Determinants of Object Persistence:

The Role of Cue Type, Cue Duration and Cue Strength

By

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Author’s Declaration

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Abstract

Four experiments investigated object persistence in conscious awareness as a function of the nature of the cues that permit the object to be segregated from the background, and identified. A number of factors were manipulated (cue type, [color, motion, color & motion] cue duration after object identification [1s vs 5s] and cue strength [strong vs weak]). Performance was fractionated into identification, maintenance and persistence components. The results show that (1) stronger cues yielded faster identification, and (2) persistence was independent of identification time, and (3) motion cues were associated with longer persistence than color cues. A distinction between dorsal and ventral visual pathways as used to segregate the object from the background provides one way to organize the data.

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Dedication

This thesis is dedicated to my family, who have guided me on the academic path of my life.

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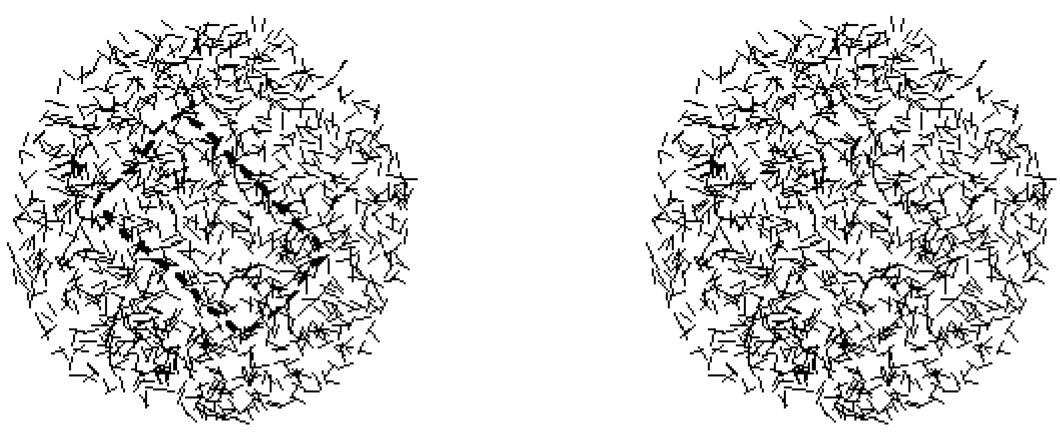
1 Introduction

Which structures and mechanisms in the brain allow us to process the multitude of information from the visual environment so as to perceive familiar and novel objects? Do various types and amounts of information affect the ability to maintain an object in conscious awareness after it is no longer present? These kinds of questions have begun to be addressed using the shape-from-motion (SFM) paradigm (Ferber, Humphrey & Vilis, 2003). In this paradigm, line segments comprising a geometric object move coherently (e.g. horizontally or in a circular pattern) relative to a background of randomly scattered lines moving in the opposite direction. The coherent motion serves to segregate the object from the background. Thus, motion (see the boldface in Figure 1, or color) can be used as a cue to define such an object in a display. Neural correlates of SFM include early visual areas of the brain (V1 and V2) processing both form and motion. Medial temporal regions (Tootell, Reppas, Kwong, Malach, Born et al, 1995) are selectively activated by moving versus stationary stimuli, and in 3-D motion and SFM displays (Peuskens, Claeys, Todd, Norman, Van Hecke et al, 2004).



Cue present Cue absent

Figure 1 – Boldface (representing motion) provides an example of one of the cues used to segregate the rectangle from the background lines (left). Without the boldface, the rectangle is not visible (right).

Object *persistence* occurs due to the brain's ability to maintain an object in conscious awareness for a short period after the cues that had initially served to segregate the object from the background are removed. Subjects then indicate (via a key press) when the object vanishes from subjective awareness. In fMRI studies, this loss of awareness of the object has been associated with a decrease in activity in the lateral occipital complex (LOC) which itself is associated with object perception (Ferber et al, 2003; Grill-Spector, 2003). The LOC shows greater activation to objects than scrambled lines in motion-defined (Peuskens et al, 2004) and non-motion-defined displays (Murray, Schrater & Kersten, 2004; Grill-Spector, Kushnir, Edelman, Itzchak & Malach, 1998).

Behavioral data reveal a longer subjective awareness of an object in the STOP condition (object remains displayed after the removal of the cue) than in the VANISH condition (the lines making up the object disappear after the removal of the cue). The VANISH condition serves as a baseline, and is thought to incorporate visual persistence (Coltheart, 1980), as well as the subjective decision and motor components of the response, while the STOP condition additionally measures the duration that the *object* persists in conscious awareness. The RTs from the VANISH condition are subtracted from the STOP condition RTs to yield a persistence *score* (Risko, Dixon, Besner & Ferber, 2006; Emrich, Ruppel & Ferber, 2008). Other studies (Ferber, Humphrey & Vilis, 2005; Large, Aldcroft & Vilis, 2005) have used RTs from the STOP condition to measure object persistence, though as noted above and in Emrich et al (2008), this measure includes various idiosyncrasies not related to the object's persistence. We look at both persistence scores and STOP condition RTs in our analysis. In fMRI data, increased RTs in the STOP condition over the VANISH condition are associated with increased activation in object-related, associative visual and higher-order brain structures (Kleinschmidt, Buchel, Hutton, Friston & Frackowiak, 2002; Ferber et al, 2003).

Ferber, Humphrey and Vilis (2005) and Risko et al (2006) reported that meaningful objects (animals and Arabic numbers, respectively) produce longer persistence than incoherent or meaningless objects. Similarly, Emrich, Ruppel and Ferber (2008) found that objects lacking points of cotermination persisted longer, perhaps because of the additional elaborative processes that can produce a richer underlying representation to support the percept. These studies have been taken to suggest a role for top-down influences in maintaining segregated objects in conscious awareness (Grill-Spector, 2003).

1.1 The Object Cycle

Ecological perception occurs in continuous time during which an object arguably goes through four ”stages” of perception (see Figure 2). Object perception begins when the object appears in a subject’s visual field. It is subsequently identified and brought into the conscious experience. The object is maintained in the conscious experience during the time the segregating cue is present (Object Maintenance) and for a short period after the cue is removed (Object Persistence). Finally, it disappears from conscious awareness, though it may still affect future experience (e.g., it could prime related objects). Vision research has predominantly focused on just two of these four states – namely Object Identification (Grill-Spector, 2003) through the manipulation of various stimulus properties, and Object Dormancy by using a previously-viewed object as a prime.

Object Maintenance, the stage following Object Identification during which the segregating cues are still present, is essential in interactions with the surrounding environment.

Yet, this stage has been virtually ignored in the literature. Following the Object Maintenance stage is the Object Persistence stage, which has been studied in a series of recent neuropsychological experiments (Ferber, Humphrey & Vilis, 2003; 2005; Large, Aldcroft & Vilis, 2006). However, much remains to be elucidated in terms of how stimulus properties and segregating cue properties determine the duration of persistence.

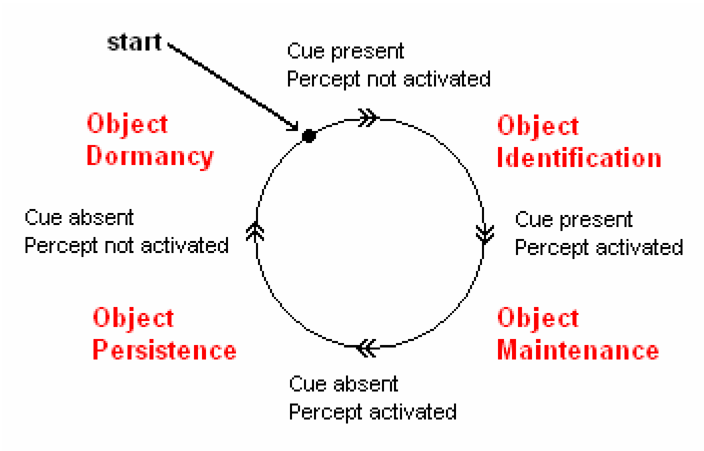


Figure 2 – The Object Cycle. Object perception begins when the object appears in an subject's visual field. It is subsequently identified, maintained in conscious experience during the time the segregating cue is present (Object Maintenance) and persists for a short period after the cue is removed (Object Persistence). Finally, it disappears from conscious awareness, though it may still affect future experiences (e.g., by serving to prime related objects).

1.2 Present Work

The present paper focuses on the joint effects of cue type, cue duration, cue strength and their effects on object identification, and persistence. We used color and motion cues which, notwithstanding significant interconnectivity between brain areas, are processed by pathways in the visual cortex that respond to one type of cue and not the other (Zeki et al, 1991; Goodale & Milner, 1992; Rolls & Deco, 2002). These investigations into the perceptual processes of object-background segregation and the ensuing conscious maintenance of the object as reflected in the context of object persistence attempt to elucidate some aspects of the development of the conscious percept of the object.

Our experiments involved measurements of both identification and persistence, which may prove useful in shedding light on the nature of the interaction of the cues at various stages in the object cycle. Thus, the present work refines and extends work by Large et al (2005) that compared the effect of these different cue types when segregating figure from ground. Large et al, along with studies by Ferber and colleagues, have all used fixed durations of the cued display, whereas the present work varied the duration of the cue after the object had been identified. This distinction is important, as the period before identification and the maintenance period after identification show different patterns of neural activity. Prior to the identification response, activation in the identification- and persistence-associated LOC rises quickly, falls slowly during the maintenance stage and rises again slightly with the onset of the persistence stage before falling sharply shortly afterwards (Kleinschmidt et al, 2002; Ferber et al, 2003, 2005). Such distinct patterns of activation and the arguably qualitative differences in processing between identification and maintenance suggest that each stage may affect persistence differently. Thus, we manipulated the time *before* identification (by manipulating the difficulty of identifying the object) and the time *after* identification (by manipulating the duration of the segregating cue following identification).

2 Experiment 1

To gain a better understanding of the development of the percept during object identification, maintenance and persistence, we varied the type of cue, and the duration of the cue during the maintenance stage immediately after identification (see Figure 3 for the timeline of a single trial). The cues that distinguish the object from the background were *color* (object and background were of a different color) *motion* (object and background moved in opposing directions) or *color and motion* combined. Cues were present from the onset of the display, they continued during the time the subject identified the object, and for a controlled period after identification. After the cue was removed, the shape either remained on the screen, (STOP condition) or disappeared, with only the background lines remaining (VANISH condition).

2.1 Design

A 2 (Display Condition: VANISH vs STOP) x 3 (Cue Type: color vs motion vs color and motion) $\times$ 2 (Cue Duration: 1s vs 5s) within subjects design was used.

2.2 Method

2.2.1 Stimuli

Sixteen objects (6 rectangle, 4 ovals, 6 triangles) were drawn on a computer using a program that ensured equal length line segments both within and across objects. Background lines were randomly oriented and placed and were of equal length (5 pixels) as the line segments making up the objects. These objects can be seen in Appendix A. Line segments making up the object were white. The background lines varied between cue condition (white or purple). These line segments appeared on a black screen.

In the *motion* condition, the shape rotated in the opposite direction to the background when the cue was present. The background lines were colored white – same as the object. There was no color change when the motion stopped. In the *color* condition, background lines were purple (analogous to the boldface cue seen in Figure 1) and both object and background lines moved together to prevent locally-based color adaptation producing a color aftereffect. When the motion stopped, the background lines turned white. In the *color and motion* condition, the object and background moved in opposite directions and the background lines were colored purple. As in the *color* condition, the background turned white when the motion stopped. All shapes were verified in a pilot study as not being identifiable in the absence of a cue.

2.2.2 Procedure

Twelve undergraduates who reported themselves as having normal or corrected-to-normal vision participated in Experiment 1. These subjects were recruited from a pool of students enrolled in undergraduate psychology courses and were given credit for their participation.

The subject was seated in front of a 17-inch computer screen. Each trial began with a 1 s fixation dot in the centre of the screen. This was followed by the presentation of the randomly oriented line segments (the background) along with the line segments making up the object. From the onset of the display to the time of cue removal, the object and background rotated clockwise and anti-clockwise, respectively, around the central fixation point between -15 degrees to +15 degrees from the upright orientation for a period of 2 s.

There were a total of 192 trials. A trial consisted of 2 parts. In the first part the subject was asked to identify the object via a key press. Three adjacent keys, (‘v’, ‘b’ and ‘n’) corresponding to the three types of shape, were used. After identification, a 1 or 5 second interval ensued, during which time the cue was still present. The cue was then removed, and the subject made a subjective judgment as to when the percept of the object disappeared, again by a key press. If the subject did not respond after 5 s, that time was noted and flagged as timed out**.** Trials were timed out in this manner to limit the duration of the experiment and thus the subject's fatigue. On STOP trials, the object remained on the screen while on VANISH trials the object was removed from the display after the motion had stopped. All conditions were randomly intermixed. Figure 3 illustrates the timeline of a single trial.

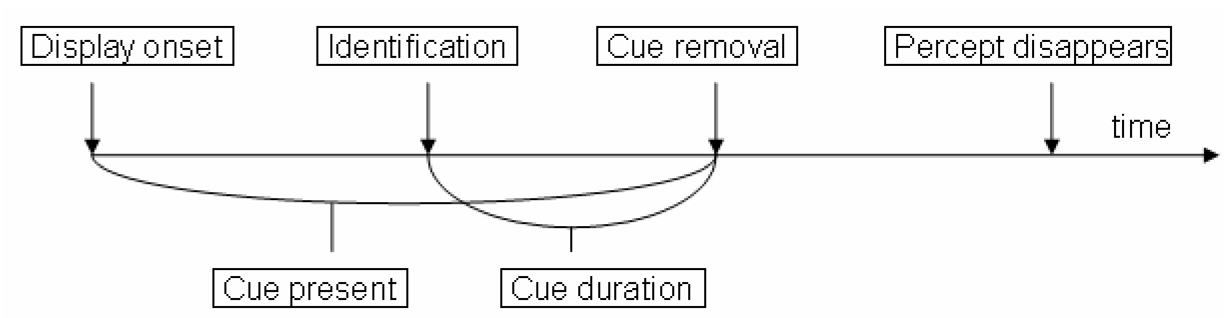


Figure 3 – Timeline of a single trial. A shape appears with the segregating cue present. After the shape is identified (by pressing one of 3 keys, each of which corresponds to one type of shape) the cue remains for some time period before being removed. Finally, the participant indicates (by key press) when the percept has disappeared from their conscious awareness.

2.3 Results

Errors in identifying the objects were low ($\bar{x}$ = 1.1%, sd = 1.0%) with no subject producing more than 3.0% errors. These errors, along with outliers (identification times more than 2.5 standard deviations from the subjects' means) and practice trials (first 10) were excluded from the analysis. Timed out trials (see below) were excluded from the analysis. The proportion of timed out trials was quite high for some subjects; those with more than one-third of such trials were excluded from further analysis (3 subjects' data was discarded in this way).

2.3.1 Timed out trials

Timed out trials represent trials with no response during 5 seconds of the persistence stage in the STOP condition (timed out trials rarely occurred in the VANISH condition). Conditions with longer RTs generally had a higher proportion of timed out trials, but a 2 x 3 x 2 repeated measures ANOVA in which the factors were display condition (VANISH vs STOP), cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*) yielded a main effect of display condition in which the higher proportion of timed out trials in the STOP condition over the VANISH condition was marginal, $F(1,8) = 3.84$, $p = .086$. The other main effects and all interactions were not significant (F's < 2). These data can be seen in Table 1.

Table 1. Proportion of timed out trials across conditions from Experiment 1

Cue duration	Short duration (1 s)			Long duration (5 s)		
Cue type	Color	Motion	Color and Motion	Color	Motion	Color and Motion
Stop	.15	.21	.16	.15	.13	.13
Vanish	.04	.04	.04	.02	.01	.02

2.3.2 Identification time

A one-way ANOVA on levels of cue type (*color* vs *motion* vs *color and motion*) for the identification time data yielded a significant effect, $F(2,16) = 16.2$, $p < .001$. Multiple comparisons showed that identification times for the *motion* cue were longer than for both the *color* cue, $t(8) = 4.06$, $p < .005$, and the *color and motion* cue conditions, $t(8) = 4.49$, $p < .005$, with no difference between the *color* cue and the *color and motion* cue conditions ($t < 1.5$). These data can be seen in Table 2.

Table 2. Identification times (ms) as a function of cue type from Experiment 1

Color	Motion	Color and Motion
1236	1573	1276

2.3.3 Persistence

As noted in the introduction, our preferred measure of persistence is the difference between the STOP and VANISH conditions. This measure was also used by Risko et al (2006) and Emrich et al (2008). A 3 x 2 repeated measures ANOVA was conducted on the persistence scores in which the factors were cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*). The main effect of cue type was significant, $F(2,16) = 6.18$, $p < .01$. The main effect of cue duration and the interaction between cue type and cue duration were not significant (F's < 3). Multiple comparisons showed that persistence scores for the *motion* cue were longer than for both the *color* cue, $t(8) = 2.70$, $p < .05$, and the *color and motion* cue, $t(8) = 2.67$, $p < .05$, with no difference between the *color* cue and *color and motion* cue conditions ($t < 1$).

A second measure of persistence is the RTs from the STOP condition. This measure was used by Large et al (2005) and Ferber and Emrich (2007). A 3 x 2 repeated measures ANOVA was conducted on the persistence times in which the factors were cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*) yielded a main effect of cue type, $F(2,16) = 16.0$, $p < .001$. The main effect of cue duration and the interaction between cue type and cue duration were not significant (F's < 1). Multiple comparisons showed that persistence times were longer for the *motion* cue than for both the *color* cue, $t(8) = 3.66$, $p < .01$, and the *color and motion* cue, $t(8) = 5.48$, $p < .001$, with no difference between the *color* cue and *color and motion* cue conditions ($t < 1.5$). These data can be seen in Table 3.

Table 3. RTs (ms) in STOP and VANISH condition and persistence scores from Experiment 1

Cue duration	Short duration (1 s)			Long duration (5 s)		
Cue type	Color	Motion	Color and Motion	Color	Motion	Color and Motion
Stop	1468	1777	1452	1430	1805	1312
Vanish	1120	1304	1030	1094	986	985
Persistence	**348**	**473**	**422**	**336**	**819**	**327**

2.3.4 Does the VANISH condition produce anomalous results?

A 2 x 2 repeated measures ANOVA of RTs from the VANISH condition in which the factors were cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*) yielded a main effect of cue type, $F(2.16) = 4.68$, $p < .05$, a marginal main effect of cue duration, $F(1.8) = 4.94$, $p = .057$, and a significant interaction between cue type and cue duration, $F(2,16) = 4.20$, $p < .05$. These effects are inconsistent with previous studies, which yielded no significant effects of any of the manipulated factors in the VANISH condition. These results are thus anomalous and undermine use of a persistence measure based on the difference between STOP and VANISH conditions. Fortunately, these effects are only seen in Experiment 1.

2.4 Discussion

As we noted in the introduction, persistence can be measured in two different ways. One is the difference between the STOP and VANISH conditions. In Experiment 1, persistence differed significantly with cue type; there was longer persistence in the *motion* condition than in both the *color* and *color and motion* conditions. The second measure of persistence is the RTs from the STOP condition. The results from comparing differences in these times show longer persistence in the *motion* condition than the *color* and *color and motion* conditions; there was no difference between *short (1s)* and *long (5s)* cue durations.

Large and colleagues used RTs from the STOP condition as a measure of persistence. These authors found no difference in persistence times between *color* and *motion* cues. Data from 9 subjects was analyzed here, compared with 7 by Large and colleagues. We therefore sought to replicate Experiment 1 so as to verify the differences in persistence with cue type, with one modification to address a possible confound described below.

The anomaly of the increased VANISH RTs in the *1s* duration *motion* condition relative to all other conditions may be an artifact of the other two conditions – the *color* and *color and motion* conditions. More specifically, the color change that occurs after the removal of the cue is abrupt and involves the entire background changing color. Because the background occupies a much larger proportion of the display than the object, the change may cause a shift in attention away from the object. This shift, compounded by the short duration of the cue after identification (1s) may result in a failure to keep a similar grasp on the vanished object in the *color* cue and *color and motion* cue conditions as in the *motion* cue condition, and hence the shorter RTs.

3 Experiment 2

In Experiment 2, we rectify the potential problem noted above by having the *object* change color instead of the background. This experiment differs from the study by Large et al (2005) but may be more natural (e.g., like an object moving from the sun to the shade – an abrupt change to the object while the background remains unchanged).

The design was the same as in Experiment 1 in which the factors were display condition (VANISH vs STOP), cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*).

3.1 Method

3.1.1 Stimuli

The difference between Experiment 1 and 2 was that the background in Experiment 2 was always colored purple. With the cue present, the object was also colored purple in the *motion* condition, but was white in the *color* and *color and motion* conditions and turned purple on STOP trials after the cue was removed.

3.1.2 Procedure

23 subjects with normal or corrected-to-normal vision participated in Experiment 2. There were 192 trials and all condition were randomly intermixed.

3.2 Results

Average percentage error rate was again quite low ($\bar{x}$ = 1.9%, sd = 2.3%). One subject had 10% errors, which was more than 2.5 standard deviations from the mean. Two other subjects had more than one-third of trials flagged as timed out. These three subjects were therefore excluded from further analysis, leaving 20 subjects. As before, timed out trials (see below) were excluded from the analysis. Trials that yielded incorrect identification as well as outliers (identification time greater or lesser than 2.5 SD from the mean) were removed from the response time analysis.

3.2.1 Timed out trials

The proportion of trials flagged as timed out followed the trend in the RTs to STOP trials as well as persistence scores more closely than in Experiment 1 (see Table 1 vs Table 4). A 2 x 3 x 2 repeated measures ANOVA was conducted on the proportion of trials flagged as timed out in which the factors were display condition (VANISH vs STOP), cue type (*color* vs *motion* vs *color and motion*) and cue duration (1s vs 5s). The main effect of display condition in which more timed out trials in the STOP condition than in the VANISH condition, was significant, $F(1,19) = 13.9$, $p < .01$, as was the main effect of cue duration in which more timed out trials in the short duration (1s) condition than in the long duration (5s) condition, $F(1,19) = 4.67$, $p < .05$. The main effect of cue type was marginally significant with multiple comparisons yielding a marginal difference between the *color* and *motion* conditions, $t(19) = 1.98$, $p = .062$, and no significant difference between the *color and motion* condition and either the *motion* or the *color* condition (t's < 1.5). All other main effects and interactions were not significant (F's < 1.5). These data are shown in Table 4.[1]

Table 4. Proportion of timed out trials across conditions from Experiment 2

Cue duration	Short duration (1 s)			Long duration (5 s)		
Cue type	Color	Motion	Color and Motion	Color	Motion	Color and Motion
Stop	.16	.23	.20	.14	.19	.13
Vanish	.03	.06	.04	.01	.03	.03

3.2.2 Identification time

A one-way ANOVA on levels of cue type (*color* vs *motion* vs *color and motion*) for the identification time data yielded a significant effect, F(2,38) = 58.9, p < .001. Multiple comparisons showed that identification times for the *motion* cue were longer than for both the *color* cue, t(19) = 8.67, p < .001, and the *color and motion* cue conditions, t(19) = 8.27, p < .001, with no difference between the *color* cue and the *color and motion* cue conditions (t < 1). These data can be seen in Table 5.

Table 5. Identification times (ms) as a function of cue type from Experiment 2

Color	Motion	Color and Motion
1269	1670	1297

3.2.3 Persistence

As noted earlier, our preferred measure of persistence is the difference between the STOP and VANISH conditions. A 3 x 2 repeated measures ANOVA was conducted on these persistence scores in which the factors were cue type (*color* vs *motion* vs *color and motion* x cue) x cue duration (*1s* vs *5s*). The main effect of cue type was significant, F(2,38) = 14.9, p < .001. The main effect of cue duration and the interaction between cue type and cue duration were not significant (F's < 1). Multiple comparisons showed the *motion* condition yielded longer times than in the *color*, t(19) = 5.09, p < .001, and *color and motion* conditions, t(19) = 4.83, p < .001, while the difference between the *color* and *color and motion* conditions was not significant (t < 1).

A second measure of persistence is the RTs from the STOP condition. A 3 x 2 repeated measures ANOVA was therefore conducted on the persistence times in which the factors were cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*). The main effect of cue type was significant, $F(2,38) = 14.8$, $p < .001$. The main effect of cue duration was also significant, with the *short duration (1s)* condition yielding longer RTs than the *long duration (5s)* condition, $F(1,19) = 4.47$, $p < .05$. The interaction between cue type and cue duration was not significant ($F < 1$). Multiple comparisons found RTs in the *motion* condition were longer than the *color*, $t(19) = 4.62$, $p < .001$, and *color and motion* conditions, $t(19) = 5.31$, $p < .001$. The difference between the *color* condition and the *color and motion* condition was not significant ($t < 1$).

3.2.4 The VANISH condition

A 3 x 2 repeated measures ANOVA on the RTs from the VANISH condition in which the factors were cue type (*color* vs *motion* vs *color and motion*) and cue duration (*1s* vs *5s*) yielded a main effect of cue duration, with the *short duration (1s)* condition yielding longer RTs than the *long duration (5s)* condition, $F(1,19) = 12.6$, $p < .005$. The interaction between cue type and cue duration was not significant ($F < 1$).

The parallel difference in the cue duration in both STOP and VANISH conditions accounts for the lack of a main effect of cue duration in persistence scores, which were calculated using the difference score. This score eliminated elements of the judgment and motor response which affected RTs from both the STOP and the VANISH conditions. These data can be seen in Table 6.

Table 6. RTs (ms) in STOP and VANISH condition and persistence scores from Experiment 2

Cue duration	Short duration (1 s)			Long duration (5 s)		
Cue type	Color	Motion	Color and Motion	Color	Motion	Color and Motion
Stop	1531	1975	1596	1503	1779	1455
Vanish	1342	1320	1233	1184	1139	1152
Persistence	**189**	**655**	**363**	**319**	**640**	**303**

3.3 Discussion

Identification times and RTs in the STOP condition show the same pattern in Experiment 2 as they did in Experiment 1, with *motion* times being longer than the *color* and *color and motion* times. Persistence scores in Experiments 1 and 2 were also similar with the exception of the one anomaly in the 1s cue duration VANISH trials. The VANISH condition in Experiment 2 was more uniform across cue conditions than in Experiment 1. This result is standard in studies of object persistence (Ferber & Emrich, 2007; Large et al, 2005) and is expected in the VANISH condition due to the absence of the object in the display to facilitate persistence. In this condition, the main component of the response are visual persistence (Coltheart, 1980), the subjective judgment and the motor response. With different cue types, these factors remain largely unaffected. However, prolonged exposure after identification (i.e., the *5s* duration condition) allows the subjects to familiarize themselves with the object, which likely accelerates the decision process resulting in shortened RTs across the board. RTs in the STOP condition followed the same pattern with respect to cue duration, further supporting this hypothesis.

Having arbitrarily chosen cue strength, (speed of motion, color contrast against background) we need to ask whether the increased persistence in the motion cue condition is attributable to the cue itself or whether other factors, such as the total effort (indexed by the identification time) involved in identifying the object, is also affecting persistence. The correlation between identification time and persistence (see Figure 4) is not significant, $r(18) = -.11$, $p = .64$, though the *motion* cue condition had longer identification times and persistence scores than both the *color* cue and *color and motion* cue conditions. Ferber and Emrich (2007) found positive but not significant correlations between identification times and persistence scores in their experiments.

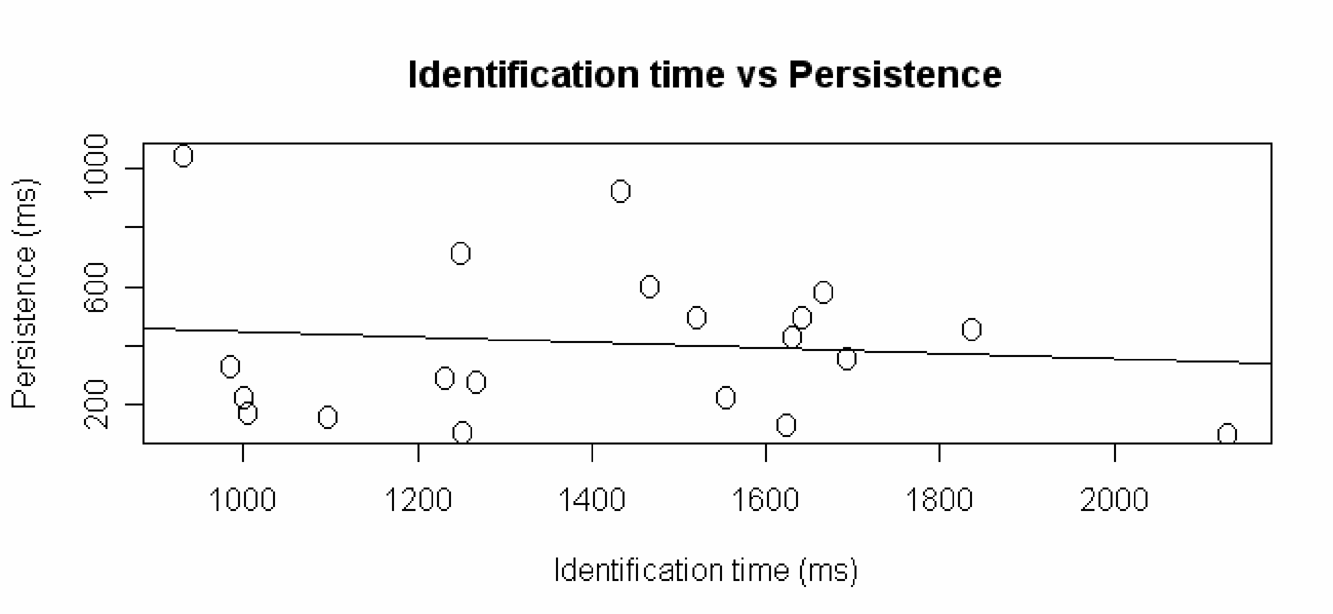


Figure 4 – Simple correlation between identification times and persistence scores from Experiment 2

4 Experiment 3

In Experiment 3, we varied the intensity of the cue used for figure-ground segregation. For the *color* condition this meant that object brightness was manipulated, and for the *motion* condition the speeds of the object and background was manipulated.

Cue duration was not varied in this experiment because both prior experiments showed no effect of cue duration on persistence scores. We therefore used the 1s cue duration.

4.1 Design

A 2 (Display Condition: VANISH vs STOP) $\times$ 2 (Cue Type: color vs motion) $\times$ 2 (Cue Intensity: weak vs strong) within subjects design was used.

4.2 Method

4.2.1 Stimuli

The stimuli consisted of the same objects and backgrounds as in Experiments 1 and 2. In varying the contrast, the object color was made 20% dimmer relative to the background. Speeds in the motion condition were 70% and 200% of the speed in Experiments 1 and 2 so as to provide a large range over which to verify the robustness of any potential difference in persistence.

4.2.2 Procedure

33 subjects with normal or corrected-to-normal vision participated in the Experiment 3.

Subjects were presented with the same display sequences and randomly-ordered condition combinations as in the previous experiments. There were a total of 128 trials.

4.3 Results

Percentage errors were slightly higher than in previous experiments ($\bar{x}$ = 2.8%, sd = 3.5%) due to the higher incidence in the low contrast condition ($\bar{x}$ = 4.9%). Trials that yielded incorrect identification as well as outliers (identification time greater or less than 2.5 SD from the mean) were removed from the RT analysis. Timed out trials were also excluded.

We again had the problem of subjects with many timed out trials, thus producing noisy data or empty cells. These trials were not analyzed separately in this experiment.[1] Six such subjects were identified. Excluding these subjects, and one due to a large number of identification errors (>10%) left 26 subjects led to decreased RTs in the VANISH condition and identification times slightly but did not change the significance of results reported below.

4.3.1 Identification time

A 2 x 2 repeated measures ANOVA was conducted on the identification times in which the factors were cue type (*color* vs *motion*) and cue strength (*strong* vs *weak*) yielded main effects of cue strength, $F(1,25) = 36.1$, $p < .001$, and cue type, $F(1,25) = 70.1$, $p < .001$, with the stronger cue yielding shorter identification times than the weaker cue and the color cue yielding shorter identification times than the motion cue. These data appear in Table 7.

Table 7. Identification times (ms) as a function of cue type and cue strength from Experiment 3

Cue type	Color cue		Motion cue	
Cue strength	Strong (high contrast)	Weak (low contrast)	Strong (fast motion)	Weak (slow motion)
Identification time	1291	1498	1415	2088

4.3.2 Persistence

As noted in the introduction, our preferred measure of persistence is the difference between the STOP and VANISH conditions. A 2 x 2 repeated measures ANOVA was conducted on the persistence scores with the factors being cue type (*color* vs *motion*) and cue strength (*weak* vs *strong*) yielded a main effect of cue type, $F(1,25) = 4.58$, $p < .05$, with the *motion* cue condition yielding longer persistence scores than the *color* cue condition. The effect of cue strength and interaction between cue type and cue strength were not significant.

A second measure of persistence is the RTs from the STOP condition. A 2 x 2 repeated measures ANOVA was conducted on the RTs from the STOP condition in which the factors were cue type (*color* vs *motion*) and cue strength (*weak* vs *strong)* found a main effect of cue type, $F(1,25) = 5.46$, $p < .05$, with increased RTs in the *motion* cue condition than the *color* cue condition, The effect of cue strength and interaction between cue type and cue strength were not significant. Data is shown in Table 8.

Table 8. RTs (ms) in STOP and VANISH condition and persistence scores from Experiment 3

Cue type	Color cue		Motion cue	
Cue strength	Strong (high contrast)	Weak (low contrast)	Strong (fast motion)	Weak (slow motion)
Stop	1930	1985	2150	2129
Vanish	1279	1345	1331	1332
Persistence	**650**	**639**	**818**	**798**

4.4 Discussion

Experiment 3 shows that increasing the strength of the cue is not associated with a change in persistence scores, despite decreasing identification times. These results are particularly interesting given the results of previous studies (Emrich et al, 2008) and the effect of cue type where both identification time and persistence are longer in the *motion* cue condition than in the *color*, and *color and motion* cue conditions. Emrich and colleagues found that decreasing the lengths of the fragmented lines (while keeping percent coverage constant) and the inclusion of non-accidental properties (e.g., corners) in the display, decreased identification times but also decreased persistence scores. These authors found no significant correlation between identification time and persistence, and attributed the parallel increase in identification times and persistence scores to more elaborate processing being required in more difficult to segregate displays, resulting in more robust access to object-related information required for persistence.

There is, however, one major difference between the present experiment and the study by Emrich et al (2008). The factors they manipulated influenced the displays in both identification and maintenance stages as well as the persistence stage. In contrast, our cue manipulations did not affect the display after removal of the segregating cue, meaning the displays were identical during the persistence stage within each display condition. Furthermore, we see that the increased time to identify the object through the use of weaker cues did not affect persistence. It seems clear from these results that subjects did not use different strategies during object identification and maintenance with weak and strong cues, as it would have likely affected the percept and hence persistence. This goes well with results from Experiments 1 and 2 where we found that cue duration did not affect persistence. With no difference in object properties between cue duration conditions, subjects engaged in elaborative processing to a similar degree on the visual properties of the object, regardless of how much time they had after identifying the object. Therefore, increased persistence due to elaborative processes (Emrich et al, 2008) must be related to specific properties of the object that stimulate these processes, and not due to differences in duration of processing during the identification or maintenance stages.

One potential concern is the 300-400 ms increase in persistence scores in Experiment 3 as compared to Experiment 2 despite similar conditions. Only one previous paper (Ferber & Emrich, 2007) on object persistence had very similar conditions repeated between experiments. In that paper, Experiments 2, 3 and 4 yielded persistence scores that ranged from 400 ms to 1800 ms for these conditions. The issue of between experiment differences in persistence scores was not addressed in their paper. We are troubled by these large differences across experiments, but we note the consistent differences between the motion and color conditions within each experiment.

5 Experiment 4

In Experiment 2, combining the two cues in the *color and motion* cue condition produced statistically equivalent identification times and persistence scores as in the *color* condition. It is not surprising that the more salient color cue determines identification time in the *color and motion* condition (see Regan & Beverley, 1984), but the motion cue information is capable of being fully processed by the persistence stage (as inferred from *motion* cue condition identification times being on average 300 ms, while the cue duration is 1000 ms) and yet the persistence score again resembles that of the *color* condition. The information from the motion and color cues in the combined condition could be interacting in one of two ways. The first is that the stronger cue (i.e., the one that is processed more quickly to the level of object identification) is attended to and the information from the weaker cue is ignored. This would result in a combined cue condition that closely resembles the single, stronger cue condition in terms of identification times and persistence scores, similar to Experiment 2.

Alternatively, both motion and color information may be used in the identification of the object with the relative strength of the cue determining to what extent the information supports the identification process. In this more complicated scenario, it is not initially apparent whether the cues act independently to support the percept in LOC or they interact. The former would yield persistence scores that resemble those of the *motion* cue condition, which has been shown to consistently yield higher scores irrespective of cue strength (in a single cue setup). The latter may yield higher or lower persistence scores depending on whether the weaker color cue improves the quality of the percept through the extra information it carries, or a form of averaging between *motion* cue and *color* cue condition persistence scores due to the division of attention between the two cues.

In Experiment 4, we varied the intensity of the cues used for figure-ground segregation in a *color and motion* condition. Similarly to Experiment 3, object brightness was manipulated in the *color* condition and object speed was manipulated for the *motion* condition. In addition to three combined cue conditions (slow motion + high contrast, medium speed + medium contrast, fast motion + low contrast), single cue conditions (pure color and pure motion cues) were included to provide a baseline and to verify consistency with results from previous experiments.

5.1 Design

A 2 (Display Condition: VANISH – STOP) $\times$ 5 (Cue Conditions: 3 *color and motion* of varying intensities + 1 *color* + 1 *motion*) within subjects design was used.

5.2 Method

5.2.1 Stimuli

The stimuli included all the objects and backgrounds as in the previous experiments but addad an oval to the set and a rectangle and triangle were removed to bring the total to 5 for each type of shape. This was done to equalize the probabilities of each shape for the quicker, identification-only task in the experiment that followed the main part (see Procedure). Data for the identification-only task appear in Table 9.

Table 9. RTs (ms) for identification-only block from Experiment 4

Cue type	Color contrast			Motion		
Cue strength	Low	Medium	High	Slow	Medium	Fast
Response time	2142	889	786	2570	1466	1035

The strengths of the motion and color cues were determined in a pilot study in the following fashion. Various motion speeds and contrasts were used in a single cue, shape identification study, and mean times for each speed and contrast were calculated. For the *slow motion + high contrast* condition the highest contrast was coupled with a motion speed where subjects in the pilot study identified the motion-defined shape on average 1s slower than the color-defined shape. Similarly, for the *fast motion + low contrast* condition, a contrast with average identification time closest to the slow motion was coupled with a motion speed where subjects in the pilot study identified the motion-defined shape on average 1s faster than the color-defined shape. The 1s difference corresponds to the 1s duration after identifying the shape after which the cue is present – an attempt to limit the amount of processing of the weaker cue. The *medium speed + medium contrast* condition used intermediate values where both cues had time to be processed before the onset of the persistence stage, when the cue was removed.

5.2.2 Procedure

21 subjects with normal or corrected-to-normal vision participated in the Experiment 4.

Subjects were presented with the same display sequences and randomly-ordered condition combinations as in the previous experiments. The persistence score was again indexed by the difference between the VANISH and STOP conditions. There were a total of 150 trials.

In addition to the conditions mentioned above, the experiment included a series of identification-only trials in which the same 15 shapes were cued with either a color or motion cue. The same 3 cue strengths were used as in combined color and motion cues from the main experiment. This identification-only task was run to verify that subjects were significantly slower in processing the weaker cues as compared to the stronger cues.

5.3 Results

The percentage of errors was low ($\bar{x}$ = 0.9%, sd = 1.3%). Of the 22 subjects, five had small (i.e., < 500ms) differences between either low and high contrast or slow and fast motion in the identification-only block of trials. Another subject had a high percentage of timed out trials that resulted in empty cells after removing these trials. These six subjects were excluded leaving 16 subjects. Trials that yielded incorrect identification as well as outliers (identification time greater or less than 2.5 SD from the mean) were removed from the response time analysis. Timed out trials were also excluded.

5.3.1 Identification time

A 2 x 2 repeated measures ANOVA in which the factors were cue type (*color* vs *motion*) and the presence of second cue (*slow motion* vs *low contrast*, respectively) found a main effect of cue type, $F(1,15) = 8.85$, $p < .01$, and a main effect of the presence of a second cue, $F(1,15) = 26.9$, $p < .001$. The interaction between cue type and the presence of a second cue was marginal, $F(1,15) = 3.45$, $p = .083$. The *medium motion + medium contrast* condition did not differ from the other combined cue conditions in terms of identification times ($t < 1.5$). These data can be seen in Table 10.

Table 10. Identification times (ms) as a function of cue type from Experiment 4

Cue type	fast motion	fast motion, low contrast	medium motion, medium contrast	slow motion, high contrast	high contrast
Identification time	1527	1302	1236	1193	1280

5.3.2 Persistence

As noted in the introduction, our preferred measure of persistence is the difference between the STOP and VANISH conditions. A 2 x 2 repeated measures ANOVA was conducted on the persistence scores in which the factors were cue type (*color* vs *motion*) and the presence of second cue (*slow motion* vs *low contrast*, respectively) yielded a main effect of cue type, $F(1,15) = 19.1$, $p < .001$. The effect of the presence of a second cue and the interaction between cue type and the presence of a second cue were not significant ($F < 1.5$). Multiple comparisons showed that adding a low contrast cue to the motion cue yielded a significant decrease in persistence, $t(15) = 5.00$, $p < .001$, while adding a slow motion cue to the color cue did not yield a significant effect, $t(15) = 1.72$, $p = .11$.

Another measure of persistence is the RTs from the STOP condition. A 2 x 2 repeated measures ANOVA was conducted on the persistence scores in which the factors were cue type (*color* vs *motion*) and the presence of second cue (*slow motion* vs *low contrast*, respectively) found a main effect of cue type, $F(1,15) = 13.2$, $p < .01$. The effect of the presence of a second cue and the interaction between cue type and the presence of a second cue were not significant ($F < 2$). The *medium speed + medium contrast* condition did not vary significantly with the other two combined cue conditions (*fast motion + low contrast*, *slow motion + high contrast*), $t < 1.5$. However, identification times and persistence scores were intermediate to the two other conditions.

All these persistence scores can be seen in Table 11.

Table 11. RTs (ms) in STOP and VANISH condition and persistence scores from Experiment 4

Cue type	fast motion	fast motion, low contrast	medium motion, medium contrast	slow motion, high contrast	high contrast
Stop	2126	2072	1922	1776	1819
Vanish	1223	1296	1370	1312	1345
Persistence	**903**	**776**	**552**	**464**	**474**

5.4 Discussion

Differences between the single cue fast motion and the single cue high contrast conditions replicated results from Experiments 1, 2 and 3 in this paper. When viewing a combination of motion and color cues, subjects were affected by the salient color cue, even in the case when it is very weak, as seen in the significant decrease in identification time with the addition of the low contrast cue. What is intriguing is that the later persistence stage shows no significant decrease. This is counterintuitive as the weaker color cue would be expected to affect the latter stage, after a more significant amount of color information has been processed. Instead, what seems to happen is that the immediately present color aides in finding the object, witnessed in the decreased identification times, but is largely neglected as a means of maintaining the percept of the object due to the presence of a stronger motion cue.

Within the combined cue conditions, as the strength of the motion cue decreases (i.e., motion speed decreases) and the strength of the color cue increases (i.e., contrast increases), identification times decrease steadily. This may inadvertently result from a slightly stronger color cue as seen in the shorter identification times in the initial identification-only task (see Table 9) as we know that identification times vary with cue strength (see Experiment 3 and Regan & Beverley, 1984).

A similar decrease can be seen in the persistence scores. Although the difference between the *medium motion + medium contrast* condition and the other combined cue condition was not significant, it is harder to detect because of the smaller differences between the conditions, and does appear to be an intermediate value. Previous experiments had shown that in single cue conditions, the more robust motion cue leads to more persistence than the color cue, independently of the strength of the cue. However, when the cues are combined, the persistence scores depend on the relative strengths of the cues. Motion information is being used in the *medium motion + medium contrast* condition, taking from the increase in persistence scores over the *slow motion + high contrast* condition. Because the motion cue's salience is close to the color cue's salience (as seen by similar identification times in the identification-only block data in Table 9), the motion cue may dominate on a significant proportion of trials, resulting in the observed increase in persistence scores. The other two combined cue conditions produced complete or nearly-complete dominance of the stronger cue, thereby suppressing of weaker information from the second cue, and yielding persistence scores that were statistically equivalent to the corresponding single cue conditions. Thus, during the initial identification stage both cues compete for dominance, with the likelihood of one winning being determined by its strength relative to the other cue. Information from the weaker cue is suppressed by processes modulating neural activation, whether this occurs by divisive normalization across a population of neurons, or direct inhibition of the neurons carrying less relevant information.

6 General Discussion

The results from the present experiments support the hypothesis that segregation by color and motion cues involves different perceptual processes, resulting in differences in identification times and persistence scores. Increases in cue strength resulted in faster identification. Furthermore, the visual pathways that support object identification also support persistence, and they compete for limited resources in the bottom-up maintenance of the conscious percept. A more detailed account of our hypothesis is provided after several further remarks.

An important concern to address first is the discrepancy between our data and those of Large, Aldcroft and Vilis (2005) where the authors failed to find a difference between the color and motion cue conditions in the STOP condition. Our first experiment was an exact replication of their experiment, except for the identification stage, the inversion of colors, and the duration the cue was present. As mentioned earlier, our initial pilot study that used identical colors had produced larger persistence times in the motion condition. We have ruled out the potential of complications due to timed out trials[1]. In Experiment 3, where we varied cue strength, persistence scores for the color and motion conditions were significantly different and persistence did not vary across cue strength. Thus, we not only replicated the longer motion persistence scores, but also showed that the difference is robust across a range of cue strengths.

One potential explanation is that Large and colleagues experiments lack the statistical power to detect the difference. Four of the seven subjects in their experiment had longer persistence in the motion cue condition than the color cue condition and the average persistence was slightly greater for the motion condition. Our results consistently yield increased RTs in the *motion* cue condition over the *color* cue condition, and we have tested many more subjects.

The cue strength manipulation in Experiment 3 discounts the possibility that the colors we chose for the object and background may be the reason that our results do not match those of Large et al (2005). The manipulation also tells us something about the development of the representation of the conscious percept. Unlike previous studies (Ferber & Emrich, 2007; Risko et al, 2006; Emrich et al, 2008) that varied objects between conditions, our cue type, cue strength, and cue duration manipulations were used on the same set of objects. Moreover, the objects repeated across conditions were the same in the identification, maintenance and persistence stages. Conversely, with different displays, results from the aforementioned studies may be affected by bottom-up processes specific to processing the visual form of the object during the persistence stage. For example, when examining the effect of non-accidental properties Emrich et al's (2008) proposed that elaborative processes may recruit higher brain areas (Doniger et al, 2000) but such mechanisms do not take into account different bottom-up processing between conditions.

The results from the present set of experiments support the hypothesis that the development of the conscious percept does not change when varying factors independent of object-specific qualities for a given visual processing stream (instantiated here by the color and motion cue conditions). Following identification, the internal percept is robust, resists deterioration through time and is unaffected by reduced cue intensity that influenced processing prior to identification. Interestingly, this independence between pre- and post-identification behavior of the percept is also seen in Experiment 4, with a shorter identification time but the same persistence score when adding a weak contrast cue to the motion-defined display. Before the object is identified, various potentially irrelevant bits of information are processed in parallel while the representation of the object is being activated. This suggests that the weaker color information that is contributing to the identification of the object is being fed through to object-sensitive areas of the brain (such as LOC). However, because of limited resources, the weaker information not essential to the maintenance of the percept is suppressed after identification. This sort of competition between weaker and stronger information is described in a computational model by Berzanskaya, Grossberg and Mingolla (2007).

Past research on color and motion processing has shown that different visual pathways in the brain process both types of visual cues (Zeki et al, 1991, Goodale & Milner, 1992; Rolls & Deco, 2002). The ventral pathway is largely implicated in color and form processing and follows V1 to the thin and pale stripes in V2 and on to V4, which is particularly sensitive to color (Zeki, 1993). The dorsal pathway follows routes directly to middle temporal areas (MT) or through V2 thick stripes, the former of which is mainly responsible for motion processing. (Rolls & Deco, 2002) The results of the present studies highlight the differences in processing between the two visual pathways. Effect of cue type and cue strength differences in identification time and persistence support our hypothesis that all available information is used in object identification while the dominant cue supports the maintenance and persistence of the object.

Footnotes

[1] In Experiment 2, subjects (total 20) with less (8) than and more (12) than 2% of trials timed out were analyzed separately. Results for both groups were consistent with those of the complete set of subjects outlined previously. Thus, timed out trials do not seem to be distorting the data.

To check whether timed out trials were distorting any of the effects we noted, the 8 subjects with fewer than 2% timed out trials (3 or less) and the remaining subjects were analyzed separately. All results for Experiment 2 were significant for both groups of subjects with the exception of the effect of cue duration in the STOP condition for subjects with more than 2% timed out trials, which was marginally significant, $F(1,11) = 3.2$, $p = .10$. Thus, the group of subjects with more timed out trials were simply slower with no qualitative difference in their behavior.

The 5s time out barrier used was quite a bit shorter than previous studies. Ferber et al (2003) and Large et al (2005) both allocated 12s before the time out occurred, though their longer time was related to the fMRI scan taking place. Ferber and Emrich (2007) used an 8s time out period. It thus seems likely that they had recorded more of the true, longer RTs of the subjects, whereas we have dealt with these as timed out trials. We have shown, by examining subjects with a similar proportion of timed out trials as those previous studies, that this does not affect the validity of our results.

References

Berzanskaya, J., Grossberg S.,& Mingolla, E. (2007). Laminar cortical dynamics of visual form and motion interactions during coherent object motion perception. *Spatial Vision, 20(4),* 337-95.

Doniger, G. M., Foxe, J. J., Murray, M. M., Higgins, B. A., Snodgrass, J. G., Schroeder, C. E., et al. (2000). Activation time course of ventral visual stream object-recognition areas: high density electrical mapping of perceptual closure processes. *Journal of Cognitive Neuroscience, 12,* 615–621.

Emrich, S.M., Ruppel, J.D. and Ferber, S. (2008). The role of elaboration in the persistence of awareness for degraded objects. *Consciousness and Cognition, 17(1),* 319-329.

Ferber, S, & Emrich, S. M. (2007). Maintaining the ties that bind: The role of an intermediate visual memory store in the persistence of awareness. *Cognitive Neuropsychology, 24(2),* 187-210.

Ferber, S., Humphrey, G. K., & Vilis, T. (2003). The lateral occipital complex subserves the perceptual persistence of motion-defined groupings. *Cerebral Cortex, 13,* 716–721.

Ferber, S., Humphrey, G. K., & Vilis, T. (2005). Segregation and persistence of form in the lateral occipital complex. *Neuropsychologia, 43,* 41–45.

Goodale MA, Milner AD. 1992. Separate visual pathways for perception and action. *Trends in Neurosciences, 15,* 20–25.

Grill-Spector, K. (2003). The neural basis of object perception. *Current Opinion in Neurobiology, 13,* 159–166.

Grill-Spector, K., Kushnir, T., Edelman, S., Itzchar, Y., & Malach, R. (1998). Cue-invariant activation in object-related areas of the human occipital lobe. *Neuron, 21,* 191-202.

Gulyas, B., Heywood, C. A., Popplewell, D. A., Roland, P. E., & Cowey, A. (1994). Visual form discrimination from color or motion cues: Functional anatomy by positron emission tomography. *Proceedings of the National Academy of Sciences of the United States of America, 91*, 9965-9996.

James, T.W., Humphrey, G,K., Gati, J.S., Menon, R.S., & Goodale, M.A. (2000). The effects of visual object priming on brain activation before and after recognition. *Current Biology, 10,* 1017–1024.

Kleinschmidt, A., Buchel, C., Hutton, C., Friston, K. J., & Frackowiak, R. S. J. (2002). The neural structures expressing perceptual hysteresis in visual letter recognition. *Neuron, 34,* 659–666.

Large, M. E., Aldcroft, A., & Vilis, T. (2005). Perceptual continuity and the emergence of perceptual `persistence in the ventral visual pathway. *Journal of Neurophysiology, 93,* 3453–3462.

Lerner, Y., Hendler, T., Ben-Bashat, D., Harel, M., & Malach, R. (2001). A hierarchical axis of object processing stages in the human visual cortex. *Cerebral Cortex, 11(4),* 287–297.

Mumford, D. (1992). On the computational architecture of the neo-cortex: II. The role of the cortico-cortical loops. *Biological Cybernetics, 66*, 241–251.

Murray, S.O., Schrater, P. and Kersten, D. (2004) Perceptual grouping and the interaction between visual cortical areas. *Neural Networks. 17,* 695-705.

Peuskens, H., Claeys, K.G., Todd, J.T., Norman, J.F., Van Hecke, P. & Orban, G.A.. (2004) Attention to 3-D shape, 3-D motion, and texture in 3-D structure from motion displays. *Journal of Cognitive Neuroscience, 16(4),* 665-682.

Posner, M.I. (1978) *Chronometric Explorations of Mind.* Hillsdale, NJ: Lawrence Erlbaum.

Risko, E. F., Dixon, M. J., Besner, D., & Ferber, S. (2006). The ties that keep us bound: Top-down influences on the persistence of shape-from-motion. *Consciousness and Cognition, 15,* 475–483.

Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects [see comments]. *Nature Neuroscience, 2(1),* 79–87.

Regan, D. and Beverley, K.I. (1984). Figure-ground segregation by motion contrast and luminance contrast. *Journal of the Optical Society of America, 1(5),* 433-442.

Regan, D. (2000). *Human perception of objects.* Sunderland, MA: Sinauer Associates.

Rolls, E. T., & Deco, G. (2002). *Computational neuroscience of vision.* Oxford University Press, Oxford.

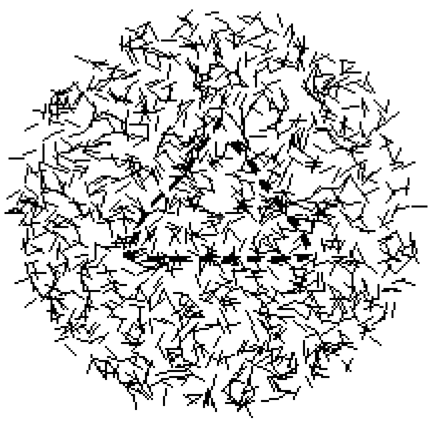
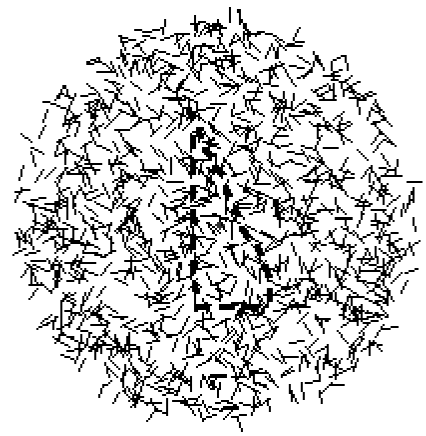
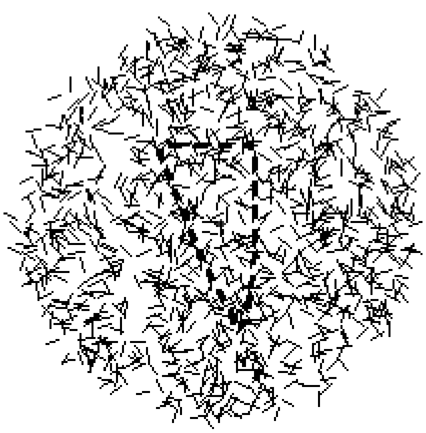
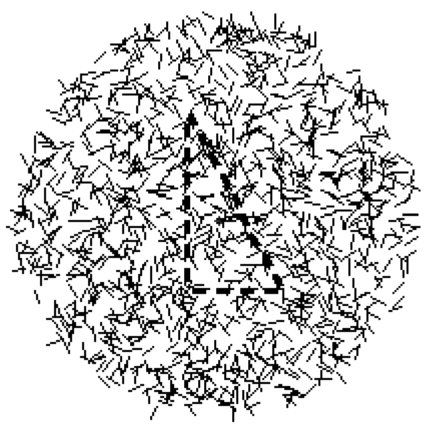
Tootell RB, Reppas JB, Kwong KK, Malach R, Born RT, et al. (1995b). Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *Journal of Neuroscience, 15,* 3215–30.

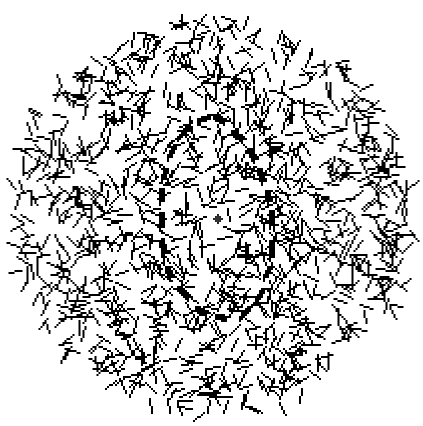
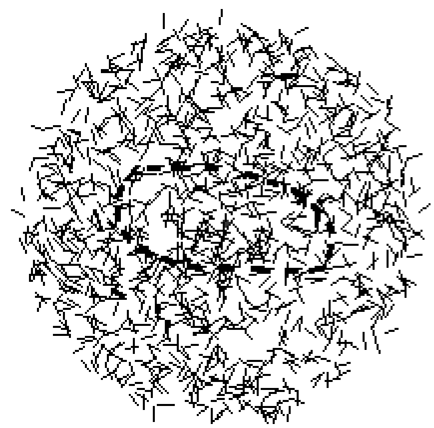
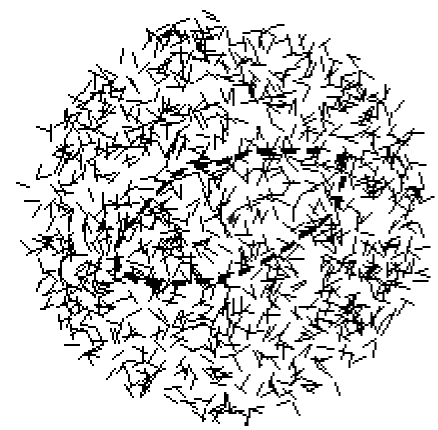
Wang, J., Zhou, T., Qiu, M., Du, A., Cai, K., Wang, Z., et al. (1999). Relationship between ventral stream for object vision and dorsal stream for spatial vision: An fMRI + ERP study. *Human Brain Mapping, 8,* 170-181.

Yantis, S. and Johnson, D. (1990). Mechanisms of attentional priority. *J. Exp. Psychol. Human Perception and Performance. 16,* 121-134.

Zeki, S. (1993). *A vision of the brain.* Blackwell Scientific Publications, Osney Mead, Oxford.

Appendix A: Shapes

Triangles		
		
		

Oval (circular shapes)		
		
		

Rectangles