention prolongs temporal integration.

What mechanisms may underlie the effect of attention on temporal integration? One possibility is an attentional mechanism that prolongs the internal response to the attended stimulus. According to this account, the internal activation generated by an attended stimulus is longer and has a slower decay compared to the activation elicited by a nonattended stimulus (e.g., Di Lollo et al., 2000; Enns et al., 1999; Mattes & Ulrich, 1998; Yeshurun & Hein, 2011; Yeshurun & Marom, 2008). This hypothesis gained some support from studies that explored the effects of attention on various aspects of temporal perception (Rolke et al., 2006; Yeshurun, 2004; Yeshurun & Levy, 2003). For instance, Yeshurun and Marom (2008) have shown that participants tend to perceive the duration of brief visual events as longer when exogenous attention is attracted to their location. Such prolongation of perceived duration was also found with endogenous attention. Mattes and Ulrich (1998) conducted a series of experiments in which they found that brief flashes appearing in cued locations are perceived as having a longer duration than those appearing in uncued locations (see also Enns et al., 1999). Indeed, longer internal responses to brief successive stimuli increase the chance that these internal responses will be integrated over time, resulting in a single unified percept (Yeshurun & Marom, 2008). Furthermore, this account is consistent with Sharp et al. (2018), who attributed their finding of attentional prolongation of temporal integration to an attentional mechanism that affects the size of the temporal window. They suggested that when there is a need for integration of temporally disparate stimuli, attention operates by biasing the system to sample the environment with longer temporal windows (Wutz et al., 2016, 2018). This account of the attentional prolongation of temporal integration is consistent with the account we suggested above because attention may extend the length of the temporal window via the prolongation of the internal responses to the stimuli. Indeed, it has been demonstrated that the length of the temporal integration window at the neural level is not fixed but rather varies with the characteristics of the input (e.g., Bair & Movshon, 2004). Thus, just as changing the characteristics of the input alters the length of the temporal window, allocating attention to a location may alter the pattern of neural firing in response to stimuli presented at this location, which prolongs the temporal interval over which information is integrated.

Our findings also provide important insights into the effect of endogenous attention on correspondence processes. As mentioned in the introduction, Stepper et al. (2020) also examined the effects of endogenous attention on the Ternus percept. In particular, they oriented attention endogenously to individual Ternus elements that could either all have the same color as in the classic Ternus display or have different color-based biases that simultaneously were compatible with element and group motion percepts (competitive bias; Hein & Schütz, 2019). Stepper et al. (2020) interpreted their findings as support for the object-based correspondence theory (Hein & Cavanagh, 2012; Hein & Moore, 2014), which suggests that correspondence is established by a higher-level process based on a one-to-one mapping of the most similar objects. That is, correspondence is established by connecting each individual element in one frame with the perceptually most similar element in the next frame. They argued that if attention was allocated to a specific element, attending that element would increase the weight assigned to it in determining the corresponding one-to-one mapping across frames, thereby affecting the final motion percept in the competitive bias display, which is what they observed in their study. With the classic Ternus display, however, directing attention to individual elements did not affect the correspondence solution. The authors concluded that the competitive Ternus display with the feature-based biases might activate different correspondence processes than the classic display for which features do not play an important role. Furthermore, Stepper et al. suggested that the effect of endogenous attention on correspondence processes is limited to the more complex feature-based correspondence situations that are resolved via object-based mechanisms in contrast to correspondence based on spatiotemporal factors. This conclusion, however, is in contrast to what we found in the present study, in which orienting attention endogenously to the entire Ternus display revealed a significant effect of endogenous attention also in the case of the simple Ternus display that did not included feature biases. Thus, the differences between these two studies suggest that spatial endogenous attention can modulate the solution of the correspondence problem through different mechanisms. In the current study, all elements were identical and attention was allocated to the entire Ternus display. Hence, in the current study, attention could not modify the solution of the correspondence problem via modification of the weights of individual elements. Instead, we suggest that the attentional effect we found operated via modification of spatiotemporal factors in a manner that consistently biases the solution of the correspondence problem toward element motion percept. Spatiotemporal factors, like the interobjects spatial distance and the time interval between objects' onset, have been shown to play an important role in establishing correspondence between objects and perceiving apparent motion (e.g., Korte, 1915). Objects that are close to each other in space or in time tend to be matched with each other (Casco, 1990; Petersik & Grassmuck, 1981). The most striking evidence for the role of spatiotemporal factors in determining the percept in the Ternus display is the IFI effect (e.g., Pantle & Petersik, 1980; Petersik & Pantle, 1979). With the short IFIs, the elements in the overlapping positions are matched with each other due to their spatiotemporal proximity, leading to element motion percept. When attention is allocated to the entire Ternus display, it prolongs the internal response to the elements of the preceding frame, thereby reducing the perceived time interval between these elements and those of the following frame. Such an increase in the temporal proximity of the frames increases the probability that correspondence will be established between the elements in the overlapping positions, resulting in more element motion percepts. Thus, establishing correspondence between objects is a complex process that can occur at different levels of processing. The current results combined with those of Stepper et al. (2020) suggest that spatial endogenous attention can affect this process in different ways, and likely at different levels, depending on the characteristics of the display and the specifics of the attentional allocation.

To conclude, in this study we examined the effect of endogenous attention on temporal integration using the Ternus display. We found higher rates of element motion percept when endogenous attention was allocated to the location of the Ternus display. This finding provides strong support to the hypothesis that covert spatial attention prolongs temporal integration. Additionally, it demonstrates that there are various manners by which spatial attention affects processes that resolve the correspondence problem.

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Received May 24, 2020
Revision received December 27, 2020
Accepted January 7, 2021 ■