COGNITIVE NEUROPSYCHOLOGY, 2007, 24 (2), 187–210

Psychology Press
Taylor & Francis Group

Maintaining the ties that bind: The role of an intermediate visual memory store in the persistence of awareness

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Segregation and feature binding are essential to the perception and awareness of objects in a visual scene. When a fragmented line-drawing of an object moves relative to a background of randomly oriented lines, the previously hidden object is segregated from the background and consequently enters awareness. Interestingly, in such shape-from-motion displays, the percept of the object persists briefly when the motion stops, suggesting that the segregated and bound representation of the object is maintained in awareness. Here, we tested whether this persistence effect is mediated by capacity-limited working-memory processes, or by the amount of object-related information available. The experiments demonstrate that persistence is affected mainly by the proportion of object information available and is independent of working-memory limits. We suggest that this persistence effect can be seen as evidence for an intermediate, form-based memory store mediating between sensory and working memory.

How does the visual system create and maintain the coherent objects and events that we experience? Different physical attributes (e.g., colour, orientation, motion, etc.) are known to be processed by separate cortical regions of the mammalian brain (see Grill-Spector & Malach, 2004). The visual system consequently has the task of integrating these distinct attributes within and across visual feature dimensions; furthermore, the visual system must also use the different attributes to segregate the figure from ground, despite the potential overlap in dimensions. These two processes are known as binding and segregation, respectively. It is currently unclear how the visual system manages to accomplish these computationally difficult tasks. Furthermore, once the coherent forms of a scene are segregated and bound, the experience of those objects is one of perceptual continuity, such that we maintain the percept seemingly effortlessly and often have no awareness of transient changes of the sensory input. But how does the visual system maintain the objects

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The authors would like to acknowledge Kendra Hollidge and Justin Ruppel for assistance with data collection. Sincere thanks also to Maha Adamo and Arin Klug for helpful comments. This research was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant awarded to the first author.

http://www.psypress.com/cogneuropsychology
DOI:10.1080/02643290601046598

in awareness once they have been segregated, and binding has occurred? Presumably, if the visual system could store these objects at least briefly, then it would not be necessary to perform these processes continually, thereby permitting resource-limited processes to be directed to more novel elements of the display.

One powerful demonstration of the visual system's ability to maintain the previously segmented and bound objects in awareness is through the persistence of objects observed in Regan's (Regan, 1986, 2000) shape-from-motion (SFM) paradigm. When a fragmented line-drawing of an object (Figure 1A) is superimposed on a background of pseudorandomly distributed lines (Figure 1B), the object is essentially camouflaged (Figure 1C); however, if the set of lines depicting the object moves in counter phase relative to the background, the object is easily detected and recognized (Figure 1D, see http://www.psych.utoronto.ca/~ferber/flash-demo2.html). This initial stage demonstrates the visual system's ability to segregate a figure from the ground (i.e., through the cue of relative motion) and bind the varying components (i.e., the distinct line-segments) of the object into a coherent percept.[1] Interestingly, when the relative motion is stopped, and the single cue inducing the segregation and binding processes is removed, the percept of the object persists briefly before deteriorating and becoming indistinguishable from the background again. This persistence is contrasted to trials in which the line-segments composing the object are removed at the offset of motion, during which no persistence is observed. The persistence of motion-defined forms in the absence of the segregating and binding cue suggests that there is perhaps some mechanism involved in maintaining a coherent representation of the previously segregated and bound elements of objects in the visual scene. It remains unclear, however, why the objects fail to persist indefinitely, given that the physical characteristics of the object remain present. In ambiguous displays, for example, permanent top-down changes in the segregation, binding, and awareness of an object are often observed after the "trick" has been revealed (e.g., Dolan et al., 1997; Rock & Mitchener, 1992). The fact that motion-defined forms fade from awareness even though all elements are still physically present may indicate that the binding of fragments into shapes has

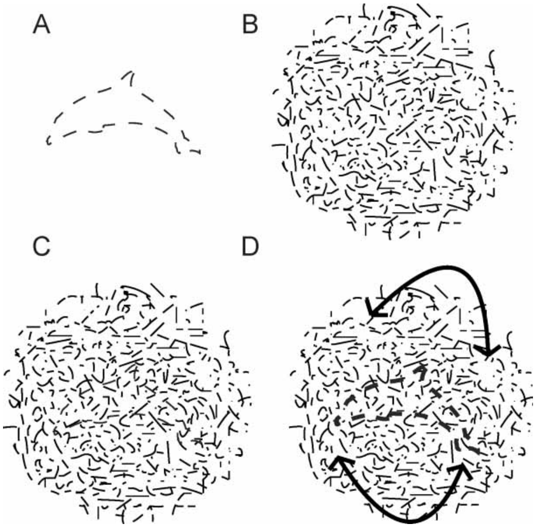

Figure 1. *Shape-from-motion experiment. (A) Example of fragmented line-drawing. (B) Pseudorandomly oriented background lines. In* vanish *conditions the fragmented line-drawings representing the object as depicted in (A) are removed from the background after the motion stops, leaving only the background lines. (C) The fragmented line-drawing depicted in (A) is superimposed on the background (B). The form of the dolphin virtually disappears in the background. In* object-stop *conditions, the motion, depicted by arrows in (D), stops, and the object again fades into the background. (D) Inducing relative motion in the object and the background makes the object recognizable instantly (note the line-segments have been enlarged to imply motion).*

[1] The term "binding" can refer to integration of information both within a dimension (e.g., binding line-segments into contours) and between arbitrary dimensions (e.g., form and colour). While binding is often discussed in general terms, Humphreys (2001) argues that binding is a multistage process based on neuropsychological evidence from patients with lesions to areas of either the ventral or dorsal visual streams: binding of form elements into contours, binding of contour information into holistic shapes, and binding of shape to surface detail. According to this distinction, binding in SFM can refer to either of the first two of these stages.

been incomplete and that the percept was only temporally stored.

The neural correlates of processing motion-defined forms have been demonstrated elsewhere in numerous neurophysiological studies (Grunewald, Bradley, & Andersen, 2002; Lamme, van Dijk, & Spekreijse, 1993; Murray, Olshausen, & Woods, 2003; Sáry, Vogels, & Orban, 1993). Typically, the motion-sensitive extrastriate motion complex (MT +), the object-sensitive inferior temporal cortex in monkeys (Sáry et al., 1993), or the lateral occipital complex (LOC) in humans (Murray et al., 2003), and early visual areas such as V1 (Grunewald et al., 2002; Lamme et al., 1993) have been found to be involved in the processing of shapes and objects defined solely by motion cues. Furthermore, patients with lesions to the parieto-temporo-occipital white matter or the superior parietal cortex showed impaired performance in motion-defined form recognition, though motion processing is still intact (Regan, Giaschi, Sharpe, & Hong, 1992; Schenk & Zihl, 1997).

In contrast, the perceptual persistence of motion-defined forms after the motion stops has only recently been studied. Ferber and colleagues (Ferber, Humphrey, & Vilis, 2003; see also Ferber, Humphrey, & Vilis, 2005) demonstrated through functional magnetic resonance imaging (fMRI) that the behavioural persistence observed in shape-from-motion displays is accompanied by persistence of brain activation in the object-sensitive lateral-occipital area (LO), part of the LOC in the inferior temporal lobe, and not in the motion-sensitive MT + complex. Accordingly, these authors have argued that area LO is the cortical region mediating the brief retention of a segregated figure.

Additional evidence suggests that area LO does indeed mediate the maintenance of objects in awareness. For example, Kleinschmidt and colleagues (Kleinschmidt, Büchel, Hutton, Friston, & Frackowiak, 2002) created segregation by gradually increasing the relative contrast of a letter from the background (pop out). Contrast was then gradually decreased until the letter was no longer visible (drop out). On initial trials, the threshold at which pop out occurs is higher than the threshold at which drop out is observed, a phenomenon known as perceptual hysteresis. Interestingly, a sustained fMRI BOLD response was observed in area LOC that was coupled to the sustained perception of the letter prior to drop out. Furthermore, Large and colleagues (Large, Aldcroft, & Vilis, 2005) have also demonstrated persisting fMRI activation that accompanies behavioural persistence of objects in SFM, and they found that this activity increases in duration and magnitude across the cortical hierarchy of the ventral visual stream. Taken together with the well-known finding that neural activation in area LOC is correlated with recognition performance (Bar et al., 2001; Grill-Spector, Kushnir, Hendler, & Malach., 2000; see Grill-Spector, Kourtzi, & Kanwisher, 2001, for a review), the findings regarding persistence-related fMRI activation in the same brain region may indicate that the LOC subserves the maintenance of objects within awareness, in addition to initial recognition processes. Furthermore, significant persistence of brain activation in the LOC is observed not only when the relative-motion cue is removed in SFM, but also when colour replaces relative motion as the sole distinguishing cue between object and background, and the colour cue is subsequently removed during the stationary epoch (Large et al., 2005). In addition, it has been demonstrated that the LOC subserves persistence of scrambled shapes without closed-loop contours (Ferber et al., 2005), and it also shows persisting activation when the initial fragments are removed, and new line-segments are presented in place of the gaps (Ferber et al., 2005); thus, persistence seems to occur—perceptually and on a neural level—when the single segregating and binding cue is removed, regardless of the presence of closed-loop contours, recognizable shapes, or identical physical features.

In this paper we examine whether persistence (i.e., the maintenance of previously segregated and bound forms in awareness) is mediated by some object-processing store localized to the LOC, or by other processes, such as working memory or attention (see Rensink, 2000a, 2000b; Wheeler & Treisman, 2002; Wolfe, 1999). Working memory can be understood as the capacity-limited set of processes or mechanisms involved in the control, regulation, and active maintenance of information (Miyake & Shah, 1999). The storage component of working memory is thought to have separate systems for spatial, object, and verbal information (e.g., Smith & Jonides, 1997) and is limited to a capacity of roughly four items (Cowan, 2000; Luck & Vogel, 1997; Todd & Marois, 2004). Thus, the failure of the objects to persist indefinitely may be a reflection of the temporal and capacity limitations of visual working memory in the absence of any segregation or binding cue. That is, the binding and segregation may act as a form of integration or "chunking", grouping the individual line-segments of the object into a coherent whole. Then, once the relative motion ceases, the numerous line-segments have to be maintained in working memory. This would involve a process of continual maintenance of the identities, locations, and configurations of those line-segments that compose the object rather than the background noise, which may create an insurmountable load for visual working memory. Accordingly, the percept of the object will fade from awareness.

The concept of a capacity-limited visual memory store has been explored by many researchers in great detail; furthermore, the neural correlates of this capacity limit have been recently explored (Todd, & Marois, 2004; Vogel & Machizawa, 2004). Interestingly, McConnell and Quinn (2004) have found that the presentation of a visual noise field with a dynamic element can interfere with the memorization of lists of words when using a visual mnemonic technique. Moreover, this interference with the visual store increases when number of dots, the density of the dots, and size of a noise field are increased, suggesting that irrelevant but complex visual stimuli can interfere with visual working-memory processes. This suggests that the failure of the visual system to maintain the percept in SFM may be due to working-memory limitations caused by interference from the noise field (i.e., the background of pseudorandomly oriented lines).

But why is the binding of elements into coherent shapes incomplete, such that the line-segments have to be stored individually and are subject to capacity limits of working memory? It has been argued that attention is the gateway to memory, which means that if focused attention is removed, the object loses its coherence and disintegrates into its constituent elements (Rensink 2000a, 2000b; Wheeler & Treisman, 2002; Wolfe, 1999). One way to test the effects of attention and working-memory load on persistence is through the use of a dual-task paradigm with a working-memory task as the secondary task. If persistence is mediated by attentional or working-memory processes, the presence of a secondary visual working-memory task should impair the maintenance of the object within awareness. A further means for manipulating working-memory load is to vary the number of line-segments that compose an object. More specifically, given the acknowledged capacity limits of visual working memory (Cowan, 2000; Luck & Vogel, 1997; Todd & Marois, 2004), one could predict that decreasing the number of line-segments will decrease the demands on working-memory load and consequently increase the duration of the persistence of the object.

Alternatively, if persistence is indeed mediated by object-sensitive regions independent of general working-memory processes, the available information depicting the object itself may have an effect on persistence and, consequently, awareness. Accordingly, the more object-specific information is available (i.e., form or shape) the more easily the object's features will remain bound together. If this latter case were true, one would predict that the more object-specific information available to the viewer, the longer the persistence of the percept.

To summarize, in the current study, we attempted to examine the underlying mechanisms mediating the persistence of objects in SFM displays by determining the attributes that promote or diminish the persistence of motion-defined groupings. Namely, we tested two contrary hypotheses that could explain persistence, the working-memory hypothesis, and the form-based short-term store hypothesis. In Experiment 1, we tested whether the disappearance of objects in SFM is owing to attentional limitations and/or the high demands on visual working memory. If so, taxing attention and visual working memory through a concurrent *n*-back task should decrease the length of perceptual persistence. Moreover, if the object's individual features are maintained in awareness by working memory, objects composed of more line-segments should demonstrate shorter persistence due to the increasing demand that each individual segment places on visual working-memory load. In Experiment 2, we examined the role of object-related information on persistence, in addition to further testing the role of working memory. Accordingly, we varied the proportion of object coverage (i.e., the object-based information) independently of the number of object features (i.e., lines). In Experiment 3, we further tested the role of object-based information on persistence; more specifically, we quantified the relation of initial object segregation in the moving displays with subsequent persistence. In addition, we also controlled for the visibility of objects in both the stationary and the moving displays. Finally, in Experiment 4, we examined the relative contribution of the familiarity of the object, as well as the presence of closed-loop contours, to the persistence of forms in shape-from-motion. The findings presented here have implications for theories of perceptual awareness and memory, as well as the neural substrates underlying visual object processing.

EXPERIMENT 1

In Experiment 1, we tested the influences of working memory and attention on the perceptual persistence of motion-defined groupings. That is, we attempted to decrease the duration of perceptual persistence by taxing working memory and attentional resources.

Wheeler and Treisman (2002) have suggested that both the binding process itself and maintaining binding in memory require the focus of attention (see also Wolfe, 1999, and Rensink, 2000a, 2000b). The maintenance of bound object representations, therefore, may be subject to interference when attention is disrupted. Though binding individual line-segments into one perceptual unit may reduce the competition for memory resources required by each individual object feature in SFM, binding cannot be maintained when the motion cue is removed due to the limits of attentional resources; thus, the bound elements disintegrate back into individual segments, causing each feature to compete for memory resources again.

The most parsimonious way of drawing attention away from the perceptual persistence task, while taxing working memory at the same time, is to present a simultaneous *n*-back task in which participants are required to decide whether a presented stimulus matches the stimulus presented *n* stimuli ago. By varying the value of *n*, the experimenter can manipulate the memory requirements of the task (i.e., no memory demands exist when $n = 0$) in terms of the load of information maintained in working-memory systems. In addition, the concurrent *n*-back task directs the focus of attention away from the line-segments, thereby weakening the binding process, causing the bound elements to fall apart more readily.

Increased cortical activity has been demonstrated in response to the additional load of increasing *n* (e.g., Smith & Jonides, 1997) and increasing memory load (Todd & Marois, 2004; Vogel & Machizawa, 2004). Increases in load-dependent activity have been observed not only in frontal and parietal regions traditionally associated with working-memory executive processes, but also in stimulus-specific regions of the ventral visual stream (Druzgal & D'Esposito, 2001; Xu & Chun, 2006). Furthermore, the role of sensory cortical structures in working memory has also been well documented (see Pasternak & Greenlee, 2005, for a review). Taken together, if persistence is subserved either by the maintenance of object features in working memory or the maintenance of binding through attention, then providing a concurrent task that utilizes the same cognitive and neural systems should limit the resources available to those systems, thereby shortening the duration of persistence as the memory and/or attentional demands increase.

Method

Participants

A total of 20 healthy participants (17 female; age 19–27 years; mean age = 20.83 years; 18 right-handed) from the University of Toronto participated in the study to receive credit for an undergraduate course. In all experiments, volunteers provided written consent, and all procedures were approved by the University of Toronto Ethics Review Board.

Procedure

Volunteers performed the experiment seated with their heads rested comfortably in a chin-rest located 57 cm from a 19-inch computer screen. Participants were told to maintain fixation on a small dot (subtending 0.2 degrees of visual angle) located centrally on the screen for the duration of the experiment, and the experimenter monitored eye movements. In each trial, the object, a fragmented line-drawing of an animal, and a background of pseudorandomly oriented line-segments rotated clockwise and anticlockwise ± 15 degrees relative to each other, with a period of 2.0 s (Figure 1D). After 12 s, the object and the background stopped moving, and volunteers indicated with a button press with their right index finger when, in their subjective experience, the percept of a coherent object had disappeared.

Concurrent with the perceptual persistence task, participants were asked to perform a 0-back, 1-back, or 2-back task. During the 0-back condition, participants were asked to make a response with their left index finger when the target (a black circle) was presented. In the 1-back condition, participants responded when the presented circle was the same colour as the circle that preceded it. The "target" circle in the 1-back condition is presented 1 s after the presentation of the reference circle without any intervening circles. During the 2-back condition, participants were told to respond when the presented circle was the same colour as the circle that was presented two circles prior. Trials were 20 s long, with 12 s of motion and 8 s of the stationary display, and participants were required to perform the *n*-back task throughout the entire 20-s trial (i.e., while the object was rotating against the background and during the stationary display).

If the participants failed to indicate that they were no longer able to perceive the object during the 8 s after the motion stopped, the trial was removed from persistence analysis. The mean number of trials per individual on which no response was made was 4.83 for the 0-back task, 5.44 for the 1-back task, and 6.94 for the 2-back task. One participant had a total of 116 of these no-response trials across all three runs, and consequently the data for this individual were removed from analysis. For the *n*-back task, small, differently coloured circles were presented centrally every 1 s, for a duration of 80 ms. The circle stimuli were arranged such that three *n*-back targets were present during each 20-s trial, for each of the *n*-back conditions. The presentation of targets was counterbalanced, such that they occur with equal frequency at all the positions within the 20-s trials. Each *n*-back condition was presented in two blocks, with a short break between each block and between each of the *n*-back conditions. Participants were randomly assigned one of two presentation orders, with the 2-back condition always being presented between the two presumably less difficult conditions (1-back, 2-back, 0-back, or 0-back, 2-back, 1-back).

A previous pilot study indicated that individuals could not reliably perceive any of the objects in stationary displays in the absence of motion.

Materials

To vary the working-memory load in addition to the manipulation of the *n*-back task, volunteers were presented with four shape-from-motion stimuli, which varied in the number of features, while keeping the amount of coverage constant at 50%. That is, for all objects, the line-segments covered 50% of a given object's outline across conditions, with lines and spaces being of identical lengths within conditions (Figure 2A).

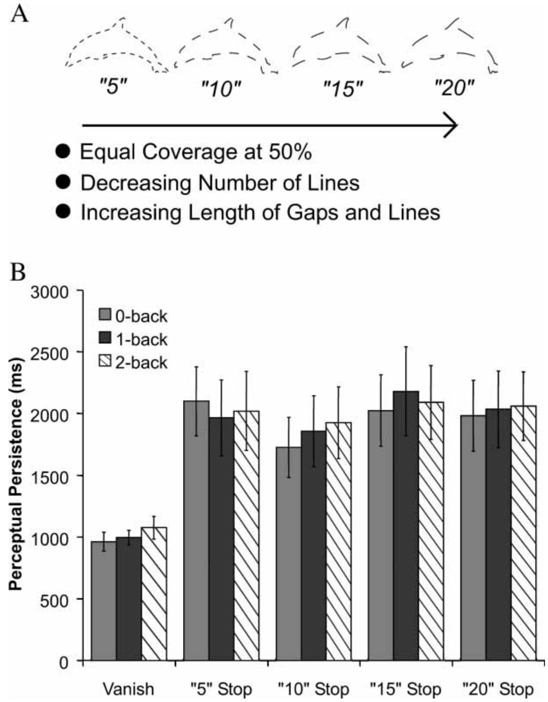

Figure 2. *(A) Examples of stimuli created for each of the object-stop conditions in Experiment 1. The condition names refer to the length of the object's features and spaces. The proportion of outline covered by the lines is kept constant at 50%, with decreasing number of features from the "5" condition to the "20" condition. The "10" stimuli were used in the vanish condition. (B) Mean perceptual persistence, measured in ms, by* n*-back condition in Experiment 1* (n = *18*). *Error bars denote standard error of the mean. All object-stop conditions were significantly different from the vanish condition. Similar persistence durations were observed across all* n*-back conditions, demonstrating that memory load* (n) *had no systematic effect on the duration of perceptual persistence.*

Participants observed a total of five shape-from-motion conditions: four object-stop conditions and an object-vanish condition. The four object-stop conditions (Figure 2A) featured segmented line-drawings that formed incomplete shapes of objects as stimuli (subtending an average maximum radius of 2.7 degrees in visual angle), which were superimposed on a background of pseudorandomly oriented lines (9 degrees of visual angle in diameter). The segmented line-drawings were rotated clockwise and anticlockwise with the background rotating in counter phase. After a total time of 12 s, both the line-drawing and background lines stopped rotating and remained on the screen (Figure 1C). The four object-stop conditions differed in their relative line and space lengths, while holding the overall coverage constant at 50% (Figure 2A); the conditions are named according to the length in pixels of the line-segments and spaces, creating the following four conditions: (a) "5" stop, (b) "10" stop, (c) "15" stop, and (d) "20" stop. Thus, the length of the line-segments, as well as the spaces between segments, were twice as large in the "10" stop objects as in the "5" stop objects, whereas the lines and spaces of the "20" stop condition were twice those of the "10" stop condition and four times greater than those in the "5" stop condition. The fifth condition was an object-vanish condition, in which the same stimuli as those in the "10" stop condition were presented in the exact method mentioned above; however, the line-segments representing the objects were removed from the display after the 12-s rotation phase (Figure 1B). One individual's data set was removed from analysis, as he demonstrated reaction times for object-stop conditions that were shorter than the object-vanish condition, thereby reducing the number of participants to 18.

There were 15 line-drawings of animals, which were then manipulated for each of the five conditions, creating a total of 75 trials, for each of the three *n*-back conditions. Trials were arranged in a pseudorandom order, and all participants received the same order of trials. Prior to beginning the experimental trials, 5 practice trials were presented to familiarize the participants with the procedure, using different stimuli from those that were presented in the experimental trials. The *n*-back stimuli consisted of seven coloured circles, each measuring 0.7 degrees in visual angle.

Results

To examine the effects of working-memory load on persistence, a repeated measures analysis of variance (ANOVA) was performed, with *n*-back task and object-stop condition as within-subjects measures, and task order as a between-subjects measure. Figure 2B displays the average perceptual persistence for each object and *n*-back condition. A main effect of SFM condition was observed, $F(4, 64) = 13.820$, $p < .001$, $MSE = 11{,}656{,}526.69$, as is expected if differences are observed between the object-vanish condition and any of the object-stop conditions. Interestingly, no main effect of *n*-back task on perceptual persistence was found, $F(2, 32) = 0.171$, $p = .844$, $MSE = 174{,}439.91$; furthermore, no interaction was observed between the factors SFM condition and *n*-back task, $F(8, 128) = 1.056$, $p = .398$, $MSE = 113{,}043.61$. Task order demonstrated no main effect, $F(1, 16) = 0.020$, $p = .889$, $MSE = 282{,}083.53$, and did not interact with either SFM condition, $F(4, 64) = 0.075$, $p = .989$, $MSE = 63{,}563.59$, or *n*-back task, $F(2, 32) = 0.203$, $p = .817$, $MSE = 207{,}422.44$. No three-way interaction was observed, $F(8, 128) = 0.530$, $p = .832$, $MSE = 56{,}696.917$.

As no main effects of *n*-back task or task order were observed, the perceptual persistence data for all participants were collapsed across all *n*-back tasks for post hoc comparisons of the SFM conditions. Bonferroni-adjusted *t* tests revealed that all object-stop conditions were significantly different from the object-vanish condition at the $p = .05$ level. Importantly, we did not observe a systematic effect of the number of features on object persistence; *t* test comparisons between the majority of object conditions were not significant at the $p < .05$ level. We did, however, observe significantly shorter persistence in the "10" object-stop condition than in the "5" and "15" object-stop conditions ($p < .05$, Bonferroni corrected).

The accuracy scores (% hits − % false alarms) for the secondary *n*-back tasks are displayed in Table 1. As expected, accuracy is very high for the 0-back task, with poorest performance in the 2-back task. A two-way repeated-measures ANOVA with *n*-back task as within-subject factor and task order as the between-subjects factor yielded a significant main effect of *n*-back task for accuracy data, $F(2, 32) = 322.365$, $MSE = 12{,}183.23$, $p < .001$. Unlike the perceptual persistence data, a main effect of task order was observed, $F(1, 16) = 9.107$, $MSE = 2{,}346.27$, $p = .008$, such that those in the first group (1-back, 2-back, 0-back) tended to be less accurate on the 1- and 2-back tasks than did those in the second group (0-back, 2-back, 1-back). An interaction between *n*-back task and task order was also observed, $F(2, 32) = 10.415$, $MSE = 393.63$, $p < .001$, due to the fact that there was no difference between groups on the 0-back task. Thus, though a main effect of order was found, along with an interaction, this did not change the overall pattern of accuracy scores, and accordingly the results were collapsed across order. Planned paired comparisons between the *n*-back tasks revealed significant differences between all three tasks.

While persistence reaction times (RTs) demonstrated no main effect of *n*-back task, it is possible that participants stopped performing the task while anticipating and experiencing persistence. Consequently, we compared accuracy on the *n*-back task during the early portion of the trial (0−8 s) to the "late" portion of the trial, immediately preceding and following motion offset (9−16 s). Scores were binned across these time periods and were compared separately. As the main pattern of responses was similar for both task orders, scores were collapsed across these conditions. A two-way repeated measures ANOVA with *n*-back task and time (early or late period) as the within-subjects factors revealed a significant

Table 1. *Accuracy scores on the secondary* n*-back tasks from Experiment 1, averaged across individuals*

	% Hits		*% False alarms*		*Accuracy score*	
n-back condition	*Mean*	*SE*	*Mean*	*SE*	*Mean*	*SE*
0-back	88.86	1.50	0.21	0.06	88.65	1.51
1-back	66.64	3.73	1.67	0.28	64.97	3.82
2-back	39.59	3.23	3.95	0.47	35.64	3.29

main effect of *n*-back task, $F(2, 34) = 204.362$, $p < .001$, $MSE = 28{,}132.87$, but no main effect of time, $F(1, 17) = 0.115$, $p = .738$, $MSE = 2.43$. Importantly, paired comparisons demonstrated that there was no difference between early and late performance for the 1-back and 2-back tasks, $t = -1.366$, $p = .190$, $SEM = 1.78$, and $t = -0.602$, $p = .555$, $SEM = 2.09$, although a significant but modest difference was observed between early and late performance in the 0-back task, $t = 4.618$, $p \leq .05$ (Bonferroni corrected), $SEM = 0.993$. This lone difference in the 0-back condition resulted in a significant interaction between *n*-back condition and time, $F(2, 34) = 4.580$, $p < .05$, $MSE = 127.38$.

Discussion

Confirming previous observations (e.g., Ferber et al., 2003), we found significantly longer perceptual persistence when the line-fragments depicting an object remain in the display after the motion stops (stop conditions) in SFM displays. Interestingly, we also demonstrated that increasing the load on working memory through a concurrent 2-back task has no significant effect on persistence when compared to concurrent 1-back and 0-back conditions. One potential interpretation of these results is that the concurrent 2-back task does not place significant demands on working-memory processes to interfere with persistence any more so than the 0-back or 1-back conditions. This interpretation is difficult to accept in light of the drastic differences in accuracy performance on the three *n*-back tasks.

Though the accuracy scores in the 1- and 2-back tasks are somewhat lower than those in typical working-memory tasks, the low accuracy is probably due to the rapid presentation rate of the *n*-back stimuli. Due to the relatively short-lived effects of perceptual persistence in shape-from-motion, the rapid presentation of the *n*-back stimuli was necessary to ensure that multiple items were not only maintained, but also updated, while participants experienced persistence. The rapid presentation ensured that the memory processes being targeted were in fact engaged and, consequently, could interfere with persistence. Thus, while the 0-back task has no memory requirement in addition to iconic representations, the 1-back and 2-back tasks require updating and maintaining visual information in memory. Although it could be argued that the low performance could indicate that participants stopped performing the task while performing the persistence task, no differences in performance were observed between the first 8 seconds and the 8 seconds surrounding the offset of motion in the 1- and 2-back tasks, demonstrating that performance did not decrease over the course of each trial.

Similarly, it could be argued that even if the concurrent *n*-back task targets working-memory processes, the specific processes and neural substrates targeted by the additional task are not the same as the working-memory processes that might mediate persistence. This, too, seems unlikely. Numerous studies have demonstrated increased cortical activity in response to increasing sets of stored information (e.g., Smith & Jonides, 1997). The rapid presentation of visual objects in our concurrent *n*-back task ensures the attentive encoding and maintenance of additional visual information not present in the independent SFM task. As was demonstrated with faces and the fusiform face area (Druzgal & D'Esposito, 2001), the presentation of coloured objects should result in increasing neural processing in areas V4 and LO with increasing *n*, precisely the areas that demonstrate the strongest persisting activation in response to persisting forms (Ferber et al., 2003, 2005; Large et al., 2005).

Instead, the absence of interference by the concurrent 1- and 2-back tasks provides evidence that persistence of objects in SFM relies on different processes from those required for the *n*-back tasks. Furthermore, despite the capacity limits of working-memory systems, we found no systematic effect of the number of features (line-segments) of an object on persistence. That is, persistence did not decrease as the number of lines decreased between the "5" and "20" object-stop conditions. In other words, persistence cannot be attributed to working-memory systems. Consequently, the persistence of forms in SFM must be accounted for by other processes. Furthermore, given the increased attentional requirements of increasing *n*, persistence (as well as the loss of awareness) cannot be attributed to attentional mechanisms. This perhaps contrasts with the results of Wheeler and Treisman (2002), who suggested that the maintenance of bound features requires attention. It is possible, however, that attention is not required for binding when the combination of features changes the relationship between those features—that is, when the whole is greater than the sum of its parts. The perception of objects in SFM is dependent not only on the binding between the features but also on perceiving the relationship between those features. Thus, persistence of forms may be critically dependent on information about the form of the object itself, rather than on mechanisms servicing the maintenance of individual features.

EXPERIMENT 2

Experiment 2 was designed to test whether information about the form of the object itself influenced persistence. That is, are objects easier to maintain in awareness if more information about the shape or form of the object is available to the visual system? The line-segments depicting the objects in Experiment 1 always covered 50% of the objects' outlines; however, there is some evidence to suggest that object-selective regions are sensitive to object completion. Doniger and colleagues (Doniger et al., 2000) demonstrated lateral-occipital source activity that increased with object completion, even though the level of completion was below the level required for recognition of the object itself. Thus, it is possible that if area LO maintains the awareness of objects after the motion stops, then increasing the level of completeness of the object may influence object-related neural activity mediating persistence.

To investigate the role of object-based information on the maintenance of object awareness, we varied the amount of coverage of objects in the SFM display. Further, while Experiment 1 demonstrated that increasing the number of object features does not affect persistence, one could argue that the additional requirements of the *n*-back task prevented us from observing differences related to the number of object features. Therefore, we further tested the role of the number of object features by varying the number of lines independently of object coverage. Consequently, Experiment 2 allowed us to compare the effects of manipulating object features to object completion directly.

Method

Participants

A total of 18 healthy undergraduates (14 female, 17 right-handed) from the University of Toronto participated in the study to receive credit for an undergraduate course. Volunteers were between 18 and 25 years old (mean age: 20.6 years) and provided written consent.

Procedure

The procedure was similar to that used in Experiment 1. However, no concurrent *n*-back task was presented. Instead, volunteers were told to maintain fixation on a small dot located centrally on the screen for the duration of the experiment, and the experimenter monitored eye movements. The moving object and background were presented for 12 s, after which the object and the background stopped moving, and volunteers indicated with a button press when, in their subjective experience, the percept of a coherent object had disappeared. If the participant failed to indicate that the percept of the object had disappeared for 12 s after the motion stopped, a sound was presented to indicate that the participant was to advance to the next trial, and these trials were discarded from analysis. These timeout trials occurred in only 7 of the 18 individuals and on a maximum of 13 trials in any one individual; the mean number of timeouts across all participants was 1.7.

Materials

Six shape-from-motion conditions were presented to participants: five object-stop conditions and one object-vanish condition. The five object-stop conditions were identical to those of Experiment 1, in that they contained segmented line-drawings that formed incomplete objects, which were superimposed and rotated over a background of randomly oriented lines. The stimuli in Experiment 2 also had identical rotation phases to those of Experiment 1. The stimuli used for the object-stop conditions in Experiment 2, however, differed from those in Experiment 1, in that the proportion of object coverage was varied, in addition to varying the number of lines (Figure 3A). The five object-stop conditions were: (a) 50%; the segmented line-drawings were composed of 50% lines and 50% spaces, the lengths of lines and spaces being equal and approximately evenly spaced; this condition was identical to the "10" stop condition of Experiment 1; (b) 25%-least; lines covered 25% of the outlines of our objects; these stimuli were created by removing every other line-segment from the 50% objects and, thus, contained only half of the lines of that condition; (c) 25%; line-segments covered 25% of the object's outline by shortening each line-segment of the 50% objects by one half, rendering each line-segment one half of its original length and each space 1.5 times that of the 50% condition; of note here is that the 25% and the 25%-least conditions have the same proportion of coverage, but differ on the number of lines; however, the number of lines is held constant between the 25% and the 50% conditions; (d) 75%; lines covered 75% of the outlines of objects by extending each line-segment of the 50% objects by one half, making each line-segment 1.5 times as long as its original length, and cutting each space between the line-segments in half; (e) 75%-most; the lines covered 75% of the objects by adding additional line-segments in the middle of each space of the 50% objects that covered one half of each space; again, the two 75% conditions have the same proportion of coverage; however, the number of lines is held constant between the 75% and 50% conditions. The sixth condition was one object-vanish condition, which was identical to that of Experiment 1, with the 50% objects being removed at the offset of motion.

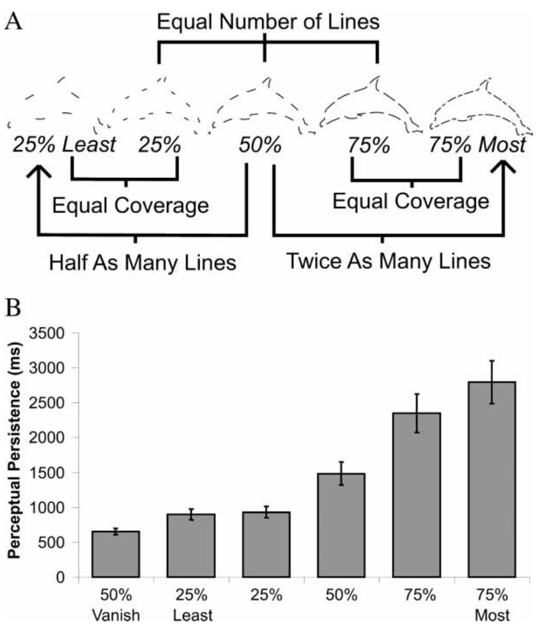

Figure 3. *(A) Examples of stimuli created for each of the object-stop conditions in Experiment 2. The conditions indicate the proportion of the object's outline that is covered. The number of features is kept constant between the 25%, 50%, and 75% conditions, while there are increasingly more line-segments between the 25% least, 50%, and 75% most objects, respectively. (B) Mean perceptual persistence measured in ms averaged across all participants* (n = 18) *for Experiment 2. Error bars denote standard error of the mean. All object-stop conditions showed significant perceptual persistence when compared to the vanish condition.*

As in Experiment 1, 15 different objects were used, manipulated for each of the six conditions for a total of 90 trials, in addition to 4 practice trials. Trials were arranged in a pseudorandom order, and each participant received the same order of trials. As in Experiment 1, the task for participants during the stationary displays was to indicate with a button press when in their subjective experience the percept of a coherent object had faded.

Results

Figure 3B displays the mean perceptual persistence that observers experienced after the motion stopped, averaged across all 18 subjects. A repeated measures ANOVA with stimulus condition as the within-subjects factor showed a clear effect of condition on reaction time, $F(5, 85) = 46.151$, $MSE = 21{,}552{,}378.1$, $p < .001$. Post hoc comparisons (t tests for paired samples, Bonferroni corrected) revealed that the percept persisted significantly longer in all stop conditions than in the vanish condition ($p < .05$). Also, all stop conditions were significantly different from each other ($p < .05$), with the exception of the comparison between the two 25% conditions, $SE = 18.709$, $p = .120$, with increasing persistence observed for more complete objects.

Discussion

As in Experiment 1, we confirmed previous experiments by demonstrating that all object-stop conditions persisted longer than the object-vanish condition. Furthermore, we again demonstrated that persistence is unrelated to the number of lines: That is, while no differences were observed between the two 25% conditions, with one half as many features in the 25%-least condition, significant differences were observed between the 25%, 50%, and 75% conditions, though these objects possessed the same number of lines. Thus, the differences observed between the stop conditions in which the number of line-segments varied were in exact opposition to a working-memory load hypothesis. Working memory is limited in capacity, and, consequently, if persistence is mediated through working memory, fewer lines should place decreased demands on working memory, thereby leading to longer persistence. In fact, the opposite effect is demonstrated here: The objects with the fewest number of lines (25%-least) persisted the shortest of the three, and those with the greatest number of lines (75%-most) persisted the longest.

Thus, taken together, the results of Experiments 1 and 2 suggest that persistence increases as objects become more complete. With the exception of the significant difference between the two 75% conditions, persistence increased only as a function of the proportion of outline coverage; thus, although all objects are impossible to detect against the background without motion, once motion is induced, those objects that form more complete wholes are more easily maintained by the visual system. A similar process has been found by Shipley and Kellman (1992) with illusory figures. They report that the strength of the perceived clarity of illusory figures demonstrated a linear relationship with the ratio of the length of the inducers to the total edge length. The persistence of the objects in SFM displays may occur due to similar effects of the object-based information available to the perceiver. That is, once the segregation and binding processes have been initiated by relative motion, the figure information is processed distinctly from the ground information, presumably by the object-sensitive LOC; then, in the absence of other bottom-up visual cues, it is this "objectness" that the LOC maintains, producing persistence.

One alternative interpretation to the observed results is that object persistence increases as the proximity between line-segments decreases. That is, the features of the object remained bound longer if the distance between them is smaller. This interpretation is relevant in the context of Gestalt psychologists' proposition, as well as the psychophysical evidence that proximity and good continuation are important laws governing object recognition and perceptual organization (Hess & Field, 1999; Hess, Hayes, & Field, 2003). Additionally, evidence from neuroimaging has demonstrated that filling-in effects can be observed in the same brain areas as those that are involved in shape-from-motion (Liu, Slotnick, & Yantis, 2004), suggesting that perhaps persistence is related to filling-in effects between nearby elements. However, though the "5" stop objects of Experiment 1 contained much shorter distances between line-segments than did the "20" stop condition, there was no observed difference in persistence. Thus, though good continuation and proximity may influence the integration of contours in stationary objects, the presence of an additional cue (i.e., motion) can also serve to initiate binding processes between features. Persistence, then, may have more to do with the ability of form-sensitive regions to maintain the binding of object representations than with the physical relation (i.e., proximity) between features.

EXPERIMENT 3

The results of Experiment 2, when taken together with those of Experiment 1, suggest that neither the number of line-segments present in an object nor the physical distance between line-segments has an effect on persistence; the completeness of objects, however, does affect the duration of the persistence of the percept, once motion, the initial cue, is removed from SFM displays. These results provide support for the idea that persistence is not a product of working-memory processes, but rather is dependent on form- or object-based information. Thus, the observed persistent brain activity in LO (Ferber et al., 2003, 2005; Large et al., 2005) may not be a reflection of the perception of the persisting object, as mediated by other processes, but rather may be mediating the persistence itself, affected by the amount of available form-based information.

If object persistence is mediated by area LO, which has been implicated in object recognition (Bar et al., 2001; Grill-Spector et al., 2000), then persistence may be related to how easily objects are recognized; that is, the same neural substrates that mediate object recognition may mediate persistence, relying on similar processes. For example, in the experiment by Doniger and colleagues (Doniger et al., 2000), increased neural processing over lateral-occipital sensors was observed as objects increased in completeness; thus, given that persistence increases with object completion, it is possible that persistence has a direct relationship to the initial recognition process. Consequently, Experiment 3 addressed the relationship between object recognition and subsequent persistence.

In addition, Experiment 3 attempted to control for how visible the object's features are in the stationary display. It is possible that the observed differences between the conditions of Experiment 2 may be attributed to differences in visibility of the object's features against the background. For example, the long features of the 75% conditions may have made them more distinct from the relatively shorter elements of the background, and therefore participants may have experienced longer persistence. Accordingly, we further controlled for the visibility of the objects in the stationary display by creating unique backgrounds for each of the object categories that contained the actual features of those objects. This control made the features of each of the task conditions identical to those of the background, thereby ensuring that persistence cannot be attributed to the relative visibility of the features themselves.

Method

Participants

A total of 23 healthy undergraduates (16 women; age range 19–32 years, mean age 21.71 years; 21 right handed) from the University of Toronto participated in the study to receive credit for an undergraduate course. All volunteers provided written consent.

Procedure

The procedure was similar to that used in Experiment 1; however, no *n*-back task was performed. In addition to making a response during the stationary epoch when the percept of the object had disappeared, participants were also asked to make a response during the motion epoch when they could detect the presence of a coherent object within the group of moving lines. Trials were advanced automatically with an intertrial interval of 1,500 ms, and participants were given two self-timed breaks. Timeouts—trials on which the individuals did not respond for 12 s during the stationary display—were not observed in Experiment 3. One participant's data was removed as she demonstrated RTs to the vanish condition that were longer than those of her stop trials, bringing the total number of participants to 22.

Materials

As in Experiment 1, 15 different objects were used, manipulated for each of the five conditions for a total of 75 trials. In addition, 15 backgrounds were created for each of the 15 objects used in the experiment. For each background, individual features of all of the “5”, “10”, “15”, and “20” conditions of Experiment 1 were pseudorandomly arranged. Thus, the backgrounds were identical across all stop and vanish conditions for each object category. Trials were arranged in a pseudorandom order, and each participant received the same order of trials. Prior to beginning the experimental trials, five practice trials were presented to familiarize the participants with the procedure, using different stimuli from those that were presented in the experimental trials. As in Experiment 1, the task for participants during the stationary displays was to indicate with a button press when in their subjective experience the percept of a coherent object had faded; to control for the effect of low-level object recognition processes on persistence, we also asked our participants to indicate with the same button press when an object was detected within the moving display.

Results

Figure 4A displays the mean perceptual persistence that observers experienced after the motion stopped, averaged across all 22 individuals. A repeated measures ANOVA with stimulus condition as the within-subjects factor found a clear effect of condition on perceptual persistence, $F(4, 84) = 16.435$, $MSE = 1{,}045{,}638.376$, $p < .001$. Post hoc comparisons (*t* tests for paired samples, Bonferroni corrected) revealed that all stop conditions differed significantly from the vanish condition, $p < .001$; however, all other comparisons were not significantly different at the $p = .05$ level after Bonferroni correction.

The mean RTs to detect the objects during the motion epoch are shown in Figure 4A. A repeated measures ANOVA with stimulus condition as the within-subjects factor demonstrated a significant effect of condition on object detection, $F(4, 84) = 2.652$, $MSE = 85{,}522.571$, $p < .05$. Post hoc comparisons (*t* tests for paired samples, Bonferroni corrected), however, revealed that only the “10” and “20” conditions were significantly different from each other, $t(21) = -3.234$, $SD = 220.132$, $SEM = 46.932$, $p < .05$.

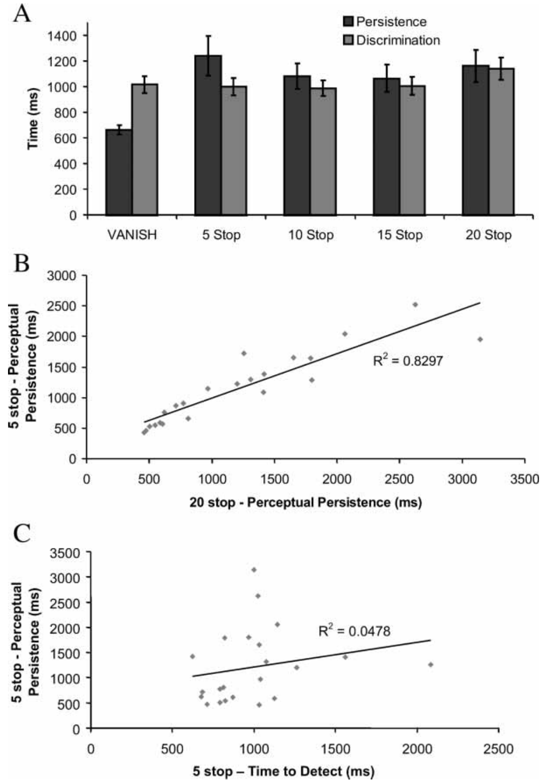

Figure 4. *(A) Mean perceptual persistence measured in ms for Experiment 3 in dark grey, time required to detect an object during the moving display depicted as light grey* (n = *22). Error bars denote standard error of the mean. Results were similar to those of Experiment 1. (B) Example of the correlation between the duration of perceptual persistence in ms for two of the object-stop conditions in Experiment 3.* R^2 *value denotes the proportion of variance in the persistence of one condition explained by persistence in the other condition. (C) Example of the correlation between the time required to detect the object during the motion display and the subsequent duration of persistence after the motion stops.*

To further examine the relationship between object detection during the motion epoch and object persistence during the stationary displays, correlations were computed between the persistence and detection RTs for all five conditions; if persistence in any of the object-stop conditions (e.g., "5") was related to the detectability of the same objects in the moving displays, participants' RTs for detection should be correlated to the duration of persistence. However, none of the correlations between detection and persistence were significant at the $p < .05$ level (see Table 2 and Figure 4C).

In addition, an individual's subjective persistence should remain relatively stable across conditions if persistence is indeed dependent on the percentage of object completion; that is, even though variability in persistence between subjects may be large, an individual's persistence in one object-stop condition should be correlated with persistence in the other conditions. Likewise, correlations should be observed between each of the object detection conditions, if object detection is equally consistent within individuals. Analysis demonstrated that the duration of persistence in each condition was positively correlated with persistence in all other conditions, with the minimum correlation exceeding $r = .79$, significant at the $p < .001$ level (see Table 3 and Figure 4B). Similarly, detection RTs demonstrated significant correlations between all conditions, with the minimum correlation exceeding $r = .44$, $p < .05$, with the remainder significant at the $p < .01$ level (see Table 4).

Discussion

As in Experiment 1, we confirmed previous experiments by demonstrating that all object-stop conditions persisted longer than the object-vanish condition. Unlike Experiment 1, however, we observed no significant differences between our object-stop conditions. Thus, this experiment replicates and extends our original finding that when the amount of object coverage remains constant, variations in proximity and number of line-segments have no effect on persistence.

The question still remains as to whether the null result between these conditions is a real effect. It could be argued that differences between the conditions exist, but that the variability between individuals is too great to observe statistically significant differences between conditions. However, we verified highly significant correlations between the persistence RTs for all conditions, demonstrating that although interindividual variability may be high, persistence is remarkably consistent and reliable across conditions. In fact, correlations of persistence between the object stop conditions explain as much as 86% of the variance in any of the other conditions, again demonstrating that the duration of persistence can be accounted for by the completeness of the object's form, even in the presence of great variations in other featural information. This finding lends additional credibility to our paradigm, and, accordingly, we conclude that the duration of perceptual persistence in SFM is not

Table 2. *Correlation between discrimination time and perceptual persistence, Experiment 3*

Condition	*r*
5 Stop	.219
10 Stop	.240
15 Stop	.210
20 Stop	.134

Table 3. *Correlation between reaction times for persistence conditions, Experiment 3*

Condition	*Stop 5*	*Stop 10*	*Stop 15*	*Stop 20*
Stop 5	—	.856**	.908**	.911**
Stop 10		—	.924**	.938**
Stop 15			—	.965**
Stop 20				—

** Correlation is significant at the .01 level.

Table 4. *Correlation between reaction times for detection conditions, Experiment 3*

Condition	*Stop 5*	*Stop 10*	*Stop 15*	*Stop 20*
Stop 5	—	.639**	.583**	.445*
Stop 10		—	.870**	.846**
Stop 15			—	.679**
Stop 20				—

* Correlation is significant at the .05 level. ** Correlation is significant at the .01 level.

mediated by the proximity between line-segments depicting the object, but instead is mediated by the information of the object form.

In addition to measuring persistence, we also examined the relationship between figure segregation during motion and object persistence after the motion stops. Unlike the persistence data, a significant difference was observed between the "10" and "20" object conditions. Thus, though differences are observed in how easily the different object conditions are identified in the moving display, these differences have no effect on persistence, suggesting that the level of difficulty at initial object discrimination is unrelated to the strength of the binding and therefore is unrelated to the subsequent duration of persistence. To corroborate this assumption, we calculated correlations between the detection and persistence RTs. Though significant correlations were observed between all detection conditions, correlations were not observed between detection RTs and persistence RTs for any of the object conditions, indicating that initial figure-segregation is unrelated to subsequent persistence.

EXPERIMENT 4

The first three experiments provide compelling evidence that the persisting awareness of objects is unrelated to working-memory load, as well as differences in the low-level qualities—namely, the proximity between the features; instead, object persistence appears to be mediated by information about the form of the object itself, as persistence increases as object completion increases, and the duration of persistence of two objects with equal completeness is highly correlated across individuals. Given the observed neural activity in the object-sensitive area LO that accompanies persistence (Ferber et al., 2003, 2005; Large et al., 2005), it appears that the neural substrates involved in the perception and recognition of objects also serve to maintain the awareness of objects in a scene.

Given the role of the LOC in object recognition processes (e.g., Bar et al., 2001; Grill-Spector et al., 2001; Grill-Spector et al., 1999; Grill-Spector et al., 1998; Grill-Spector et al., 2000), as well as the lack of relationship between initial segregation processes and subsequent persistence demonstrated in Experiment 3, questions remain about the mechanisms underlying persistence. For example, if area LO is involved in object-recognition processes, to what extent are unrecognizable objects maintained by similar processes? Though it has been demonstrated that top-down influences may play a role in persistence (Risko, Dixon, Besner, & Ferber, 2006), unrecognizable forms demonstrate persistence that is similar to that of recognizable objects. Furthermore, identical persisting LO activity was observed for scrambled and intact objects (Ferber et al., 2005), although phenomenological persistence was somewhat shortened for the scrambled objects. Though these experiments demonstrated that persistence can occur for nonobjects as well as objects, closed-contour nonobjects have not been directly compared to familiar objects with similar outlines. Furthermore, if persistence of objects parallels persistence of nonobjects with similar form completeness, it may provide evidence that persistence is in fact related only to the colinearity between features (Hess & Field, 1999; Hess et al., 2003). Experiment 4 examined the persistence of nonobjects, both with and without perceived closed-loop contours.

Method

Participants

A total of 18 healthy undergraduates (16 female, 18 right-handed) from the University of Toronto participated in the study to receive credit for an undergraduate course. Volunteers were between 20 and 34 years old (mean age 22.05 years) and provided written consent.

Procedure

The procedure was similar to that used in Experiment 3. Participants were asked to perform a discrimination task during the motion epoch: They were to indicate with a button press with either their index or middle finger whether the stimulus was a familiar object or a novel shape. Button responses were counterbalanced between individuals, as they were assigned randomly to one of the two responses. We examined two measures from the responses during the motion epoch: accuracy in correctly categorizing recognizable objects, and RTs. Instructions emphasized accuracy for identifying an object as such in addition to speeded responses.

Materials

We created three different stimulus conditions for Experiment 4: (a) real objects; the same 15 objects as those used for the first three experiments, identical to the "10" stop objects; (b) nonobjects; closed-contour nonobject shapes; the nonobjects were created by distorting the forms of objects until they maintained a similar level of complexity but were no longer recognizable as objects (see Figure 5A); (c) scrambled; the line-segment features of the individual objects were rearranged with pseudorandom orientations within the shape defined by the contours of the nonobject stimuli. Thus, the scrambled conditions contained similar number and complexity of features as the real and nonobjects, however, they contained no contour-defined outline and no recognizable shape. We used the discrimination task to test how the real and nonobjects were categorized by participants.

All of the conditions contained 15 stimuli each, and each was presented in both stop and vanish conditions, for a total of 90 trials, in addition to 6 practice trials. All objects were created to be as similar as possible, with all stimuli having a maximum radius of between 2 and 3 degrees of visual angle. Trials were arranged in a pseudorandom order, and each participant received the same order of trials. As in Experiment 3, participants made two responses, one during the motion epoch to indicate whether the stimulus was a recognizable object or not, and one during the stationary epoch to indicate when they could no longer perceive a coherent form.

Results

The object discrimination task during the motion epoch verified that participants only recognized the objects in the real-object condition. One participant falsely identified two thirds of the nonobjects as real objects, and thus this participant's data set was removed, reducing the total number of participants to 17. The remaining participants correctly categorized all real objects on an average of 98% of the trials, with a total average accuracy of 97% across all object conditions. Thus, participants could reliably recognize and identify real objects in the SFM display from the closed-contoured nonobjects and scrambled objects.

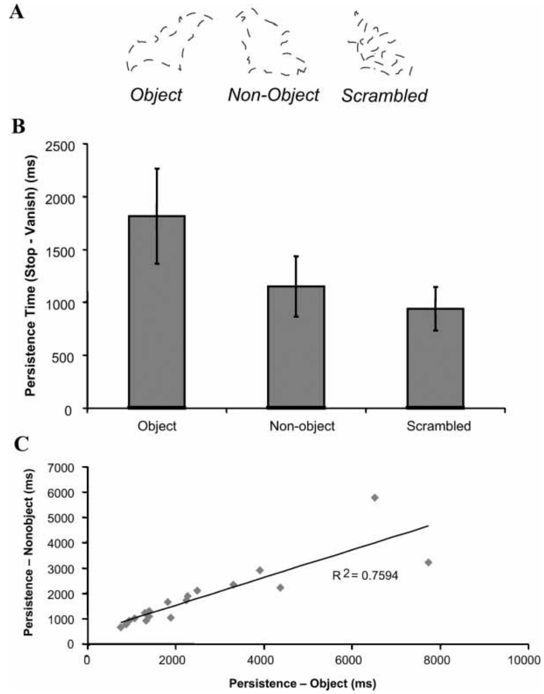

Figure 5. *(A) Examples of the stimuli used in Experiment 4. Nonobject stimuli were created by distorting the object stimuli until they were unrecognizable. Scrambled objects were created by randomly arranging the features of the object condition within the outline of the nonobject condition. (B) Mean perceptual persistence measured in ms for Experiment 4* (n = *17). Error bars denote standard error of the mean. The object condition demonstrated significantly longer persistence than the two nonobject conditions. The nonobject and scrambled conditions did not differ at the* $p < .05$ *level. (C) Correlation between perceptual persistence in the object condition and nonobject condition in Experiment 4. Similar correlations were observed between all stop conditions.*

Table 5. *Time required to categorize a stimulus during the motion epoch, Experiment 4*

Condition	*Mean RT (ms)*	*SE*
Object	1,202.12	73.93
Nonobject	2,318.69	318.56
Scrambled	1,763.87	250.72

Table 7. *Correlation between reaction times for persistence conditions, Experiment 4*

Condition	*Object*	*Nonobject*	*Scrambled*
Object	—	.872**	.952**
Nonobject		—	.931**
Scrambled			—

* Significant at the .01 level.

The mean RTs for correctly categorizing the objects are displayed in Table 5. A repeated measures ANOVA reveals a significant main effect of object condition, $F(2, 32) = 14.486$, $p < .001$, $MSE = 5{,}308{,}151.60$, with Bonferroni-corrected t tests revealing significant differences between all three conditions at the $p < .05$ level. Thus, while real objects require the least amount of time to recognize in the moving display, closed-contour nonobjects require much longer processing.

Because each stimulus was presented in both stop and vanish conditions, difference scores were obtained by subtracting the vanish RTs from the stop RTs for each of the three conditions. The results are displayed in Figure 5B. Repeated measures ANOVA demonstrated significant differences between the three object conditions, $F(2, 32) = 7.604$, $p = .002$, $MSE = 3{,}811{,}547.77$. Bonferroni-corrected t tests demonstrate that while the real-object condition is significantly different from the nonobject and scrambled conditions, $t(16) = 2.58$, $p < .05$, $SE = 273.569$, and $t(16) = 3.14$, $p < .05$, $SE = 286.309$, respectively, the two nonobject conditions were not significantly different from each other, $t(16) = 1.38$, $p = .186$, $SE = 141.744$.

As in Experiment 3, we examined the role of initial object processing in persistence by calculating the correlation coefficients between segregation and persistence RTs. The results are displayed in Table 6. As with Experiment 3, no significant correlations were observed between the time necessary to identify the object during the motion epoch and the subsequent duration of persistence. However, the duration of persistence in one object condition was strongly correlated with the duration of persistence in the other object conditions, with the persistence in one condition explaining between 76% and 90% of the variance in persistence for the other conditions (see Table 7 and Figure 5C). The correlations between recognition RTs are also displayed in Table 8.

Discussion

The results of Experiment 4 extend the results of Experiment 3 by further demonstrating that persistence is unrelated to the recognition of objects during the motion epoch. Thus, the processing time required to recognize familiar objects correctly is unrelated to the maintenance period of that object in awareness. Furthermore, the results demonstrate that the maintenance of object awareness is not dependent on object familiarity, as both closed-contour nonobjects and scrambled

Table 6. *Correlation between discrimination time and perceptual persistence, Experiment 4*

Condition	*r*
Object	.452
Nonobject	.230
Scrambled	.317

Table 8. *Correlation between reaction times for categorization conditions, Experiment 4*

Condition	*Object*	*Nonobject*	*Scrambled*
Object	—	.688**	.700**
Nonobject		—	.951**
Scrambled			—

* Significant at the 0.01 level.

shapes demonstrate significant persistence. Thus, persistence cannot be attributed to mechanisms serving the maintenance of familiar objects only.

The perceptual persistence of both familiar objects and nonobject shapes provides further evidence that the LOC subserves the maintenance of object awareness, as the LOC is sensitive to both familiar objects and novel shapes (Grill-Spector et al., 1998). We also observed no differences in persistence between closed-contour shapes and scrambled shapes. This finding has further implications for the neural mechanisms subserving the maintenance of these figures. Though contour integration and colinearity may be important to the initial perception of objects, the colinearity between features does not seem to be essential to the cognitive and neural mechanisms subserving the maintenance of forms once the objects' features have been segregated and bound.

At first glance, the absence of a difference in persistence between the nonobject and scrambled conditions seems at odds with the neuroimaging evidence (e.g., Grill-Spector et al., 1998) that the LOC prefers "novel" objects (much like the nonobject condition here) to textures or scrambled images (similar to the scrambled condition in this experiment). There are two probable reasons for this apparent discrepancy. First, while scrambled objects in fMRI experiments are "scrambled" in that they contain no well-defined contour, the use of a relative-motion cue in our experiment separates both the scrambled objects and nonobjects from the background; thus, the scrambled objects are segregated from the background and are processed as novel forms, in contrast to static scrambled images in which there is nothing to bind, and no form can be segregated. Second, Experiments 3 and 4 both demonstrate that persistence is at least uncorrelated with recognition, suggesting that while shared by similar cortical regions, the two processes are not equivalent.

GENERAL DISCUSSION

In the presented experiments, we attempted to examine the mechanisms underlying the persistence of objects in shape-from-motion displays. Experiments 1–3 provide evidence against a working-memory hypothesis of persistence. Increasing the number of lines that compose an object does not inversely affect persistence (Experiments 1 and 3), as would be predicted if persistence were mediated by capacity-limited working memory. Furthermore, placing an additional load on working-memory processes by performing a concurrent 2-back task does not produce detrimental effects on persistence when compared to concurrent 1-back or 0-back tasks (Experiment 1), even though accuracy performance is dramatically impaired. Both of these experiments provide evidence against the hypothesis that persistence is mediated by visual working-memory processes. In addition, if focal attention were required to maintain the binding of object features into coherent shapes, as has been proposed by a number of theories, including *coherence theory* (Rensink, 2000a, 2000b) and the *inattentional amnesia hypothesis* (Wolfe, 1999), then the additional attentional demands of the dual-task paradigm in Experiment 1 should disrupt the maintenance of fragmented line-drawings representing a coherent form. Our results show, however, that the coherent representation of the objects remains unaffected by the division of attention required by the additional tasks, as indicated by unaltered perceptual persistence.

If persistence of objects in SFM is not accomplished through working-memory processes, what are the processes that maintain the awareness of the percept? One intuitive alternative is that the persistence is a demonstration of *iconic* memory. However, there are a number of reasons why this hypothesis cannot be supported. First, the percept persists for periods that well exceed what is typically identified as an "iconic" representation, where the persistence of information degrades in less than 1 second (Coltheart, 1980; Sperling, 1960). Iconic memory is in the order of hundreds of milliseconds, whereas the perceptual persistence of forms in SFM is observed for seconds. Second, the duration of object persistence can be varied by the degree of object completion (Experiment 2); if persistence were a product of iconic memory it would be largely unaffected by these changes to the higher order information. Furthermore, persistence is observed even when the features that compose the object are replaced with its complement (Ferber et al., 2005), suggesting that persistence is related more to the global perceived structure or form of the figure, rather than a low-level iconic representation of individual features. Finally, persistence is sensitive to semantic information (Experiment 4), providing further evidence that persistence is not related to the physical properties of the stimulus alone. Persistence is not dependent, however, on the recognition of a familiar form, suggesting that persistence cannot be attributed to processes specific to these higher level representations.

Furthermore, though the maintenance of a given form in SFM clearly involves the persistence of information, it appears to differ from memory processes in a number of ways. Unlike most demonstrations of iconic and working memory, the visual features comprising the information are themselves not removed from the display. This means that the maintenance of the features themselves is theoretically not required; as the percept fades from awareness, the visual features themselves remain present. The alternative to the working-memory hypothesis, and the position we would like to argue for here, is the form-based memory store hypothesis. It was demonstrated in Experiment 1, and replicated in Experiment 3, that persistence is generally unaffected by changes in the features of the objects, but is instead affected only by the degree of object information available. In Experiment 2, as forms become more complete (and, thus, present more information regarding the "objectness" of the form), the forms persist longer; when the degree of object-related information is held constant, but the lengths and proximity of the object's features are altered as in Experiments 1 and 3, no changes in persistence are observed. The "store", then, seems to service the subjective awareness of global form. That is, it is the maintenance of awareness itself, rather than the mnemonic maintenance of low-level perceptual features, that is demonstrated by persistence. We propose here that the functional significance of a mnemonic store mediating this type of process is to maintain the awareness of unified forms and objects as those objects rotate or move in the scene, or as attention and fixation move throughout the scene, thereby creating a unified phenomenological experience. Though it is already well documented that LO plays a critical role in mediating the awareness of objects (Bar et al., 2001; Grill-Spector et al., 2001; Grill-Spector et al., 2000), the maintenance of that awareness may also be mediated by the same neural substrate.

All of this evidence strongly supports the argument originally made by Ferber and colleagues (Ferber et al., 2005) that persistence is indeed mediated by an object-based intermediate store, localized to the object-sensitive LOC. The neurophysiological evidence obtained to date also supports these conclusions. Persistent neural activity in the LOC is observed to perceptually persisting objects (Ferber et al., 2003, 2005). Other evidence (Large et al., 2005) suggests that the persistence of forms is an emerging property of the ventral visual stream, as the duration of persisting activity gradually increases across the cortical hierarchy, with the greatest persistence observed in the LOC. Other psychophysical studies have also suggested the possibility of a brief mnemonic store for visual representations. It has been demonstrated that when ambiguous patterns are presented intermittently, the perceptual state of that pattern will remain constant for much longer than during continuous viewing (Leopold, Wilke, Maier, & Logothetis, 2002). It was later suggested that this stabilization of a perceptual state may be due to memory processes specific to a perceptual state, and that these representations are dependent on the global aspects, rather than on the basic perceptual features, such as motion (Maier, Wilke, Logothetis, & Leopold, 2003).

Given that the features of the object are still physically present during persistence, some reciprocal activity may occur between area LOC and early visual areas, including V1, in order to maintain the segregation and binding already processed. It has been suggested previously that the synchronization of rhythmic oscillations of neural activity could provide a neuronal mechanism for bottom-up visual feature binding (e.g., Eckhorn, 1999; Engel, Roelfsema, Fries, Brecht, & Singer, 1997). Furthermore, the same oscillatory activity has been proposed as a mechanism for object representation (Tallon-Baudry & Bertrand, 1999). The maintenance of awareness of the segregated objects and its associated binding may depend on such neural synchrony, both within and between the LOC and early visual cortex; for example, the loss of awareness (i.e., the degradation of the representation) may be a product of the desynchronization between neuronal populations, although this hypothesis has yet to be tested.

In addition, we also provide further evidence that the maintenance of objects in awareness is not crucially dependent on the familiarity of the object. Although objects persist longer than nonobjects with closed-loop contours and without, the persistence of forms is not dependent on whether the form is familiar. This provides further evidence that the maintenance of awareness is mediated by the LOC, as it has been demonstrated that the LOC is sensitive to novel shapes as well as familiar objects (e.g., Kourtzi, Erb, Grodd, & Bültoff, 2003; Malach et al., 1995); furthermore, the LOC is ideally located to receive both feed-forward information about the low-level features of forms, as well as feedback information about the semantic content of the form. Both processes may influence the maintenance of awareness.

Though the evidence presented here and elsewhere (e.g., Ferber et al., 2003, 2005; Kleinschmidt et al., 2002; Large et al., 2005; Maier et al., 2003) suggests the presence of a brief memory store different from working memory and iconic memory, specific to and affected by object or form information, the complete nature and extent of such a store are unclear. While the proposed form-based store localized to the LOC may not represent the only possibility, the persistence of objects in SFM cannot be understood in terms of traditional working-memory systems. However, it is important to state that we are not arguing that the proposed store operates entirely independent of traditional working-memory systems, but rather that the current framework of working memory cannot explain the phenomenon of perceptual persistence in SFM. In contrast, the proposed buffer may play a significant role in the encoding stage of working memory, and it may also serve as an intermediate stage between sensory and working-memory systems, as suggested by Ferber et al. (2005); in other words, a form-based store may mediate encoding processes essential to working memory. Alternatively, the proposed short-term object store may be in line with the recent proposal made by Postle (2006) that working memory is not a distinct set of systems, but instead is a property of the brain that emerges when attention is directed towards sensory, representation, or action-related systems.

By briefly maintaining visual representations, a form-based store may provide a mechanism to reduce the computational load necessary for repeatedly segregating and binding the features of a scene into objects. This may also serve to assist in the experience of perceptual continuity, helping to maintain the coherence of a visual scene, despite the rapid changes to the physical stimuli impinging on the retina. Paradoxically, the proposed buffer could also help to explain some failures of perception; for example, “change blindness” could occur due to the presence of stored representations in this memory system and maintaining the sense of awareness of figures and forms, thereby making the viewer unaware of small and rapid changes to the visual scene (Rensink, 2000a, 2000b).

The proposed intermediate store for visual information is also supported by other existing physiological findings. Xu and Chun (2006) recently demonstrated that the LOC is involved in visual short-term memory, with a capacity that does not have a fixed number of objects, but rather is sensitive to the amount of visual information stored. Furthermore, Mukamel and colleagues (Mukamel, Harel, Hendler, & Malach, 2004) demonstrated that a four-fold increase in presentation rate produces only a 25% increase in the fMRI signal of higher visual areas, roughly half the observed increase of lower visual areas. The authors suggest a short term "iconic" memory system in these areas, which could preserve and integrate information over time.

To summarize, we have demonstrated that the persistence of objects in SFM outlasts the possible duration of iconic memory, and yet we provided strong evidence here that persistence is different from working-memory systems. Furthermore, we showed that persistence is dependent on the degree of object completeness (that is, the degree of "object" information within a form), and not on the physical relationship between those object's features. These behavioural findings fit nicely with existing evidence for a form-based memory store from other behavioural studies, fMRI, and single-cell literature. While the experiments presented here do not elucidate fully the nature of persistence of motion-defined forms, they help clarify the mnemonic processes involved in perceptual persistence.

Manuscript received 1 July 2004
Revised manuscript received 11 August 2006
Revised manuscript accepted 2 October 2006
First published online 5 December 2006

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