CONTENT SPECIFICITY OF THE CONTRALATERAL DELAY ACTIVITY

by

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Abstract

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The neural signature and cognitive architecture of how a visual stimulus reaches conscious awareness have not been conclusively determined. Recently, we have reported an ERP activity corresponding with a period of perceptual persistence which has been typically reported in working memory research, known as the contralateral delay activity (CDA). Specifically, we reported how the CDA can be used to track how an object fades in and out of consciousness. Here, we report on the behaviour of the CDA when the type of item in this paradigm is manipulated between face, animal and object stimuli. We recorded EEG activity while participants viewed a bilateral Shape-from-Motion display and analyzed where and how large a CDA is observed. Our findings show that the CDA is generalizable to different item types fading from awareness, with no differences between item conditions. This work supports the content-invariant involvement of working memory processes in sustaining conscious awareness.
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Introduction

Despite tremendous advances in understanding how the brain works, the question of how conscious awareness arises from neuronal processes has not been conclusively answered (Miller, 2005). An influential framework of how neural activity may eventually result in conscious experience has been proposed by Crick and Koch (2003). Building on the idea of Hebbian cell assemblies (Hebb, 1949), they propose that neurons form transient but sustained coalitions that embody our conscious percepts. These percepts rarely consist of individual features but rather depict a coherent representation of an object of interest. In Crick and Kochs framework, this process of binding of elements into wholes emerges through neurons representing unique features joining the same coalition (Crick & Koch, 1995; Treisman, 1996; Treisman, 1998). The exact nature of these coalitions is unclear but it has been hypothesized that driving and modulating connections are essential building blocks (Crick & Koch, 2003). These connections constitute feed-forward and feedback relationships, such that connections from early visual areas to more frontal areas are largely driving, whereas connections from frontal areas to more posterior ones are largely modulating. Other researchers have built on this framework to suggest that the initial feedforward sweep of information through primary visual areas is unconscious (Lamme & Roelfsema, 2000; Lamme, 2010). A percept then reaches conscious awareness after a brief processing time during which input propagates to higher-order frontal areas and feedback loops are instantiated.

These feedfoward and feedback sweeps of information processing have been linked
with attentional processes. While rapid, saliency-driven bottom-up processes are largely connected with the initial feedforward sweep and as such, can be considered driving connections, top-down controlled aspects of attention require feedback loops and can be considered modulating connections (Bullier, 2001; Juan & Walsh, 2003). Attention biases competition amongst coalitions and thus helps bringing a percept to the forefront. Synchronized neural firing may aid a given coalition in biasing competitive processes in its favour. For example, it has been argued that sustained neural firing across widely distributed networks is a crucial component to consciousness (Edelman, 2003). Once a percept has reached conscious awareness, it may require re-entrant cortical feedback loops to keep activity above threshold levels to maintain a conscious representation of this percept (Edelman, 1989).

This framework for the neural correlates of consciousness shows striking similarities with a more cognitive model of how conscious experience arises from the brain. The Global Workspace Theory (GWT) presumes that multiple cortical and subcortical networks operate in parallel and conscious awareness emerges when the neural representation of a stimulus is propagated throughout these networks through attentional processes (Baars, 2005; Dehaene & Naccache, 2001). As such, both models agree that attention is a crucial cognitive faculty biasing which input will receive prioritized access to conscious awareness. Once a winning percept has emerged, the GWT assumes working memory process sustain the subjective experience (Baars, 2005).

While some aspects of these frameworks could be tested by recording simultaneously from multiple neurons in different areas, it has been challenging to find neural correlates of consciousness in humans. One avenue that has been proven successful is to study transitions in states of awareness. In binocular rivalry paradigms, competing images are presented to each eye and perception alternates between the two images. Tong et al. (1998) used such a paradigm, presenting overlapping images of houses and faces at equal intensity, combined with functional magnetic resonance imaging (fMRI) to show
that during alternating perception, the current percept causes the corresponding brain area subserving that percept to be more active. In other words, when the participants perceived a face, the fusiform face area (FFA) was more active but when participants perceived a house, the parahippocampal place area (PPA) showed the strongest activation. While the relationship between binocular rivalry and attention has long been debated (James, 1890), it has been recently argued that the selection process between the alternating percepts builds on object-based attention (Mitchell, Stoner, & Reynolds, 2004). As such, there seems to be mounting evidence that attention is a crucial component for a percept to reach conscious awareness.

Once a percept has reached the stage of consciousness, what are the processes that sustain it? As mentioned earlier, it has been argued that on a neural level, sustained firing may be required (Crick & Koch, 2003) and that on a cognitive level, working memory processes are engaged (Baars, 2005). While binocular rivalry paradigms are useful to study how the brain resolves competition, the shape-from-motion (SFM) paradigm may prove more fruitful to explore how a percept is maintained in awareness. In this paradigm, a fragmented line drawing of an object is shown on a background of random line segments and is essentially camouflaged (Regan, 1986). When the object line segments move relative to the background line segments, however, the object is easily and instantly recognized. When the motion stops, the object consistently fades from conscious awareness over a brief period of time. Because the motion-defined forms fade from awareness when the line fragments remain, it seems that the binding of the fragments can only be temporarily stored (Ferber & Emrich, 2007). On the other hand, if the line segments representing the object are removed when the motion stops, no persistence of awareness is observed (Ferber, Humphrey, & Vilis, 2003, 2005) (see http://www.psych.utoronto.ca/users/ferber/flash-demo.html ). Using functional MRI, Ferber and colleagues (2003, 2005) have shown that while both the object-sensitive lateral occipital complex (Grill-Spector et al., 1998) and the motion-sensitive area MT
(Newsome & Pare, 1988) are activate during the motion phase, only the LOC maintains its activation level during the stationary phase when observers perceive perceptual persistence. Ferber and colleagues (Ferber & Emrich, 2007) have argued that the LOC involvement represents a form-based memory systems mediating between iconic memory and working memory (Baddeley, 1992).

Other evidence also supports the notion that LOC mediates maintaining objects in awareness. Kleinschmidt et al. (2002) applied a separate paradigm, distinct from SFM, where the contrast of a letter on a background is manipulated until it is noticeable or not noticeable. Sustained LOC activity was observed when the perception of the letter drops out. This LOC activity continued to be observed when colour became the distinguishing cue between the object and the background, and when the colour cue was removed (Large, Aldcroft, & Vilis, 2005). Strother et al. (2011) show that faces and objects elicit somewhat different voxel activity in a SFM display, but both elicit activity in object- and face-sensitive regions of the brain. Activity in the OFA and FFA is of a higher magnitude when responding to faces versus animals (Strother et al., 2011). On the other hand, objects and faces both elicit approximately equal LOC activity. As such, it seems that while the LOC seems to be generally involved in the maintenance of a percept, there is also some evidence for content-specific correlates in those brain areas that subserve the perceptual analysis of the visual input. Thus, while there is some research that speaks to the role of content-invariant versus content-specific neural processes, there is little research that speaks to how this is related to working memory processes.

Working memory has been described as a cognitive faculty that allows one to hold information online after it has been removed from view (Baddeley, 1992). It is typically considered to consist of a central executive component that controls the flow of information and three temporary storage systems: a phonological loop for auditory information, a visuospatial sketchpad for spatial and visual information and an episodic buffer to link and time-stamp the other components (Baddeley, 2000). Over the past ten years or
so, there has been a surge in the number of studies aiming at understanding the visual component of working memory. These studies have typically used a change-detection paradigm, in which participants are asked to maintain an array of items in memory over a brief delay period. After the delay, a memory probe display is shown and participants have to indicate whether or not a change occurred. On average, participants can maintain 3-4 items of the original display (Luck & Vogel, 1997). Combining such change-detection paradigms with electroencephalography (EEG), it has been shown that about 300 ms into the delay period a sustained negativity emerges over posterior electrodes contralateral to the side on which the memory sample items have been shown (Vogel & Machizawa, 2004). The amplitude of this contralateral delay activity (CDA) is modulated by the number of items maintained in memory, plateaus at a given participants capacity (Vogel & Machizawa, 2004), and is seen as the electrophysiological correlate of visual working memory (VWM) engagement.

Recently, this event-related potential (ERP) has been used to track how a percept enters and exits conscious awareness. Pun et al. (2012) used an SFM paradigm and adapted it to work with EEG recording. They presented two animations on the left and the right of a fixation cross, and participants were asked to focus on one of the animations following an arrow cue. Each animation consisted of an animal line drawing rotating in one direction while the background of random line segments rotated in the other direction. The last frame either had the animal removed or still present, and this determined whether awareness persisted. The authors found that a noticeable sustained posterior contralateral negativity (i.e., the CDA) occurs when the animal slowly fades from awareness, but not when it is removed from the display immediately following motion offset. As such, given that the electrophysiological marker of VWM engagement was observed during a period of visual awareness, the authors argued that awareness and working memory draw on the same resources and that this ERP component may serve as an online correlate of consciousness. Not much is known, however, how content-specific
the CDA is. Pun et al. (2012) used line drawings of animals as their stimuli, with no stimuli from other categories. Using a different paradigm, Wilson et al. (2012) reported that the CDA at one electrode site was modulated by the number of items regardless of their feature complexity, however, at a different electrode site, the CDA responded to complexity but not the number of items.

This MA thesis will expand on the research by Pun et al. (2012) to test whether the CDA during the persistence period (called the stop condition) of an SFM paradigm serves as a general index of conscious awareness (i.e., content-invariant), or whether it carries unique information about its contents (i.e., content-specific)? As such, the hypotheses are that if the CDA is indeed content-specific, then differences in amplitude and/or the recorded electrode sites should be observed when the stimulus category changes. If, however, the CDA is content-invariant, a hypothesis in line with the global workspace theory, then regardless of stimulus category, no differences should be observed in amplitude or electrode sites. The stimulus categories chosen for this thesis were line drawings of animals to replicate Pun et al. (2012), line drawings of faces as face stimuli have known neural substrates (Kanwisher & Yovel, 2006) and line drawings of common objects, as images of living and non-living objects are thought to be processed by different areas of the brain (Perani, Cappa, & Bettinardi, 1995). The main dependent variables are CDA amplitude and CDA electrode site.
Methods

Two experiments were conducted, where the first assessed judgements about the length of perceptual persistence with no EEG recording, and the second tested the CDA using EEG. A group of 10 individuals (9 female, mean age: 20.7 years, SD: 1.6) with normal or corrected-to-normal vision participated in experiment 1, and 21 individuals (15 female, mean age: 21.9 years, SD: 2.7) participated in experiment 2. All participants provided informed consent, and procedures were approved by the University of Toronto Research Ethics Board. Stimuli and procedure were based on the second experiment conducted by Pun et al. (2012). Methods for both experiments were identical except for the following: In experiment 1, participants judged the duration of persistence by pressing a key when they could no longer perceive the target. In experiment 2, participants wore an EEG recording device and made a key press that qualitatively judged the length of persistence of the target, which avoided the problem of muscle movement adding noise to the EEG recording and also avoided the potential confound of differences in response inhibition between different conditions. The following describes methods common to both studies.

Stimuli and procedure

Shape-from-motion task

A bilateral display was generated in Matlab version 2009a which involved an identical circular animation presented on either side of a fixation cross. The animations were
generated in Adobe Flash, and included a background of random curved line fragments and a foreground fragmented line drawing. The background and the foreground moved in opposite directions during the motion phase. Each trial began with a 300-ms displayed fixation cross, followed by an arrow near the center of the screen appearing 2° of visual angle above the fixation cross. After the 200-ms presentation of the arrow, there was a jittered delay of 200, 250, 300, 350 or 400 ms during which only the fixation cross was presented. Participants were asked to attend only to the animation on the side of the display to which the arrow points, without moving their eyes from the fixation cross in the center of the screen. The background line fragments were presented statically for 200 ms, after which the foreground and background began to move in counterrotation to one another. During the 1,200 ms animation, the images rotated at a rate of 25 frames per second. The initial orientation of the animation frame in which the animation began was randomized. When the motion stopped, the line fragments in the foreground, representing an object display, would either remain in the display (stop condition) or be removed to leave only background lines (vanish condition). The display would remain for 2,000 ms statically, during which a person might experience the fading of awareness described earlier. In experiment 1, participants pressed a button when in their subjective experience the complete object has faded from awareness. In experiment 2, participants had no button-press task until the animation was complete. After it ended, participants were cued on whether the animation remained on the screen for a short, medium or long amount of time. Participants were instructed to use their own judgement to define these lengths of times, as in experiment 2 our interest was primarily neural and not behavioural. After the participant pressed an arrow key which corresponded with their response, the trial was complete (See Figure 1 for complete trial depiction). Participants were engaged in 540 trials in total, with 45 trials in each combination of item type (animals, faces and objects), stop/vanish condition and arrow direction. The 18 objects shown were divided equally into 6 animals, 6 human faces and 6 household objects (See Figure 2). The human
faces were traced from real faces photographed to represent neutral facial expressions.

**Electrophysiological recording and analysis**

EEG recordings for experiment 2 were obtained using a BioSemi ActiveTwo system (www.biosemi.com) with 64 active Ag/AgCl electrodes, recording at 512 Hz and mounted on an elastic cap with channel locations configured in the international 10/20 layout. Analysis was done using the EEGLAB and ERPLAB software. First, the data were downsampled to 256 Hz, and a band-pass filter of 0.01-30 Hz was applied to the EEG. Trials with larger than a 30 Hz horizontal electrooculogram or 80-uV vertical electrooculogram were excluded from the analysis.

ERPs were computed for a 3000 ms window and time-locked to the onset of the static image, with a baseline correction of 200 ms preceding motion onset, coinciding with the delay following the arrow cue. Difference waves for the CDA were calculated by subtracting ipsilateral from contralateral channels, for all channels, and then collapsing across presentation sides.
Figure 1: Animation sequence for this experiment. A fixation cross is presented temporarily, followed by an arrow cue pointing in the direction the participant is asked to focus their attention, without moving their eyes. In this case, the participant would be asked to focus on the animal on the left side of the screen. The animation consists of an item (either face, animal or object) rotating in one direction while the background of random line segments rotate in the other direction. The last frame either has the item removed (vanish) or still present (stop), and this determines whether awareness persists. There were 25 animation frames randomly initialized. Both on the left and the right would be the same item, so if, for example, a mug was presented on the left, the same mug would be presented on the right, and they would rotate in unison. Thus there were no differences between the visual cues on the left and the right, and all lateral differences in ERP activity were the result of choosing where to move attention. Note that here the dolphin image is enhanced for clarity, but during the experiment the thickness of the lines is not distinguishable from the background. The arrows in the animation frame represent rotation and are not present in the experiment.
Figure 2: Stimuli used in this experiment separated by category. The first row represents animal stimuli, which have previously been used in this paradigm to elicit a CDA (Pun et al., 2012). The second row shows common objects which are novel to this experiment. The third row shows human faces in the portrait orientation, which were created by drawing overtop of real human faces photographed in a neutral expression. These faces were rated as neutral previously, and so we consider them to be a good representation of a neutral facial expression. There is more internal detail in the human faces than in the other types of stimuli, but Experiment 1 showed no difference in the length at which they persisted in a button press judgement. Each of the stimuli were designed to be as close as possible to 100 pixels by 100 pixels in size, and contain 400 to 600 pixels of dark lines. When the stimuli were turned into line segments, 50% of the pixels were erased, leaving 50% behind. This was confirmed in MATLAB.
Results

Experiment 1

To assess potential differences in how participants respond to the different stimulus categories, the duration of perceptual persistence for the different categories was measured (Figure 3). A $2 \times 3$ ANOVA with display type (stop versus vanish) and stimulus category (animals, faces, household objects) as the within subject factors shows a main effect of the stop/vanish conditions $F(1,9) = 60.337 \ p < 0.01$, confirming that participants indeed perceived persisting awareness and that there were no differences in perceptual persistence between stimulus categories. On average, the duration of subjective perceptual persistence was 1445 ms (after motion offset which equates to, 2645 ms after stimulus presentation). In light of this, the CDA time window for experiment 2 was computed to be 400 ms after the stimulus stopped to just before the average judged persistence, as determined by this study (1400 ms after the motion stops).

Experiment 2

To confirm that qualitatively the same judgement of persistence is made as in experiment 1, participants rated after stimulus presentation whether the stimulus persisted for a short, medium or long duration. A chi-square test of independence determined that the reported duration of awareness significantly differed based on the display type, $\chi^2(21, N = 12556) = 6142.18, \ p < .001$, with the duration in the stop condition more
frequently reported to be medium or long, while the duration in the vanish condition is most commonly reported as short (See figure 4).

In order to determine significant differences between ERP amplitude in the stop and vanish conditions, a within-subject repeated measures ANOVA with ERP amplitude as the dependent variable was performed at two time windows of interest. ERP amplitude is assessed as the difference between an ipsilateral and contralateral electrode pair. The time windows are shown in Figure 5. The first time window is during the animation motion, at a point in time in which the stop and vanish conditions are identical (1100 to 1300 ms post stimulus onset). The second is during a time period (1800 to 2600 ms post stimulus onset) where the average participant has the sustained percept of the image in the stop condition but not the vanish condition, as shown by experiment 1. In each time window, a repeated measures 2 x 3 x 6 ANOVA was conducted with display type (stop or vanish), stimulus category (animals, faces and objects) and electrode channel (CP5/CP6, P3/P4, P5/P6, P7/P8, PO3/PO4) as factors.

In the first time window, which occurs during the motion phase, there are no main effects and no interactions. Importantly, the stop/vanish manipulation has no effect at this time point $F(1, 20) = 0.108, p = 0.746$, because at this point in the paradigm both conditions are in fact identical. In the second time window, which occurs when we expect to see a CDA, there is a main effect of the stop/vanish manipulation on the measured CDA $F(1, 20) = 14.182 p < 0.001$. There are no other main effects and no interactions, and statistically significant findings with respect to item category.

One might ask what the power of this ANOVA is to reject the null hypothesis given the data found with respect to item category. Power was calculated using SPSS, which asks what the post-hoc observed power of this study was to reject the null if the sample we collected does indeed reflect true population differences. Because the sample we collected showed very small, unreliable differences with respect to item category and larger variability within subjects than between groups, we find a low statistical power.
to reject the null hypothesis if it is false. This tells us that if our measured sample
parameters do exactly reflect the population, we would need an extremely large sample
size to prove that a small difference is significant. The power to reject the null if it is
false with respect to item category is 0.166, and the power to reject the null hypothesis
with respect to the interaction of item category and electrode site is 0.111. On the other
hand, there exists a large, reliable difference in amplitude between the stop and vanish
conditions, and the power to reject the null hypothesis if it is false for this comparison is
0.947.

To look for broad trends in scalp topography of the CDA, the difference between the
ipsilateral and contralateral electrodes are shown in Figure 9 across time window 2 (w2
= 1800-2600 ms). In each condition, the same posterior electrodes show the CDA, with
the peak site of the CDA not significantly different across conditions, but always close
to P5/P6 and P7/P8.

Additionally, we might expect differences in the amplitude of the N170. This ERP
is typically found during the neural processing of a face image, over occipito-temporal
electrode sites (Bentin, Allison, & Puce, 1996). It can be seen in experiment 2 170-190
ms after the stimulus presentation but before the motion. The N170 with respect to item
category in the stop condition is shown in Figure 8. No collapsing across presentation
sides is done when computing the N170 amplitude. There are no differences between
stimulus conditions in the amplitude of the N170. There are also no physical stimuli
differences between the stop and vanish conditions at this point in the experiment.
Figure 3: Behavioural reaction time for perceptual persistence responses in experiment 1. In this experiment, participants responded with a key press at the moment they could no longer distinguish the item, indicating that it no longer persisted in conscious awareness. There are large differences between the stop condition, and the vanish condition, where the item remained onscreen or was taken away, respectively.
Figure 4: Behavioural keyboard responses for experiment 2. In this experiment, participants indicated whether the target persisted for a short, medium or long duration. In the stop condition, subjects consistently reported that the target persisted for a long or medium duration, as opposed to a short duration in the vanish condition.
Figure 5: EEG difference wave plots for the animals conditions. The contralateral side electrode were subtracted from the corresponding ipsilateral side electrode. Negative is plotted up. Plotted channels include CP5/CP6, P3/P4, P5/P6, P7/P8, P9/P10, and PO3/PO4. Shaded area around the graph represents standard error. Window 1 (W1) corresponds to 1100-1300 ms and window 2 (W2) corresponds to 1800-2600 ms following the onset of visual stimuli.
Figure 6: EEG difference wave plots for the faces conditions. Plot comes from subtracting the contralateral side electrode from the corresponding ipsilateral side electrode. Negative is plotted up. Plotted channels include CP5/CP6, P3/P4, P5/P6, P7/P8, P9/P10, and PO3/PO4. Area around the graph represents standard error.
Figure 7: EEG difference wave plots for the objects condition. Plot comes from subtracting the contralateral side electrode from the corresponding ipsilateral side electrode. Negative is plotted up. Plotted channels include CP5/CP6, P3/P4, P5/P6, P7/P8, P9/P10, and PO3/PO4. Area around the graph represents standard error.
Figure 8: EEG wave plots for the stop condition. Plot is the average of the basic channels CP5, CP6, P3, P4, P5, P6, P7, P8, P9, P10, PO3 and PO4 without side of head subtraction. Negative is plotted down. Highlighted is the N170 period. To improve image clarity, standard error is not shown.
Figure 9: Scalp topography of the CDA at the second time window 1800 to 2600 ms following the beginning of the recording at the onset of a stimulus. Only one half of the head is shown. Each location represents an electrode pair derived from the subtraction of the contralateral side from the ipsilateral side.
Discussion

The purpose of this study was to find further evidence for the involvement of working memory processes in the maintenance of conscious awareness and to determine whether this is content-specific or content-invariant. The electrophysiological correlated of VWM engagement, the CDA, was used as a measure of working memory. To assess continued awareness, the SFM paradigm allowed us to present an item that suddenly disappears (vanish condition) or gradually fades away (stop condition) from conscious experience. We expected the CDA to be present in the stop condition, but to disappear along with the stimulus in the vanish condition, in a replication of the research by Pun et al. (2012). If content manipulation has an effect on the CDA, I hypothesize that we might detect it from the amplitude, or scalp topography of the recording. Two experiments were conducted: the first used reaction times to assess prior differences in judgements of persistence with respect to the item categories, and the second used EEG recordings to answer the question of the content specificity of the CDA.

We first carefully assessed from Experiment 1 whether our conditions do indeed induce continued awareness in the stop condition but not in the vanish condition. As expected, the time it took for participants to cease perceiving the target, as measured by response time, was sharply different between these two conditions. In support of this quantitative finding, Experiment 2 demonstrated that participants distinguish the two conditions qualitatively. Participants more frequently reported that the persistence lasted for a medium or long duration in the stop condition, but typically reported a short duration...
in the vanish condition. We can then assess whether the duration of the conscious experience changes with our item categories of interest.

In Experiment 1, there were no detectable differences in the duration of the persistence as a function of item condition (See Figure 3). Having established in Experiment 1 that conscious awareness differs sharply with the stop and vanish manipulation but not item category changes, we turn to investigating the recruitment of the CDA in the task.

In Experiment 2, EEG results showed that a sustained difference in negative amplitude at posterior electrode sites began at the onset of motion in both the stop and vanish conditions (see Figure 5, time window 1). I interpret this to be the initialization of the CDA. There were no detectable differences between the stop and vanish conditions at this point in time, as predicted. Once motion ended (Figure 5, time window 2), the sustained negative amplitude persisted for the stop but not for the vanish condition, as evidenced by the main effect of display type at this time window. These findings are highly consistent with Pun et al. (2012), and indicate that the stop condition does induce a maintained contralateral negativity that corresponds with the maintenance of the item in subjective awareness. The results also support the previous finding that CDA is present under conditions of continued stimulus awareness.

The goal of Experiment 2 was to test whether the CDA is content-invariant or varies as a function of the item category held in conscious awareness. In light of this hypothesis, no differences in the CDA as a function of item category were statistically significant, and there were no identifiable trends. While we cannot rule out low statistical power in identifying a difference if it does exist, there were no data trends in mean CDA amplitude across channels in support of the alternate hypothesis. We can conclude that we are unable to find evidence against the null hypothesis that the CDA is invariant regardless of the type of item held in awareness (between animals, objects and faces).

Having found no clear evidence for CDA content-specificity with respect to manipulating the item category held in continued awareness (between faces, animals and ob-
jects), we should assess how this result fits in with past research into the CDA. A lack of content specificity fits well with the Global Workspace Theory of conscious awareness, for instance. This theory proposes that a percept which reaches awareness is sustained through a working memory process (Baars, 2005). The discovery of a CDA in response to continued awareness of a visual target then represents a compelling piece of evidence in favour of such a model. If the recruitment of the CDA reflects a working memory process, we expect the CDA in this experiment to behave in a similar manner to the CDA recorded during typical working memory tasks.

The CDA as measured during working memory tasks has an established relationship with the number of items held in memory, and some conflicted literature points to the CDA varying with item complexity. Ikkai, McCollough, and Vogel (2010) found that the CDA amplitude at three posterior electrode pairs is affected only by the number of items held in memory but not by colour contrast. Luria and Vogel (2011) found that the CDA scaled mostly with the number of objects but not the number of features within an object. Thus, typical research into the CDA does not detect differences based on the content of one item held in memory, but only the number of visual working memory items. On the other hand, item complexity may also modulate the CDA. Woodman and Vogel (2008) found that maintaining multi-feature objects results in a greater amplitude for a feature conjunction than for a simple feature at a single electrode (PO1/PO2). Expanding on this research into object complexity, Wilson et al. (2012) found a double dissociation between the CDA as measured at channels P7/P8 and at channels P1/P2. In this experiment, the CDA at P7/P8 was affected by object complexity but not the number of objects, but the CDA at P1/P2 was modulated by the number of items being encoded and not by object complexity. Similarly, an enhanced CDA has been shown for polygons relative to simple colour stimuli (Gao et al., 2009). This suggests that the number of items held in VWM is the primary influence on the CDA, but occasionally a less reliable relationship with feature complexity is found as well. If these are the only influencing factors on this
ERP component, we would not expect differences in our experiment, given that feature complexity was not directly manipulated across item categories here.

Failing to find a difference with respect to item category fits well with the known factors that influence the measurement of the CDA, but a null result is challenging to interpret. The low statistical power to find a difference with respect to object category in this study could be attributed to large intersubject variability in the data. EEG data typically shows tremendous variability across subjects (Luck, 2005). In addition, this variability is larger than the within-subject variability (Luck, 2005). The main contributors to between-subject variability are the unique folding patterns of the cortex, which vary across individuals, as well as differences in the location and orientation of the cortical generator source of an ERP component (Luck, 2005). Within-subject variability is also a concern, which is why it becomes necessary to average over many trials in order to identify an ERP component common to a specific condition (Luck, 2005). To increase within-subject power, we employed a large number of trials (540), and to increase between-subject power, we used a large sample size (n = 21). Given the extraordinary amount of evidence required to disprove a null hypothesis and the lack of any trends in the data to suggest an alternate hypothesis, I conclude that the best course of action is to retain the null hypothesis that the CDA is invariant with respect to item condition.

After analyzing the CDA, one might look for other components of interest in attributing attention to an area of space. Our paradigm does not lend itself to looking for the N2pc, which reflects attentional filtering (Luck & Hillyard, 1994), because participants attention was drawn to the target location before the onset of motion when an arrow was presented onscreen. Similarly, we might expect faces to elicit a face-specific ERP in our paradigm, specifically, an increased N170 effect. However, the N170 occurs at a display onset, whereas in this experiment, the type of item shown to the participant could not be perceived until the motion started 200 ms later (See Figure 8). Because the N170 was measured before motion, there are no differences in the amplitude of the N170 as a
function of item condition in this study.

Future research into attributes which influence the CDA may investigate the differences between VWM and the continued conscious awareness of a form, using the CDA as a measure. Although we have established that both situations produce a reliable CDA, we still do not know what differentiates the two sources of this ERP. Our results, as well as the results of Pun et al. (2012), confirm that the CDA is present in tasks that test conscious awareness without explicit memory demands. One line of research might involve testing the presence or amplitude of the CDA in memory tasks to look for dissociations between this recruitment and the recruitment during a continued awareness task. In addition, it may be useful to investigate the CDA in clinical patients who suffer from memory impairment and corresponding damage to the Medial Temporal Lobe. Some researchers report that such patients have intact VWM (Jeneson, 2012), whereas others report the opposite (Hannula, Tranel, & Cohen, 2006). As is often the case in the field of cognitive neuroscience, a combination of lesion and neuroimaging research can elaborate on the differences between VWM and conscious awareness without explicit memory demands.

These findings show that the CDA does act as a reliable index of subjective conscious awareness of a visual item and is a useful measurement for continued research into consciousness. We are able to support and inform past research by Pun et al. (2012), and suggest that the CDA is present and invariant regardless of whether object, animal or face stimuli are held in continued subjective awareness.
Bibliography


