

The role of elaboration in the persistence of awareness for degraded objects

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Abstract

When a fragmented line-drawing of an object moves relative to a background of randomly oriented lines, the previously hidden object can be segregated from the background and consequently enters awareness. In this shape-from-motion paradigm, the percept of the object briefly persists after the motion stops, demonstrating the maintenance of a bound percept in awareness. This study investigated how the manipulation of object features that are crucial to recognition influences both the binding process and the maintenance of objects in awareness. Overall, we found that objects that took longer to recognize (i.e., objects missing their vertices) were nonetheless maintained in awareness for longer. We argue that this effect is mediated by additional elaborative processing that is required to bind these less recognizable forms, which generates stronger and more robust representations. These representations are then more easily maintained in awareness, suggesting an important role of elaborative mechanisms for conscious representations.

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1. Introduction

Although the different visual features of an environmental stimulus, such as color, orientation, and motion are processed in different cortical areas (see Grill-Spector & Malach, 2004; for a review), the visual system manages to combine these features into a stable representation of objects in awareness. This difficult task of combining separate features into a coherent percept is referred to as the “binding problem.” While numerous studies have investigated how humans initially recognize and become conscious of visual objects, little is known about the equally difficult task of maintaining stable representations once separate features have been bound and a stimulus has reached awareness. Which areas of the visual cortex contribute to the maintenance of object awareness, and does the maintenance of a coherent percept rely on the same features involved in its initial representation? The purpose of the present study was to observe how featural changes that affect binding and recognition processes modulate the subsequent maintenance of object awareness.

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Regan's shape-from-motion (SFM) paradigm provides a demonstration of how objects are maintained in awareness after initial object recognition has occurred (Regan, 1986, 2000). When a fragmented line-drawing of an object (Fig. 1a) is embedded in a background of randomly distributed lines (Fig. 1b), the object cannot be distinguished from the background (Fig. 1c). However, the addition of relative motion between the object and the background enables instantaneous perception and recognition of the object (Fig. 1d). Motion acts as the cue that allows the object features to be segregated from the background, and importantly, to be bound together into a coherent representation. Interestingly, when the motion stops (and therefore the initial segregation cue is removed), perception of the object is maintained for a few seconds before the object fades into the background and becomes indistinguishable again. This perceptual persistence can be compared to conditions in which the object is removed from the background at the offset of motion and subjects do not experience significant persistence. Thus, object awareness is sustained in the former condition for far longer than would be available with iconic memory alone. Studying persistence enables us to examine the circumstances under which perceptual consciousness is first maintained and then lost, as once motion stops, the transition between the presence and absence of a conscious percept occurs without changes to the physical stimulus.

To be aware of an object embedded in the background of the SFM display, the individual line-segments of that object must be bound into a coherent representation. Binding in vision can refer to a number of different processes. For example, when observing a red square, the visual system must not only bind features within a modality, that is binding between four oriented lines, but also between modalities, that is the binding between the lines and the color of the square's surface. While the binding problem is commonly discussed with regard to these surface features (e.g., Treisman, 1998), Humphreys (2001) argues that binding is a multi-level process, as evidenced from case studies of patients with lesions to the ventral or dorsal visual streams. For example,

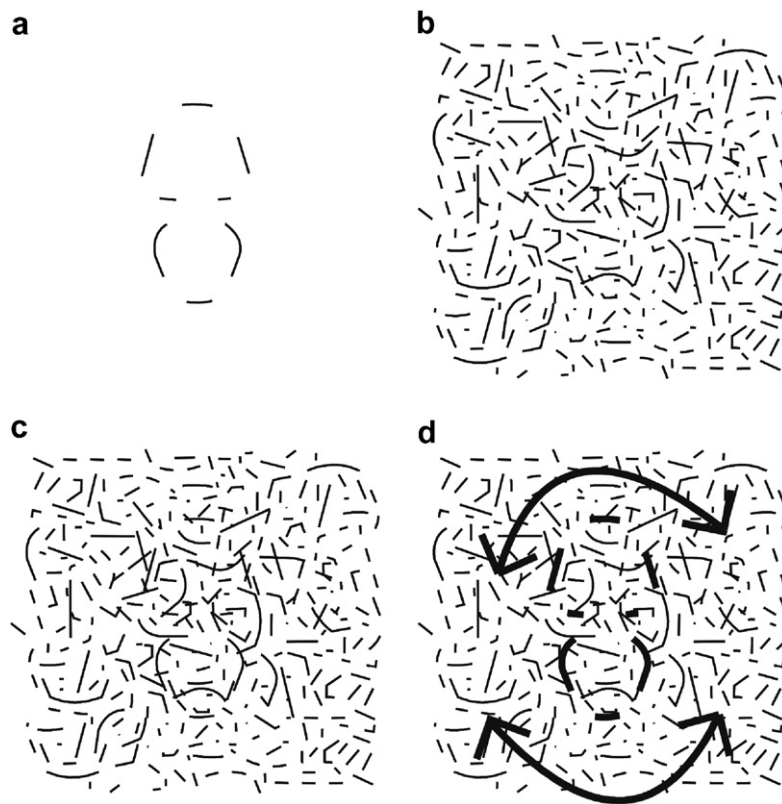


Fig. 1. The shape-from-motion paradigm. (a) An example of a fragmented object. (b) The line-segments from all the objects in the same category (e.g., lamps) are arranged pseudorandomly to create the background for that category. (c) When the object is superimposed on the background, the object is invisible. (d) When the object is rotated relative to the background (as indicated by the arrows), the object becomes recognizable (simulated here by the bolded lines). Although motion is initially required to recognize the object, when motion stops the object persists in awareness for a few seconds.

patients with parietal damage are unable to bind surface features, but are still able to bind contours into complete object forms. Humphreys maintains that a number of different types of binding can be distinguished: binding of form elements into contours, binding of contours into complete object forms, and the binding of surface features previously mentioned.

The SFM paradigm involves the first two types of binding mentioned above. The individual line-segments must be bound into contours, which are subsequently bound to create a complete representation of the object, enabling the object to be stored in awareness. Humphreys (2001) notes that individuals with lesions to object recognition areas in the ventral stream have difficulty binding contours into shapes, particularly with degraded objects (Humphreys, Cinel, Klempe, Olsen, & Wolfe, 2000). This finding fits nicely with results from functional neuroimaging studies with healthy participants showing that activity in the object-sensitive lateral occipital complex (LOC) corresponds to the persistence of object awareness in SFM displays (Ferber, Humphrey, & Vilis, 2003, 2005; Large, Aldcroft, & Vilis, 2005). Taken together, these findings provide compelling evidence that the LOC may in fact bind line-segments into a coherent whole and store this representation temporarily. Accordingly, we argue that the disappearance of objects from awareness observed in SFM most likely reflects the un-binding of global-forms in the LOC back into its component features (Ferber & Emrich, *in press*; Ferber, Humphrey, & Vilis, 2005).

It is unclear what object features and cognitive processes influence the initial binding and subsequent persistence. Ferber and Emrich (*in press*) found that placing an increased load on attention and working memory with a concurrent *n*-back task did not result in significant changes in persistence, suggesting that object awareness in SFM is not mediated by general working memory processes. Furthermore, persistence was not influenced by the number, length or distance between the line-segments. The degree of object completeness, however, did affect persistence such that objects with greater percentage coverage tended to persist longer than the same objects with less coverage. This finding demonstrates that the maintenance of objects in awareness depends on object-related information. In line with these findings, Ferber and colleagues (2005) demonstrated that when the original features of a SFM stimulus were replaced by their complements after the motion stopped, LOC activation and object persistence was maintained, suggesting that the LOC maintains the global representation of the object independent of the physical cues present. In addition, greater persistence is observed for recognizable objects over novel-shapes or scrambled-objects (Ferber & Emrich, *in press*; Ferber et al., 2005; Risko, Dixon, Besner, & Ferber, 2006), further demonstrating the important effect of information about object-form on the maintenance of object awareness in the LOC; importantly, however, object-form information can influence persistence from both bottom-up (Ferber & Emrich, *in press*) and top-down (e.g., Risko et al., 2006) modulation.

These previous experiments have suggested that information contributing to the representation of global object form influences the persisting awareness of objects in SFM. These behavioural findings fit nicely with the above mentioned results from neuroimaging studies showing that the LOC is active during persistence (Ferber et al., 2003, 2005) and that LOC activity is correlated with object recognition (Grill-Spector, Kushnir, Hendler, & Malach, 2000). That is, if the persistence of objects in awareness is related to the amount of object information available to the LOC, then persistence may be related to the ease with which features are initially bound into coherent and recognizable forms. However, Ferber and Emrich (*in press*) demonstrated that persistence is uncorrelated with the amount of time required to recognize an object. Thus, although both processes involve reporting a conscious percept, the two processes appear to be distinct. The current study addresses this apparent discrepancy by testing more directly the relationship between the initial binding of features into objects and the subsequent maintenance of those bound representations. In other words, is the length of perceptual persistence related to the amount of processing required to bind features into coherent objects?

What factors contribute to object recognition? A number of experiments have shown that the removal of vertices, defined as points of cotermination, severely impairs object recognition compared with the removal of the same quantity of midsections (see Fig. 2; e.g., Biederman, 1987; Guyette & Koch, 2002). According to Biederman's recognition by components (RBC) theory (Biederman, 1987), vertices are non-accidental properties (NAPs) that aid in the generation of the fundamental component of objects, geons. For example, occlusion of objects at the midsection is readily compensated for by NAPs, which aid in the recovery of lost components. However, if objects are degraded at regions of concavity (such as a vertex), recognition is more difficult because the component geons cannot be created by NAPs. Object features crucial for recognition may assist

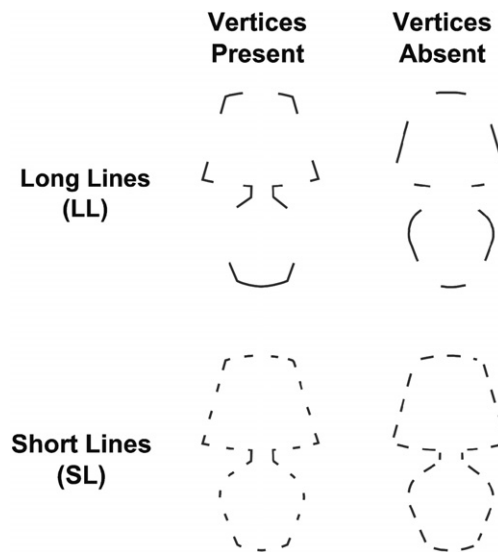


Fig. 2. Examples of the four stimulus conditions used in the experiment. The points of cotermination (vertices) or the midsections of 10 objects were removed. The remaining line-segments were also manipulated, making the length of the gaps and segments large or small. All objects covered 50% of the contour outline.

the visual system in readily binding the individual line-segments into a global representation of the object. Accordingly, one can predict that objects that lack NAPs require additional processing to bind the remaining features successfully into a coherent form which may lead to a less stable representation of the object, resulting in shortened perceptual persistence. By comparing the perceptual persistence of objects with or without vertices in SFM displays, we can investigate interactions between the initial feature-binding processes in object recognition on subsequent persistence while maintaining the amount of other object-related information (including percent coverage) between conditions equivalent.

To summarize, previous evidence suggests increasing amounts of object form information lead to greater perceptual persistence, suggesting that the level of processing required to bind features into a coherent representation determines object persistence. However, persistence has been shown to be uncorrelated with recognition, despite a common neural substrate. Here, we investigated more closely the role between initial binding (recognition) processes and the maintenance of bound percepts in awareness by manipulating the binding and recognition processes through NAPs.

2. Methods

2.1. Participants

Thirty five healthy undergraduate students (19 females) from the University of Toronto participated in the experiment to receive partial credit for an undergraduate course. Participants were on average 22.1 years old, and 29 identified themselves as predominantly right handed according to a modified Edinburgh handedness test. All volunteers provided written consent, and experimental procedures were approved by the University of Toronto Ethics Review Board. The data of 5 subjects were removed from analysis for failing to understand the task instructions, or for failing to remain vigilant during the task as indicated by a large number of deviations from fixation during the task.

2.2. Procedures

The experiment procedures were similar to those of previous experiments (Ferber & Emrich, *in press*). Subjects were seated with their chins resting comfortably on a chin rest located at 57 cm from a 19 in. computer

screen. Participants were instructed to maintain fixation on a small red dot (0.2° of visual angle) located in the center of the screen. The experimenter monitored eye movements and recorded any divergence of fixation.

Subjects were presented with 90 SFM trials (see Figs. 1 and 2). In each trial, the object and background rotated $\pm 15^\circ$ relative to each other with periods of 2 s for a duration of 12 s. In the recognition phase, subjects were asked to make a button response at the moment they were able to say whether the shape was a familiar object (in addition to the object stimuli, 10 scrambled objects were presented, and button responses were considered as false alarms). After 12 s, the motion stopped and participants then indicated with a button response when the percept of the object had disappeared in their subjective experience. In half of the SFM trials, the object was simply removed after the motion stopped leaving only the background on the screen. These ‘vanish’ trials serve as a baseline, as observers do not experience any perceptual persistence. In the other half of the SFM trials (the stop trials), the object remained present against the background once the motion stopped.

2.3. Materials

Participants were presented with a number of different object conditions in the SFM trials (see Fig. 2). The fragmented objects, which were created in Macromedia Flash MX (Adobe Systems, Inc. San Jose, CA) by removing line-segments from whole objects, were manipulated with respect to two features. The first feature manipulated concerned the points of cotermination (or vertices); line-segments were removed at the points of cotermination, leaving only the midsections between the vertices intact, or the midsections between vertices were removed, with the points of cotermination still present. The second feature that was manipulated concerned the length of the remaining and removed line-segments; the length of the segments was altered so that objects were composed of either short, closely spaced line-segments (SL), or long, distantly spaced line-segments (LL). Line length was manipulated to examine interactions between the low-level features of the object and NAPs and was included as a manipulation check. If the presence or absence of NAPs has robust effects on recognition and persistence, then changes in the physical length of those remaining features should not change the main effect. The remaining line-segments in all four conditions covered an average of 50% of the given object. To ensure equal coverage between all object conditions, a MATLAB script was used to measure surface coverage of the objects and to trim the remaining line-segments until coverage between the four conditions was equal. The horizontal extent of the objects covered an average of 3.9° of visual angle. Examples of each of the four conditions for the same stimulus are presented in Fig. 2.

Participants were presented with 10 objects in each of the manipulations described above (short and long lines, present and absent vertices), with both stop and vanish conditions for each stimulus, for a total of 80 experimental trials. The background for each object was composed of the line-segments from each of the conditions of that object (Fig. 1b), to ensure the object was equally salient against the background in all the conditions. In addition, 10 catch-trial objects composed of randomly oriented lines (taken from Ferber & Emrich, *in press*) were added to ensure participants were accurately responding in the recognition phase of the SFM experiment. Persistence data was not recorded for these catch trials. To familiarize participants with the experimental task, 5 practice trials containing different objects were presented at the beginning of the experiment.

3. Results

All responses more than 2.5 standard deviations from subjects’ mean reaction time (RT), were removed from analysis. For the recognition data, a total of 3.2% of the data was removed. For the persistence phase, standard deviations and means were calculated separately for stop and vanish trials, resulting in a deletion of 2.9% (stop: 4.7%; vanish: 1.2%) of the data.

3.1. Recognition phase

Fig. 1 shows the mean RTs required to recognize the moving object across all subjects, and raw data are reported in Table 1. False alarms to non-object trials were minimal, occurring on only 3.8% of catch trials. A repeated measures ANOVA with line length (SL, LL) and vertex condition (present, absent) as within subjects factors and RTs as the dependent variable found significant main effects of line length ($F_{(1,29)} = 21.574$,

Table 1
Average RTs (ms) required to recognize the object during the motion phase

Condition	Reaction time (ms)		Standard error
	Vanish	Stop	
<i>Long lines</i>			
Vertices absent	1168		78
Vertices present	1124		61
<i>Short lines</i>			
Vertices absent	1000		36
Vertices present	962		44

MSE = 817,181, $p < 0.001$, power = 0.994) and vertices ($F_{(1,29)} = 8.705$, MSE = 50,038, $p < 0.01$, power = 0.814). The interaction between line length and vertices was not significant ($F_{(1,29)} = 0.021$, MSE = 331, $p > 0.05$, $\eta^2 = 0.001$).

3.2. Perceptual persistence

Mean RTs for each of the conditions are displayed in Table 2. An initial t -test was performed between the mean RTs for stop and vanish trials to establish that significant persistence is observed when the object is stopped and remains on the background compared to when it is removed. The analysis demonstrated a significant difference between conditions ($t_{(29)} = -5.039$, SEM = 236, $p < 0.001$), confirming previous results that the object stop trials persist for longer than the object vanish trials. To obtain persistence scores that are not influenced by any idiosyncrasies related to a particular object condition, we subtracted the object vanish RTs for a given condition from the object stop RTs for the same condition. Fig. 3 displays the resulting mean perceptual persistence subjects experienced after the motion stopped, measured in ms. A 2 (LL, SL) \times 2 (with and without vertices) repeated measures ANOVA found a significant effect of line length ($F_{(1,29)} = 8.447$, MSE = 4,334,343, $p < 0.01$, power = 0.802), as LL objects persisted for longer than SL objects. A main effect of the presence or absence of vertices was also observed ($F_{(1,29)} = 8.526$, MSE = 3,258,640, $p < 0.01$, power = 0.806), as objects without vertices persisted for longer than objects with vertices. The interaction between vertices and line length was not significant at the $p < 0.05$ level ($F_{(1,29)} = 3.227$, MSE = 701,350, $p = 0.083$, $\eta^2 = 0.1$).

3.3. Correlations between recognition and persistence

To further assess the relationship between recognition and persistence processes, correlations were computed between the recognition and persistence RTs (Ferber & Emrich, in press). This analysis revealed that there was no significant correlation between recognition and persistence across all conditions ($p > 0.05$).

4. Discussion

This study investigated how the manipulation of object features that affect recognition would influence the subsequent maintenance of objects in awareness. In keeping with past SFM experiments (Ferber et al., 2003,

Table 2
Mean RTs (ms) observed during the persistence phase

Condition	Reaction time (ms)		Standard error	
	Vanish	Stop	Vanish	Stop
<i>Long lines</i>				
Vertices absent	776	2283	50	383
Vertices present	741	1768	42	236
<i>Short lines</i>				
Vertices absent	767	1733	48	221
Vertices present	764	1598	48	177

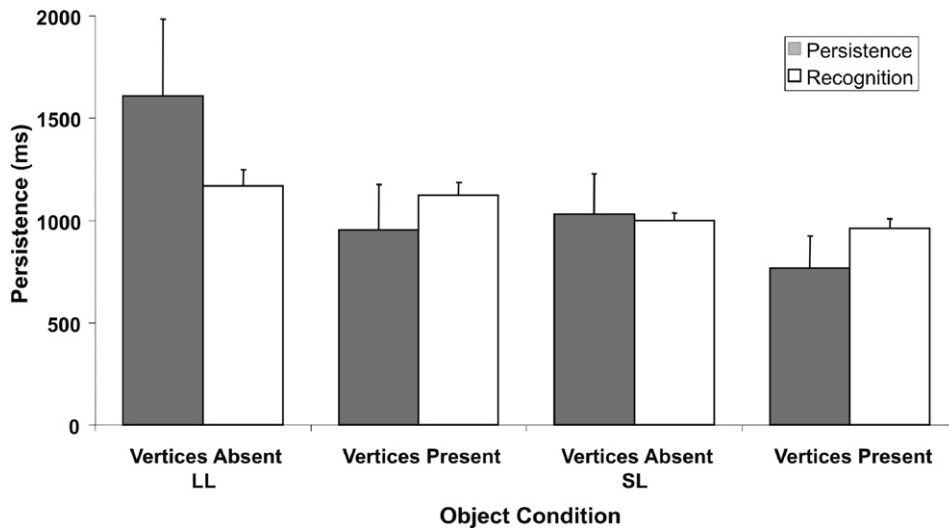


Fig. 3. Observed average reaction time (RT) for recognition and persistence ($n = 30$) for each of the four conditions, measured in milliseconds. Persistence is measured by subtracting vanish trials (trials in which the object is removed from the background after motion stops) from stop trials (objects remain on the display). Objects without vertices require more time to be recognized than objects with NAPs intact. Objects in the long-line condition also take longer to recognize. In the persistence phase, the differences observed parallel those that occur during recognition. Objects without vertices are maintained in awareness for longer than objects with vertices. Objects in the long line condition also persist longer than those with short lines. Error bars denote standard errors of the mean.

2005), objects in the stop condition persisted for significantly longer than objects in vanish trials. This suggests that an object can continue to be held in awareness despite the loss of the initial segregating cue.

In the recognition phase of the experiment, subjects demonstrated shorter RTs for recognizing objects with their vertices intact. This confirms earlier findings (Biederman, 1987; Guyette & Koch, 2002), and supports the RBC theory, which predicts that objects with missing vertices would be more difficult to recognize since vertices convey crucial object-related information. The missing line-segments in objects with intact vertices are easily compensated for by NAPs. Likewise, objects in the SL condition were recognized faster than objects in the LL condition. Despite the equivalent proportion of coverage between the two conditions, the length of line-segments evidently conveys important information about remaining object features, with short lines perhaps conveying more information about object geons.

In the persistence phase, objects without vertices persisted for longer, and were therefore maintained in awareness for longer. Thus, in contrast to the initial recognition of objects, the presence of NAPs does not confer any advantage for maintaining object awareness. In fact, when objects are presented without the NAPs, a condition under which recognition is difficult, objects persist for longer. This finding is contrary to the prediction that features which promote object recognition will also lead to increased perceptual persistence. Likewise, objects in the LL condition, which took longer to recognize than the SL objects, also demonstrated longer perceptual persistence. Again, this is contrary to the prediction that the low-level feature manipulation should not have an effect on persistence. The pattern of longer-recognition and greater persistence, however, reflects the same pattern observed for the NAPs manipulation.

The results appear to conflict with previous experiments (Ferber & Emrich, *in press*) in which more degraded objects (objects with less coverage) demonstrated less persistence than more complete objects. Numerous experiments have demonstrated that increasingly degraded objects take longer to recognize (e.g., Biederman, 1987). Furthermore, given the observed persistence of neural activity in the object-sensitive LOC (Ferber et al., 2003, 2005) and the observed correlation between LOC activity and object recognition (Grill-Spector et al., 2000), it would appear that persistence is inextricably linked to recognition processes. However, here we demonstrate that objects that take longer to recognize are maintained in awareness for longer. In other words, we a factor that is known to have a *negative* impact on recognition, namely the removal of NAPs, leads to increased persistence. Furthermore, no direct correlation between object recognition and object persistence was

observed, consistent with past SFM experiments (Ferber & Emrich, *in press*). Therefore, the results here seem to suggest that the maintenance of object awareness is distinct from recognition processes, and may even indicate that objects which are more difficult to recognize, due to the absence of certain features, are more easily held in awareness (although a negative correlation between persistence and recognition was not demonstrated). Accordingly, it appears that additional processes or mechanisms that are distinct from those enabling the explicit recognition of objects contribute to the maintenance of object awareness.

What mechanism allows the less recognizable objects to be held in awareness for longer? One possibility is that the longer persistence time reflects increased attentional processing. Objects lacking vertices are more difficult to recognize and, thus, subjects may purposefully exert more effort to focus on and attend to the object after the motion stops. However, evidence suggests that this explanation cannot be true. Recently, Ferber and Emrich (*in press*) demonstrated that a concurrent *n*-back task has no effect on the length of persistence in SFM. Given the substantial increase in attentional resources required for a 2-back compared to a 0-back task, it is unlikely that the differences in persistence reflect differences in attention on behalf of the observer.

A convincing solution is that binding processes required to create a coherent percept can account for these differences between recognition and persistence. Biederman (1987) proposed that objects missing their vertices would be much more difficult to recognize because the brain would need to engage in more elaborate processing to attempt to identify the fragmented geons. Accordingly, it is likely that when perceiving less recognizable objects, additional neural processing is needed to successfully bind and maintain the object in awareness. This mechanism may function similarly to long-term memory systems, in which more elaborative processing enables more robust future access (Craik & Tulving, 1975). For example, when trying to remember a given piece of information one can employ different rehearsal techniques. A simple, maintenance rehearsal would be to continuously repeat the information. This basic processing would allow for some degree of retrieval but would likely not allow for robust, flexible access to the information in the future. Elaborative rehearsal, on the other hand, involves more complicated processing such as drawing meaningful connections between the information and contemplating the information from different perspectives. This additional elaborative processing allows for more effective retrieval and more flexible processing in the future (Craik & Tulving, 1975). A similar mechanism likely underlies the persistence results observed in this experiment. In order to successfully create a global representation of the less recognizable objects, more elaborative processes would be required, and would result in more robust access to object-related information. This elaboration may not necessarily require categorically different processes, but rather may simply require additional neural resources or computation time relative to the examples for which recognition is more immediate.

We also observed longer persistence for objects consisting of longer lines. At first glance, this finding seems to be at odds with our previous report that line length does not affect persistence (Ferber & Emrich, *in press*). We would like to argue here, however, that in the current experiment feature length becomes important because it conveys information about the NAPs and the relationship between them. In the previous experiments, line-segments were deleted from all areas of the object equally. The segments deleted in the present experiment, however, were arranged to specifically indicate the presence or absence of cotermination. Manipulating feature size, then, affects the amount of information about the NAPs that is available to the observer, with longer lines providing less information about the removed vertices and the relationship between intact vertices. This means that feature size *per se* does not affect persistence, but when feature size also conveys information about critical object features we do see an effect on persistence.

The argument that line-length *per se* does not affect persistence is supported by the observation that line-length affects recognition RTs as well. That is, in the previous experiments (Ferber & Emrich, *in press*), manipulating line-length had no systematic effect on recognition time; however, because the line-segments in the present experiment convey information about features critical to object recognition, namely vertices, feature length significantly affects the time required to recognize an object. This increased time required to recognize objects with long lines and spaces may be responsible for the subsequent effects on persistence. That is, it is the effect of the specific manipulations on binding and recognition that produces the effect on persistence, rather than affecting persistence directly. As such, future studies should test additional properties which may affect binding and recognition processes independently of those that affect segregation and persistence.

Findings from the priming literature indicate how elaborative mechanisms may mediate this phenomenon. Through a number of experiments, it has been demonstrated that moderately fragmented images produce

greater priming effects than completed or entirely fragmented images (Snodgrass & Feenan, 1990; Snodgrass & Kinjo, 1998; Srinivas, 1993). Further investigation indicated that recognition of these degraded objects (also referred to as perceptual closure) was most likely the result of top-down and bottom-up process occurring simultaneously (Snodgrass & Kinjo, 1998). For example, more recognizable objects would likely activate largely top-down processing. It was proposed that less complete objects, however, would activate an optimum level of both top-down and bottom-up processing in order to properly recognize the object. In other words, relative to complete objects less recognizable objects trigger more bottom-up processing to achieve perceptual closure. Thus, we find more extensive processing for less recognizable objects and that may enable more robust object processing in the future.

What brain areas are mediating this effect? Doniger et al. (2000) measured activity in the LOC while subjects were presented with sequences of fragmented images of objects, starting with the most degraded, and getting progressively more complete. Activity in the LOC increased with the degree of object completion peaking at around 290 ms, even when the objects were still below the recognition threshold. It was proposed that a feedback mechanism between the LOC and lower visual areas subserves these initial perceptual processes (Doniger et al., 2000). Higher visual areas such as the LOC have extensive feedback connections to the lower visual areas, and evidence suggests that sustained activity in the lower areas is moderated by higher areas (e.g., Lamme, Super, & Spekreijse, 1998). Doniger et al. (2000) argued that the latency of the LOC activity was the result of feedback between the LOC and earlier visual areas. This additional feedback was required to complete the perceptual closure task (that is, to bind the object features). The extent of relevant feedforward and feedback modulation may explain observed differences in persistence. For example, non-objects take longer to ‘recognize’ than familiar objects (e.g., Ferber & Emrich, *in press*), but familiar objects persist longer due to the feedback modulation of regions encoding semantic information; on the other hand, objects with NAPs and objects without NAPs may both receive feedback modulation from higher regions, however, the extent of modulation may be greater for those objects that require more neural processing in the recognition phase (those without NAPs). It has been shown that neurons in the inferior temporal cortex of the macaque monkey, a region involved in object processing, are more sensitive to manipulations of NAPs than to similar manipulations of metric shape properties (Vogels, Biederman, Bar, & Lorincz, 2001). Interestingly, some of these neurons demonstrate *increased* activity in response to changes in NAPs, relative to the original stimulus.

This provides evidence that cortical regions involved in object processing are in fact sensitive to changes in NAP information, and that changes to NAPs can lead to increased cortical processing, suggesting a neural mechanism for elaboration. However, fMRI evidence suggests that objects which are more difficult to recognize actually demonstrate reduced activity in the LOC relative to objects which are easily recognized (e.g., Lerner, Hendler, & Malach, 2002). This finding is difficult to reconcile with the observed increase in neural processing in response to the removal of NAPs in monkeys (Vogels et al., 2001). It is possible that there are subsets of neurons in object sensitive regions which respond more to objects that are difficult to recognize, such as those lacking vertices. To examine this question, future studies should employ high-resolution fMRI of object-sensitive areas.

Additionally, both lower-level and higher-level information may modulate representations in the LOC through neural synchrony. Neural synchrony has been suggested as a mechanism by which the nervous system may solve the ‘binding problem’. This hypothesis postulates that synchronized oscillatory activation allows for the component features of an object, each coded by different neurons, to be represented as belonging to the same object (e.g., Eckhorn, 1999; Engel, Roelfsema, Fries, Brecht, & Singer, 1997; Singer & Gray, 1995). To recognize the object effectively (i.e., to become conscious of a coherent percept), neural synchrony may be required not only between the object features, i.e., between low-level regions and LOC (bottom-up), but also between medial or anterior temporal regions and the LOC (top-down). Objects that are more easily recognized may achieve synchronization more easily, whereas objects which are difficult to recognize may take longer to establish necessary synchronization, potentially over a more widely distributed network of brain areas. The increased time or larger number of neural populations required to establish synchronized connections may lead to longer subsequent persistence; that is, objects which require increased processing to establish a conscious percept are again devoted additional processing in the maintenance of that percept in awareness. This proposal is consistent with a framework of consciousness outlined by Crick and Koch (2004). According to this framework, synchronized neural firing of a coalition of neurons can assist in *establishing* a conscious

percept (represented by a particular coalition of neurons) over other competing coalitions. A winning coalition is somewhat sustained, and its associated percept enters into consciousness. If a percept is established in consciousness easily it requires only brief synchronization, whereas those coalitions which have substantial competition may require more sustained synchronization. Persistence of objects in awareness, then, may reflect the re-recruitment of coalitions of neurons used to identify the object, in an attempt to maintain the percept in conscious awareness. It would be interesting to examine neural synchrony in response to the manipulation of NAPs using electroencephalography (EEG) or magnetoencephalography (MEG). According to the suggestion here, it would take longer to establish synchrony during recognition for objects without vertices, with the recruitment of additional neural resources, which would result in greater and longer synchrony during persistence.

The value of the increased object persistence due to elaboration is somewhat unclear. Persistence could simply be an aftereffect of the more elaborate binding process. It is possible, however, that the object is held in awareness for longer to allow additional conscious processing. For example, an ambiguous and therefore less-recognizable object may nonetheless have important implications for an observer's behavioral goals (such as survival), and thus, maintaining an object in awareness for longer may allow the individual to further evaluate the object based on task demands. Since the inferior-temporal cortex of the macaque monkey, the homologue of the human LOC, appears to be interconnected with the frontal cortex (Schmahmann & Pandya, 2006), persisting consciousness of the object (maintained by the LOC) could allow for such conscious evaluation. This hypothesis is in accordance with the proposal by Postle (2006) that working memory is an emergent property of the cortex, not a set of specialized systems. According to this proposal, cortical regions which have evolved sensory or representational functions are recruited to maintain information specific to those systems. Thus, the awareness for stimuli which are still physically present (SFM persistence) and the mnemonic representation of stimuli which have been removed from the environment may ultimately reflect a common functional objective; that is, the maintenance of information in consciousness.

Interestingly, a similar relationship between the amount of information available at encoding and phenomenological persistence has been obtained in the study of iconic memory. Erwin (1976) presented participants with strings of letters with varying similarities to real English words. Persistence was observed to be shortest for strings of letters most closely reflecting real words (or those with the most redundancy), but only when participants had to report the contents of the letters. While persistence in SFM differs from iconic persistence in several important ways (see Ferber & Emrich, *in press*, for a discussion of the differences between iconic memory and SFM persistence), this provides further evidence that the conscious awareness of visual stimuli appears to be prolonged when the informational contents at encoding requires deep or elaborative processing.

To summarize, we observed that objects that took longer to recognize (objects without vertices) showed longer perceptual persistence compared to objects that were more easily recognized (objects with vertices present). We believe that our results point to a more general mechanism underlying conscious processing in the human cortex. Considering perceptual closure and elaborative rehearsal experiments, results suggest that information requiring additional processing may be more easily accessed in the future, enabling additional conscious processing. Accordingly, we conclude that when more elaborative steps are necessary to process information, the ease with which this information enters or is maintained in consciousness increases due to the stronger neural connections and associations. That is, elaboration at encoding will aid in the future accesses of those contents to consciousness.

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