

Evidence for parallel consolidation of motion direction and orientation into visual short-term memory

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Keywords: motion direction, orientation, parallel consolidation, visual short-term memory

Running title: PARALLEL CONSOLIDATION OF DIRECTION AND ORIENTATION

Abstract

Recent findings have indicated the capacity to consolidate multiple items into visual short-term memory in parallel varies as a function of the type of information. That is, while colour can be consolidated in parallel, evidence suggests that orientation cannot. Here we investigated the capacity to consolidate multiple motion directions in parallel and re-examined this capacity using orientation. This was achieved by determining the shortest exposure duration necessary to consolidate a single item, then examining whether two items, presented simultaneously, could be consolidated in that time. The results show that parallel consolidation of direction and orientation information is possible, and that parallel consolidation of direction appears to be limited to two. Additionally, we demonstrate the importance of adequate separation between feature intervals used to define items when attempting to consolidate in parallel, suggesting that when multiple items are consolidated in parallel, as opposed to serially, the resolution of representations suffer. Finally, we used facilitation of spatial attention to show that the deterioration of item resolution occurs during parallel consolidation, as opposed to storage.

The limits of memory: Evidence for parallel consolidation of motion direction and orientation into visual working memory

A great deal is known about the capacity of visual short-term memory (VSTM), i.e. the number of items that can be stored; for a review, see Ma, Husain and Bays (2014). However, relatively little is known about *how* information is consolidated from sensory memory into VSTM, i.e. the formation of VSTM representations. Sensory memory is characterized as high capacity memory whose contents decay within a few hundred milliseconds (Sperling, 1960, 1963), whereas VSTM has a considerably lower capacity which is more sustainable (Cowan, 2001). A number of studies have examined the time course of this consolidation, and determined that the transfer of information from sensory to VSTM takes around 50ms per simple item (Jolicoeur & Dell'Acqua, 1998; Vogel, Woodman, & Luck, 2006). Importantly, these studies do not attempt to discriminate between serial and parallel models of consolidation, noting that both could account for the data. While items could be processed serially, each taking 50ms, multiple items might be processed in parallel, together requiring a longer total duration. Given the importance of the mechanism that transfers information from sensory memory to VSTM, understanding the nature of this process, i.e. whether information can be consolidated in parallel, is essential to a complete understanding of memory processes.

Recently, a number of studies have addressed this question. Huang, Treisman and Pashler (2007) used a task where observers were shown simple items (coloured squares), either serially or simultaneously and then asked to respond whether a probed colour was present. As matching performance was worse in the simultaneous condition even when only two items were presented, the authors concluded that consolidation occurs serially. However, Mance, Becker and Liu (2012) argue that a number of presentation contingences in these experiments, i.e. certain pairs of items consistently being presented in the same locations, led

Huang, et al. (2007) to underestimate participants' capacity to consolidate items in parallel. Their results supported this, indicating that these presentation contingencies had selectively handicapped performance in the simultaneous condition. In conditions where the contingencies were removed, observers were capable of performing the simultaneous task with the same accuracy as the serial task with two, and possibly three, items. To account for these results, the researchers proposed that parallel consolidation is possible but may be limited to two items.

Becker, Miller and Liu (2013) extended this work by using a similar paradigm to investigate whether orientation information can be consolidated in parallel. Over a series of experiments they consistently found better performance when two items were presented serially compared to simultaneously, leading them to conclude that orientation information, unlike colour information, cannot be processed in parallel. The notion that such marked differences exist between categories in the capacity to process simple information is unexpected. Initially the researchers proposed the difference between the perceptual spaces of the two types of information, i.e. colour and orientation, may account for the findings. That is, while colour has a rich space, varying in hue, saturation and luminance, orientation has a relatively poor space, only varying along a single dimension. They argued that this difference may have led to greater interference between feature intervals used to define items within the orientation dimension than those used within colour as a result of the proximity of these items in their corresponding perceptual spaces.

In a follow-up study, Miller, Becker and Liu (2014) demonstrated that a combination of colour and orientation information could not be consolidated in parallel, which the authors interpreted as suggesting that the inability to consolidate orientation information in parallel may not be due to interference within a small perceptual space. However, the unknown impact of using features from within different dimensions makes it difficult to compare these

results with previous studies involving only a single feature type. Some evidence for a shared mechanism was found for the consolidation of colour and orientation, and to account for the difference in the capacity of this mechanism to consolidate these two features, the authors proposed that while only a small information bandwidth is required to encode colour, the information bandwidth required to encode orientation is too large for the system to consolidate in parallel.

Thus, currently the answer to the question posed previously regarding the debate between parallel and serial consolidation is not a simple yes or no, but appears to be contingent upon the type of information being consolidated, e.g. colour or orientation. Given the importance of this question, if the nature of the consolidation process does vary between serial and parallel as a function of the type of information being processed, it is of interest to determine how other types of basic information are consolidated. Determining this is not only useful in isolation, but will ultimately lead to a deeper understanding of the nature of information processing in memory consolidation.

One type of information that would be a good candidate for parallel consolidation is motion direction. Previous studies have investigated simultaneous processing with global motion signals defined by direction, presented in the same spatial region (transparent motion) or in different spatial regions (Edwards & Greenwood, 2005; Greenwood & Edwards, 2006; Qian, Andersen, & Adelson, 1994). Over a number of studies, the researchers consistently found that observers were capable of making n vs. $n + 1$ motion signal discriminations with up to $n = 3$ signals. The researchers interpreted these findings as indicating a higher-order limit restricting the simultaneous processing of motion to three directions. More recently, this research has been extended by the demonstration that during brief presentations of multiple spatially localized motion signals, observers are capable of extracting direction information from up to three items (Edwards & Rideaux, 2013; Rideaux & Edwards, 2014).

Importantly however, none of these motion studies explicitly differentiated between rapid serial and parallel accounts of consolidation; due to the length of presentation durations in these studies, it is impossible to discriminate between these accounts. Given the similarity between orientation and motion direction information (Clifford, 2002), it is likely that the factors preventing parallel consolidation of orientation information proposed by Becker et al. (2013) may also apply to direction. For instance, while the range of possible directions is twice the size of possible orientations, i.e. 360° as opposed to 180° , the perceptual space appears to be equivalent. Adaptation studies show that the tuning bandwidths for motion direction are twice that for orientation (Albright, 1984; Britten & Newsome, 1998; McAdams & Maunsell, 1999), and the threshold orientation required for discrimination of motion direction is about twice the size of that needed for orientation (De Bruyn & Orban, 1988; Webster, De Valois, & Switkes, 1990). Thus, if interference resulting from proximal intervals within a small perceptual space does account for the inability to consolidate in parallel, we would expect to find the same results using motion direction, even though it has a larger physical range. Additionally, it is conceivable that the size of the information bandwidth required to encode direction, like orientation, is larger than needed for colour, as information must be pooled over space and time. Thus, if the ability to consolidate in parallel is related to the size of the information bandwidth required to process a given feature, it is likely that parallel consolidation of motion direction will not be possible.

In summary, in the light of recent findings indicating that the capacity to consolidate information into VSTM varies as a function of the type of information encoded, we set out to determine whether motion direction information is capable of being consolidated in parallel. To the best of our knowledge this will not only be the first test of whether motion direction can be consolidated in parallel, but the first test of this kind with a dynamic feature, i.e. motion.

Experiment 1: parallel consolidation of motion directions

Using a similar paradigm to that employed by Mance et al. (2012), here we directly investigate whether motion direction information can be consolidated into VSTM in parallel or if, like orientation information, it is limited to rapid serial processing. Specifically, the aim of the experiment was to determine the shortest stimulus duration necessary to consolidate a single item and then examine whether observers were capable of consolidating two items presented simultaneously for this duration. To balance other factors associated with processing and storing multiple items between the methods of consolidation, performance consolidating n number of items in parallel was compared to performance processing n number of items serially, with sufficient time between serial presentations for optimal performance. If direction information can be consolidated in parallel, we would expect observers to perform equally well when items are presented simultaneously as when they are presented sequentially.

Method

Observers

Ten observers participated in the study: one of the authors (RR) and nine others who were naïve with respect to the aims of the study. All had normal or corrected to normal acuity and gave informed written consent to participate in the study.

Apparatus

Experiments were run under the MATLAB (version R2013a) programming environment, using software from the PsychToolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a Phillips Brilliance 202P4 CRT monitor that was driven by an Intel Iris

graphics card in a host MacBook Pro computer. The monitor had a spatial resolution of 1024 x 768 pixels and a frame rate of 120Hz.

Stimuli

The stimulus presentation sequence consisted of a motion sequence, a fixation period and a probe sequence, respectively. The motion sequence contained one or more motion stimuli presented either simultaneously or sequentially. The motion stimuli were square apertures ($8^\circ \times 8^\circ$ visual angle) positioned evenly around an imaginary circle (8° radius) centred on fixation. Each stimulus contained 100 Gaussian blobs (0.3° radius), which moved in a consistent direction within each square, wrapping around when they reached the edges, to form the percept of a coherent motion within each aperture. For each trial the direction of the motion stimuli was randomly selected from the four possible oblique directions without replacement, i.e. 45° , 135° , 225° and 315° , avoiding presentation contingencies, e.g. only presenting certain items in some locations, which have been shown can selectively hinder parallel consolidation (Mance, et al., 2012). Oblique, as opposed to cardinal, directions were employed to encourage observers to use visual rather than verbal short-term memory, i.e. it should be more difficult to verbally encode diagonal directions than up/down/left/right. During the motion sequence the motion stimuli were presented for a predetermined duration, the determination of which is later described, and then replaced by a 200ms dynamic mask. The mask consisted of an aperture equal to the size and shape of the motion stimuli containing 300 blobs which were rapidly randomly positioned and repositioned for its duration, giving a similar impression to the static observed on a television without reception. The mask was employed to interrupt sensory persistence of the motion signal, and has previously been shown to be effective (Rideaux & Edwards, 2014).

When motion stimuli were presented sequentially, each stimulus was separated by a 500ms fixation period, where only the fixation cross was present. To reduce temporal uncertainty, a tone was played 200ms before each motion stimulus was presented. Following the motion sequence/s there was another fixation period; in the sequential condition this was 500ms and in the simultaneous condition this was the combined duration of the fixation periods in the corresponding sequential condition. That is, when two motion stimuli were presented in the simultaneous condition, the fixation period was 1000ms; when three were presented, it was 1500ms. This was done in order to balance the duration that information needed to be maintained in VSTM between the simultaneous and sequential conditions; otherwise this may have selectively handicapped performance in the sequential condition (Mance, et al., 2012). In the sequential condition, the interval between each item presentation and the probe varied depending on the order of presentation, whereas in the simultaneous condition the duration of this interval was equal to the longest interval in the corresponding sequential condition for all items. Thus, information in the simultaneous condition was required to be maintained for longer on average and similar performance between these conditions cannot be interpreted as reduced performance in the sequential condition resulting from longer retention periods. Finally, the probe sequence, consisting of a motion stimulus similar to that used in the motion sequence, centred on fixation, was presented for 500ms followed by a fixation period. The probe stimulus moved in either one of the directions presented in the preceding motion sequence (match) or one of the remaining directions (mismatch). Examples of the presentation sequences are shown in Figure 1.

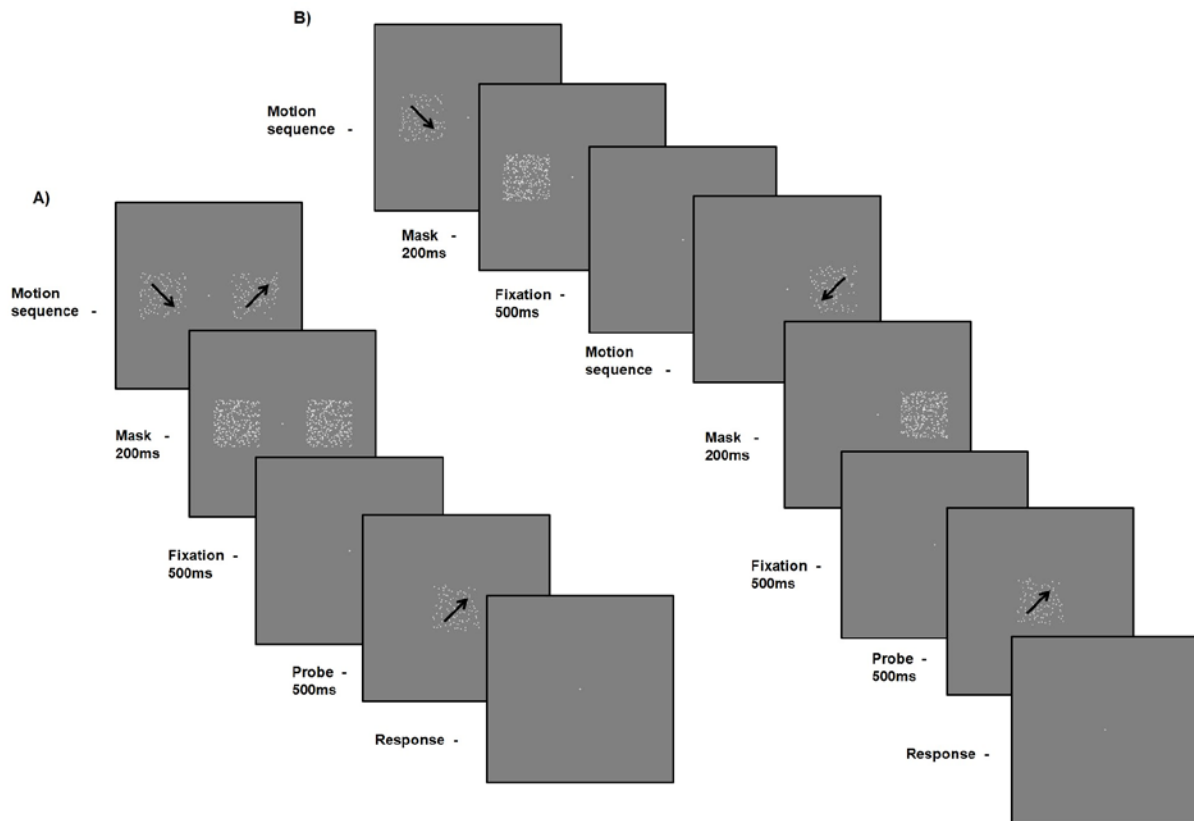


Figure 1: An example of the stimuli used in Experiment 1. A) An example of the presentation sequence in the simultaneous condition (match trial). B) An example of the presentation sequence in the sequential condition (mismatch trial). The black arrows in the motion sequence and probe frames have been added to illustrate the motion direction of the blobs.

The background was grey (mean luminance, 12 cd/m^2) and the blobs were white (mean luminance, 63 cd/m^2). The blobs were displaced 0.082° each frame, resulting in a speed of $9.8^\circ/\text{s}$. The observer sat 50 cm from the monitor, with their head supported on a chin rest.

Procedure

Observers were instructed to maintain fixation on the fixation cross throughout the experiment. Their task was to indicate whether the probed direction was present or absent in the preceding presentation using the ‘z’ and ‘1’ keys. The minimum duration mentioned

earlier was determined by taking the mean of five 3 down/1 up staircases to find the 79% threshold duration for which observers were capable of serially consolidating two items using the stimulus described above. This duration was determined for each observer and used to test this observer in all subsequent presentations, to account for individual variation in consolidation efficiency. The frame rate was 120Hz, i.e. 8ms per frame, and at least two frames are required to produce motion, thus the minimum possible duration was 16ms. To balance experience with the stimuli, observers also ran five staircases using simultaneous presentation during threshold determination; however this data was not used.

Following determination of the minimum duration for consolidation, 240 trials were run using both simultaneous and sequential presentation of two and three motion signals. Thus, the experiment was a 2×2 design (simultaneous/sequential presentation \times 2/3 items) with a total of 960 trials. Trials were run in blocks of 48, with the condition held constant within blocks and randomly interleaved between blocks. Blocks were counterbalanced so on half the trials the probe matched one of the test directions, and each test location had an equal probability of being the target. Finally, for match trials within the sequential condition blocks targets selected as a function of presentation order was also counterbalanced.

Results and discussion

The average threshold duration was 82ms (range, 37 – 154ms; SD, 44ms). This is somewhat longer than the corresponding mean thresholds found for colour (60ms) (Mance, et al., 2012) and orientation (55ms) (Becker, et al., 2013); however, this is unsurprising, given that colour information can be extracted from a single static image whereas motion direction requires at least two frames before information extraction is possible. Furthermore, a number of studies indicate that colour is processed more rapidly than motion direction (Arnold & Clifford, 2002; Moutoussis & Zeki, 1997; Nishida & Johnston, 2002).

In the subsequent trials examining proportion of correct responses, the same pattern of results was found for all observers. Average performance is plotted in Figure 2. A repeated measures ANOVA was used to compare performance across the four conditions. Significant main effects for both presentation type (simultaneous/sequential) and item number (2/3) were found, $F(1, 9) = 11.65$, $p < .001$ and $F(1, 9) = 120.96$, $p < .001$ respectively. A significant interaction effect was also found, $F(1, 9) = 19.29$, $p < .01$. Paired t-tests revealed that while mean performance between simultaneous/sequential conditions was the same when two items were presented, $t(9) = 0.60$, $p > .05$, performance was significantly higher in the sequential condition when three items were presented, $t(9) = 3.96$, $p < .001$. Note that the average performance in the two item conditions is higher than the threshold used to determine the exposure duration, 79%. This is likely due to the increased temporal certainty in the main experiment compared to the threshold determination experiment, i.e. the exposure duration during the latter experiment varied constantly from trial to trial, and also a practice effect as observers were more familiar with the stimuli/task during the main experiment.

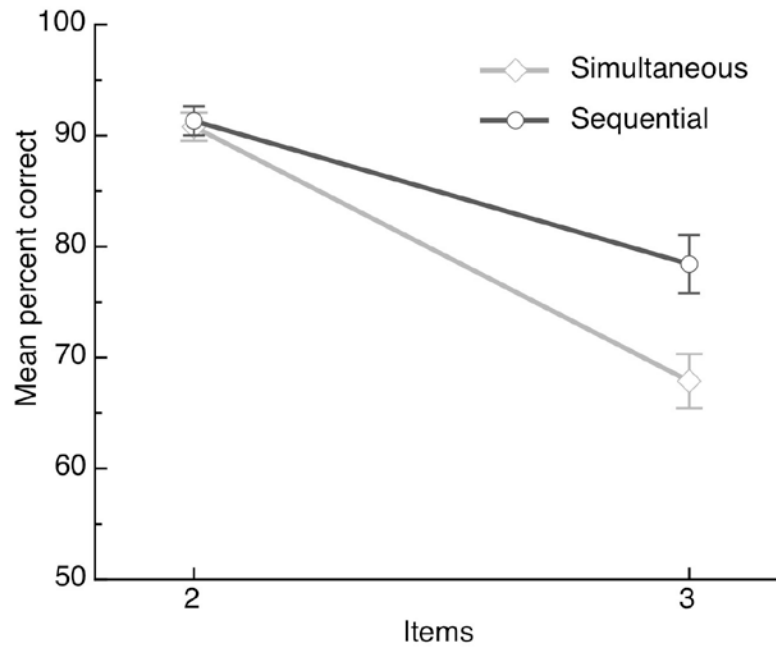


Figure 2: Mean performance across observers in Experiment 1 for each presentation type (simultaneous & sequential) as a function of the number of items presented. Error bars indicate ± 1 SEM.

Interestingly, performance was higher when only two items (as opposed to 3) were presented in the sequential condition, $t(9) = 6.54$, $p < .001$. To examine whether this was due to information decay resulting from increasing the number of directions which were required to be held in VSTM, performance as a function of the order in which the target item was presented (for match trials) within the sequential three item condition was analysed (mean performance is shown in Figure 3). A significant main effect of target presentation order was found, $F(2, 9) = 5.12$, $p < .05$, demonstrating that observers performed worse at the task when the target was presented earlier in the sequence. This indicates that the reduction in performance between two and three items presented sequentially was, at least partially, due to the information decay of older items. This is surprising given that storing three motion directions is within the capacity of VSTM (Blake, Cepeda, & Hiris, 1997) and no difference in performance was found between targets presented first and second in the corresponding two-item condition $t(9) = 1.55$, $p > .05$.

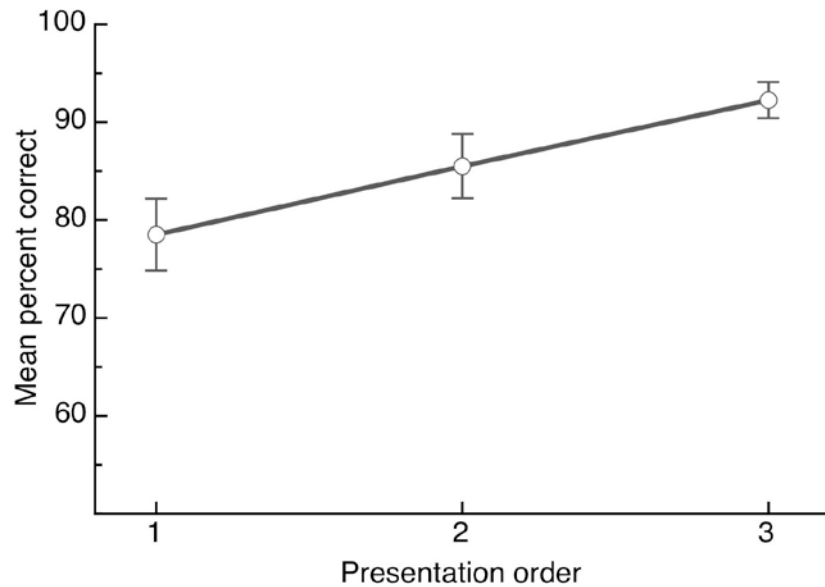


Figure 3: Mean performance across observers within the 3 item sequential condition (match trials) of Experiment 1 as a function of target item presentation order. Error bars indicate ± 1 SEM.

The results show that parallel consolidation of motion direction information from sensory to VSTM is possible and suggest that this process is limited to two items. Indeed, if observers were only capable of consolidating two items during the three item/simultaneous presentation condition, with the exception of trials where one of the consolidated items was probed (0.33), all other trials would be performed at chance because it would be unknown whether the probed item was the missed item or not. Thus, the expected performance level would be equal to the product of mean performance in the two item condition and the proportion of trials where the consolidated items were probed ($.91 \times .33 = .30$), plus the product of chance performance and the remaining proportion of trials ($.5 \times .66 = .33$), i.e. 63%. Given that performance in the three item/simultaneous condition is not significantly different from this value, $t(9) = 1.76, p > .05$, the results support this interpretation.

Experiment 1 demonstrated that two motion directions can be consolidated in parallel from sensory to VSTM. Given that evidence suggests that the perceptual space available to direction is equivalent to orientation, this finding is inconsistent with the claim that the

incapacity to consolidate orientation information in parallel is due to its relatively smaller (than colour) perceptual space. However, given that the physical range of directions is twice that of orientation, caution must be taken when comparing the perceptual spaces of these features. This finding appears to be inconsistent with the claim that the size of the information bandwidth required to encode orientation is responsible for the inability to consolidate this feature in parallel (Miller, et al., 2014), as the information bandwidth required to encode motion is likely the same as if not larger than orientation, e.g. to extract motion direction information must be pooled over both space and time.

However, in addition to using motion direction (as opposed to orientation) to examine parallel consolidation, another potentially important difference relating to the presentation of items may have been responsible for the distinct results found here. That is, spatial attention, which allows localized enhancement of perceptual processing (Lee, Itti, Koch, & Braun, 1999), was facilitated through the use of consistent item locations. In contrast, Becker, et al. (2013) presented orientation items randomly in four possible locations. If consolidating information in parallel results in reduced resolution of encoded information, when information encoded serially is already encoded at high resolution, facilitation of spatial attention may be more beneficial for parallel than serial consolidation. Liu and Becker (2013) found no evidence for this interpretation, their results indicating that when presented with two orientation items simultaneously, observers consolidated one item at high resolution and failed to consolidate the other. However, the task used in their experiment required observers to respond with the precise orientation of a single probed item, which may have resulted in observers using a single consolidation strategy rather than consolidating two items at low resolution. In contrast, the resolution required to complete the task in the current experiment is considerably lower, possibly encouraging the employment parallel consolidation, at the cost of resolution.

Given the relative proximity of feature intervals used to define targets by orientation and direction compared to colour, the susceptibility to interference of information encoded at reduced resolution is greater for these types of information. Thus, while it may not be necessary to consolidate colour in parallel, facilitation of spatial attention may be required to achieve this with motion direction and orientation information. Experiment 2 investigates whether these explanations account for the ability to consolidate direction information in parallel.

Experiment 2: effects of spatial attention and feature interval separation

Becker, et al. (2013) found that observers were not capable of consolidating orientation information in parallel, which contrasted with their previous finding indicating that this was possible using colour information (Mance, et al., 2012). To account for this discrepancy the authors proposed that the size of the perceptual space afforded to orientation, considerably smaller than that of colour, may have resulted in interference between the two items, preventing parallel consolidation. The results of Experiment 1 would appear to be inconsistent with this account, given that evidence indicates the perceptual space of motion and orientation are equivalent (Clifford, 2002). However, although adaptation/discrimination studies suggest that the perceptual spaces of these features are equivalent, it is possible that motion direction has a larger perceptual space, afforded to it by its wider physical range, which allows direction to be consolidated in parallel where orientation cannot. Alternatively, spatial attention was facilitated in Experiment 1 by presenting items in consistent locations, i.e. observers could anticipate the location of items being presented and direct their attention to those locations, and may be necessary to achieve parallel consolidation of direction information. Here we explore these two possibilities by a) reducing the range of motion directions used in the task and b) increasing the spatial ambiguity of targets, using the same design as Becker, et al. (2013), i.e. presenting the targets pseudo randomly in four possible

locations. If either of these factors plays a significant role in parallel consolidation, this should result in differential performance compared to that found in Experiment 1.

Method

Observers

Ten observers participated in the study: one of the authors (RR) and nine others who were naïve with respect to the aims of the study. All had normal or corrected to normal acuity and gave informed written consent to participate in the study.

Stimuli and procedure

The stimuli and procedure were largely the same as that used in Experiment 1. Given that we found observers were only capable of parallel consolidation with two items in Experiment 1, here we only compared performance between sequential and simultaneous presentation using two items.

To examine whether parallel consolidation is possible when the physical range of directions used is reduced to that available to orientation (180°), a condition was run where the directions used were changed from the four diagonals to 0° , 45° , 90° , and 135° , where 0° was represented by leftward motion. To investigate whether spatial certainty is necessary to achieve parallel consolidation, another condition was run where the targets were randomly presented in two of four possible locations on each trial, as opposed to the same locations on every trial. The four possible target locations were on the corners of an imaginary square ($12^\circ \times 12^\circ$), centred on fixation. Thus, the experiment was a 2×2 design (simultaneous/sequential presentation \times reduced range/spatial uncertainty). The same stimuli and procedure used in Experiment 1 was employed to determine observers' minimum threshold duration. Examples of the presentation sequences used in the spatial uncertainty conditions are shown in Figure 4.

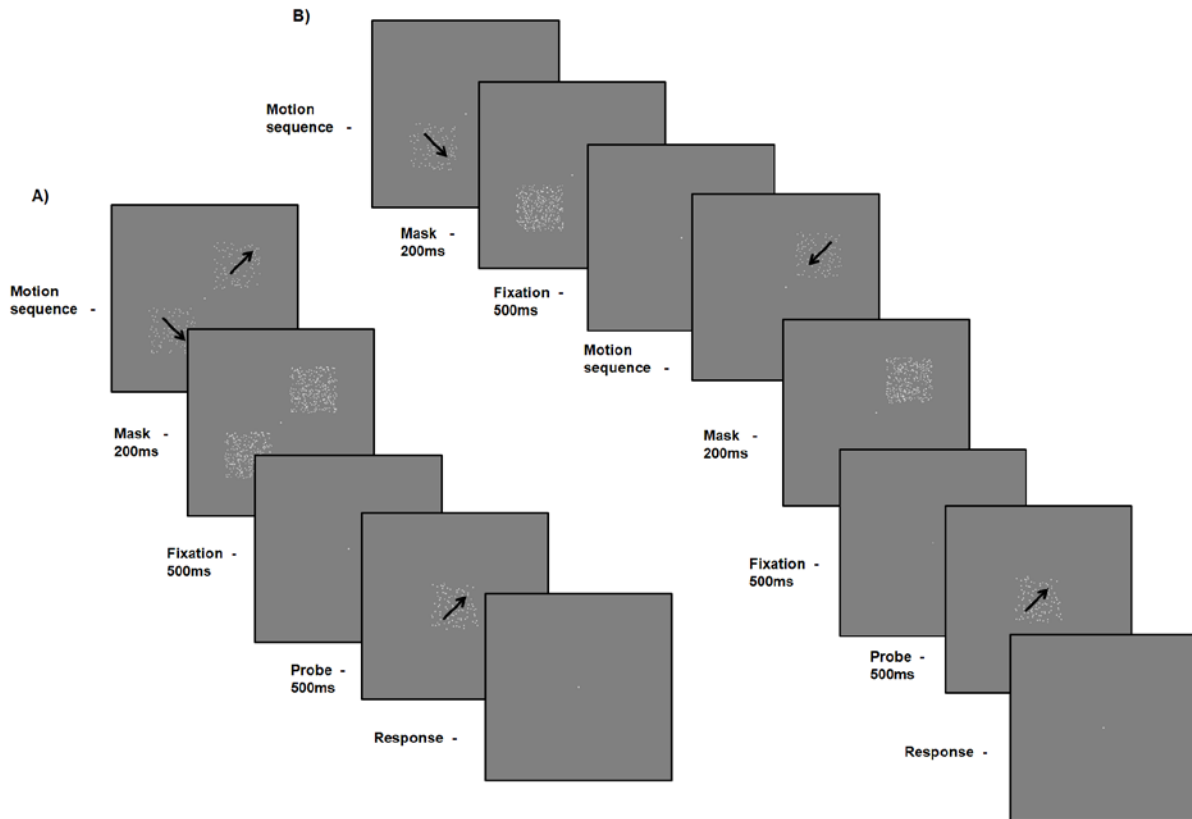


Figure 4: Examples of the stimuli used in the spatial uncertainty condition of Experiment 2. A) An example of the presentation sequence in the simultaneous condition (match trial). B) An example of the presentation sequence in the sequential condition (mismatch trial). The black arrows in the motion sequence and probe frames have been added to illustrate the motion direction of the blobs.

Results and discussion

The average threshold duration was 64ms (range 32 – 192ms, SD = 56ms). In the main experiment, a similar pattern of results was found for all observers; mean performance across all observers is shown in Figure 5. While performance for items presented sequentially was significantly better in the reduced range condition, $t(9) = 4.16, p < .01$, no difference was found between sequential or simultaneous presentation in the spatial uncertainty condition, $t(9) = 0.31, p > .05$.

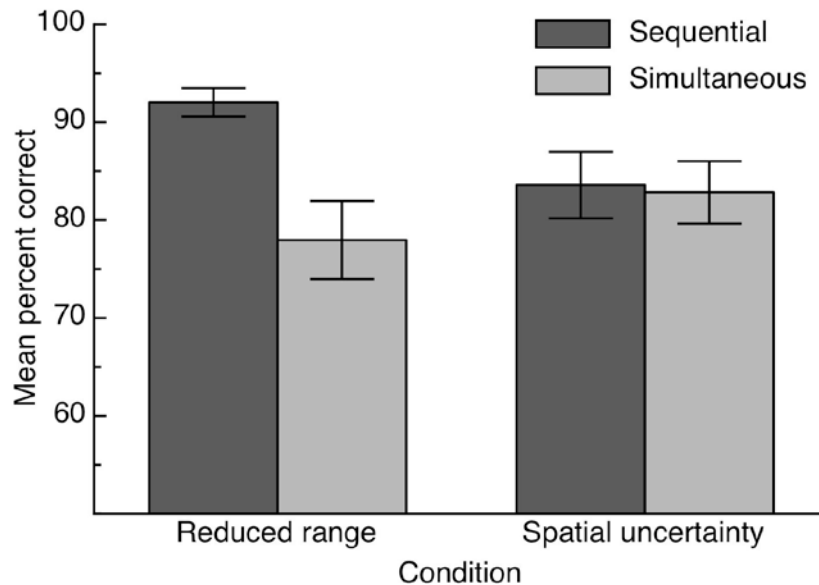


Figure 5: Mean performance across observers in Experiment 2 for each presentation type (simultaneous & sequential) as a function of the condition (reduced range & spatial uncertainty). Error bars indicate ± 1 SEM.

These results could be interpreted as indicating that reducing the range of directions presented resulted in an inability to consolidate items in parallel, while increasing the spatial uncertainty of item presentation did not. However, by applying the same logic used in Experiment 1 to predict performance based on the number of items consolidated, it is clear that even in the condition where performance was the lowest (reduced range/simultaneous) the mean was still significantly higher than the most conservative estimate of performance assuming a single item was consolidated at 100% accuracy, i.e. 62.5%, $t(9) = 3.87$, $p < .01$. Thus, a more likely interpretation of the results is that in both the simultaneous conditions parallel consolidation was possible.

The results show that by reducing the range of feature intervals used to define items, parallel consolidation was significantly more adversely affected than serial consolidation. This suggests that the perceptual space of direction may not be equivalent to that of orientation, despite proportional discrimination thresholds and tuning bandwidths, and that

this may explain the difference in performance between serial and parallel consolidation for orientation information found by Becker, et al. (2013). The finding that a combination of orientation and colour information cannot be consolidated in parallel appears to be inconsistent with this interpretation (Miller, et al., 2014); however, the increased complexity of consolidating different types of information may introduce additional restrictions unrelated to perceptual space size. For example, in visual search, while search for a single feature is a parallel process, search for a conjunction of features is restricted to serial processing (Treisman, 1982). In contrast, increasing spatial uncertainty had an equivalent effect on serial and parallel consolidation. This effect is illustrated by the significantly lower performance in the spatial uncertainty condition than in the two item condition of Experiment 1, both of which can be collapsed across presentation type conditions due to their similarity, $t(19) = 3.45, p < .01$.

Experiment 2 demonstrated the importance of adequate feature interval separation for parallel consolidation and equivalent effect of spatial attention on both serial and parallel consolidation. Experiment 3 investigates whether parallel consolidation of orientation information can be achieved when spatial attention is facilitated.

Experiment 3: parallel consolidation of orientation

Two factors influence the degree of decision uncertainty when comparing representations held in VSTM to a probed item: the separation between feature intervals used to define items and the resolution of the representations held in VSTM. If separation is relatively small and the resolution of representations is low, the probability of mistaking one item held in VSTM as a neighbouring item is increased. Physiological and psychophysical studies show that spatial attention locally enhances information processing by increasing the signal gain of a stimulus (Luck, Chelazzi, Hillyard, & Desimone, 1997; McAdams &

Maunsell, 1999), resulting in higher resolution encoding. Thus, if poorer recall performance when orientation information is presented simultaneously, rather than sequentially, is due to a combination of inadequate feature interval separation and low resolution encoding, facilitation of spatial attention may overcome this by narrowing the signals' bandwidths and increasing the resolution of the encoded items. However, if it is due to the size of the region from which information must be pooled in order to encode a meaningful signal, i.e. information bandwidth, increasing the resolution of this information by facilitating spatial attention should not overcome this.

Method

Observers

Ten observers participated in the study: one of the authors (RR) and nine others who were naïve with respect to the aims of the study. All had normal or corrected to normal acuity and gave informed written consent to participate in the study.

Stimuli and procedure

The stimuli and procedure were similar to that used in the previous experiment, except now instead of moving dots, the items presented to observers were sinusoidal gratings (contrast, 0.7; spatial frequency, 1 cycles/deg) within a circular aperture (4° radius). The edge of the aperture was smooth, leaving no sharp contrast between target and background. The gratings had four possible orientations: 0° , 45° , 90° , and 135° , where 0° was horizontal. The mask was a circular aperture (4° radius) containing pixel noise of random luminance levels with a uniform distribution ($0 - 63 \text{ cd/m}^2$). An example of an orientation stimulus and mask are shown in Figure 6.

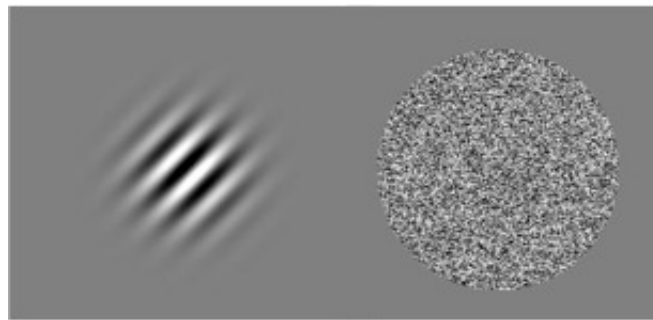


Figure 6: An example of an orientation stimulus (left) and mask (right) used in Experiment 3.

To investigate whether facilitation of spatial attention would improve performance during parallel consolidation of orientation information, two conditions were employed: a condition where items were presented in one of four possible locations and another where items were always presented in the same two locations. The presentation locations used in the spatial uncertainty condition here were the same as those in Experiment 2, whereas only the upper left and right locations were used in the spatial certainty condition. Across all conditions, only two items were presented. Thus, the experiment was a 2×2 design (simultaneous/sequential presentation \times spatial un/certainty). The stimuli described above and the procedure used in Experiments 1 and 2 was employed to determine observers' minimum threshold duration.

Results and discussion

The average threshold duration was 32ms (range, 16 – 112ms; SD, 18ms). In the main experiment a similar pattern of results was found for all observers; mean performance across all observers is shown in Figure 7. A repeated measures ANOVA revealed main effects of both spatial (un/certainty) and presentation (sequential/simultaneous) conditions, $F(1, 9) = 5.78, p < .05$ and $F(1, 9) = 5.56, p < .05$ respectively, and a significant interaction effect, $F(1, 9) = 13.84, p < .01$. While performance was better in the spatial certainty condition for items presented simultaneously, $t(9) = 3.14, p < .05$, no difference was found between the

conditions when items were presented sequentially, $t(9) = 0.16, p > .05$. However, this is likely due to a ceiling effect in the sequential conditions. Performance for items presented sequentially was significantly better in the spatial uncertainty conditions, $t(9) = 2.75, p < .05$, while no difference was found between sequential or simultaneous presentation in the spatial certainty condition, $t(9) = 1.54, p > .05$.

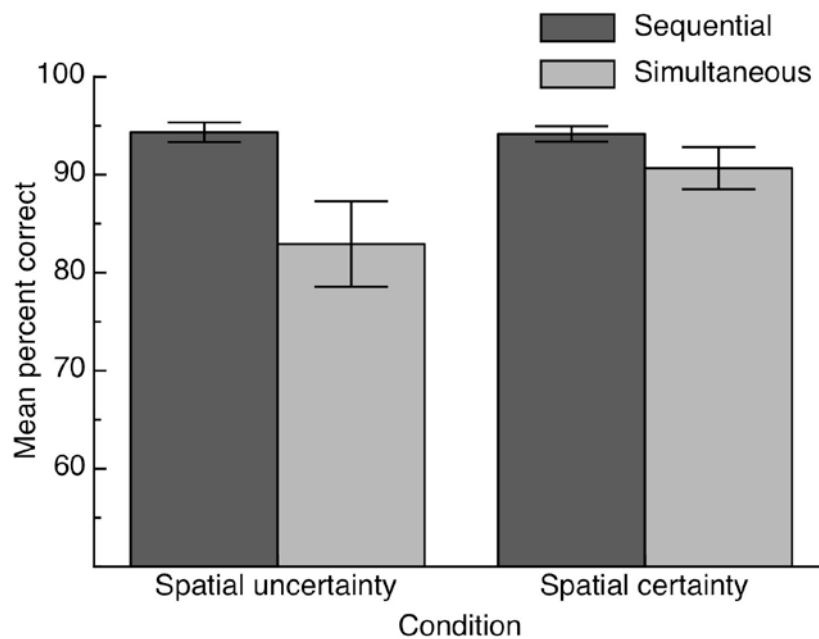


Figure 7: Mean performance across observers in Experiment 3 for each presentation type (simultaneous & sequential) as a function of the condition (spatial un/certainty). Error bars indicate ± 1 SEM.

One interpretation of these results is that parallel consolidation was possible in the spatial certainty condition but not in the spatial uncertainty condition, and thus facilitation of spatial attention overcame the inability to consolidate orientation information in parallel. However, for the same justification provided in Experiment 2, it is more likely that even in the spatial uncertainty condition parallel consolidation was achieved, i.e. performance is significantly higher than the predicted accuracy for consolidation of a single item, $t(9) = 4.68, p < .01$. Thus, a more fitting interpretation of the results is that orientation information that is consolidated in parallel is encoded/stored at a lower resolution than when consolidated

serially, but that facilitation of spatial attention can mitigate the effect of this by enhancing the resolution of items at the encoding stage. Note that while Mance, et al. (2012) found no evidence for an advantage of simultaneously presenting items in the same or different hemifields using colour, it is possible that spatial attention was, at least partially, facilitated here by presenting items in different hemifields (Alvarez & Cavanagh, 2004; Delvenne & Holt, 2012), as opposed to by reducing spatial ambiguity.

General discussion

Our main findings indicate that both motion direction and orientation information can be consolidated from sensory to VSTM in parallel. Experiment 1 demonstrated that multiple directions can be consolidated in parallel and indicated that this process is limited to two items. Experiment 2 showed that adequate separation between feature intervals used to define items, and thus the size of the perceptual space, is more important for parallel than serial consolidation. Finally, Experiment 3 demonstrated that orientation information can be consolidated in parallel and that facilitation of spatial attention can be used to improve performance of parallel consolidation.

It appears that the capacity for parallel consolidation does not vary as a function of type of information. That is, while previous research has shown that colour can be consolidated in parallel, and suggested that orientation cannot, here we provide powerful evidence indicating that both motion direction and orientation can be also consolidated in parallel.

Rather than a model that excludes certain features from parallel consolidation due to their informational bandwidth (Miller, et al., 2014), our results indicate the heightened importance of feature interval separation during parallel consolidation, compared to serial consolidation. The finding that facilitating spatial attention mitigated the effects of inadequate

feature interval separation suggests that items consolidated in parallel are encoded at a lower resolution than those consolidated serially. That is, by spreading cognitive resources to consolidate two items in parallel, the items become encoded at a lower resolution than if all resources were used to process a single item; consistent with our previous study that found the capacity of motion processing varies as a function of the detail of information extracted (Rideaux & Edwards, 2014). Items encoded at a lower resolution have an increased susceptibility to being mistaken for neighbouring items along a feature dimension, especially when the separation between intervals used to define items along that dimension is small. This results in greater uncertainty during the comparison stage of the task and subsequently reduces performance. However, by facilitating spatial attention, which locally enhances processing, the resolution of encoded items is increased, mitigating this effect.

If reduced resolution encoding is a limiting factor on the capacity/effectiveness of parallel consolidation, this may explain why colour appears to be consolidated more effectively than orientation. That is, recent evidence suggests that colour may be consolidated in a qualitatively different way than orientation, such that its representations are not subject to resolution degradation (Ye, Zhang, Liu, Li & Liu, 2014). Future research could explicitly address this question by measuring parallel consolidation performance with a reduced range of colours, e.g. red/yellow/orange.

This interpretation conflicts with Liu and Becker (2013), who directly examined this possibility and found evidence for a strictly serial, high-resolution, consolidation mechanism for orientation. However, in addition to spatial ambiguity of item presentation, in their study a high-resolution representation was required to perform the task, i.e. indicating the orientation of an item drawn from a set of items separated by 14° increments, here the task could be performed with a low-resolution representation. Thus, these distinct task demands

may have led observers to employ different strategies; high-resolution serial processing to perform the task in the Liu and Becker (2013) study and low-resolution parallel consolidation here. Clearly, further research is required to determine the impact of task demands on the employment of parallel consolidation.

Importantly, we believe that a significant difference between recall performance when orientation information is presented sequentially and simultaneously is not necessarily accounted for by an inability to consolidate this information in parallel. Rather, the evidence indicates that parallel consolidation of orientation information is possible, but that the resolution of items suffers.

Acknowledgements

This work was supported by an Australian Postgraduate Award to R.R., an NHMRC Early Career Fellowship (1054726) to D.A., and an Australian research Council Grant (DP110104553) to M.E.

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