Representing dynamic stimulus information during occlusion

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ABSTRACT

Human observers maintain a representation of the visual features of objects when they become occluded. This representation facilitates the interpretation of occluded events and allows us to quickly identify objects upon reappearing. Here we investigated whether visual features that change over time are also represented during occlusion. To answer this question we used an illusion from the time perception domain in which the perceived duration of an event increases as its temporal frequency content increases. In the first experiment we demonstrate temporal frequency induced modulation of duration both when the object remains visible as well as when it becomes temporarily occluded. Additionally, we demonstrate that time dilation for temporarily occluded objects cannot be explained by modulations of duration as a result of pre- and post-occlusion presentation of the object. In a second experiment, we corroborate this finding by demonstrating that modulation of the perceived duration of occluded events depends on the expected temporal frequency content of the object during occlusion. Together these results demonstrate that the dynamic properties of an object are represented during occlusion. We conclude that the representations of occluded objects contain a wide range of features derived from the period when the object was still visible, including information about both the static and dynamic properties of the object.

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1. Introduction

During daily life, objects constantly move in and out of sight, temporarily depriving us of direct visual information about these objects. However, even though retinal input is disrupted we tend to experience these objects as persisting in space and time (Michotte, 1950). Several studies have shown that both animals and human observers behave as if the occluded object is still present (e.g. Baillargeon, 1986; Churchland, Chou, & Lisberger, 2003; Von Hofsten, Kochukhova, & Rosander, 2007; Van Wermeskerken et al., 2011). This suggests that we maintain an internal representation of an object while it is occluded. This representation of occluded objects has been a topic of interest in several fields investigating situations of both partial and full occlusion. Behavioral studies investigating amodal completion – the process of filling in occluded parts of an object – have shown that both the shape (Rensink & Enns, 1998) and color (Albertazzi, Canal, & Micciolo, 2012; Pinna, 2008) are completed for the occluded segment of the object. This representation of the occluded segment is formed automatically (Murray, Imber, Javitt, & Foxe, 2006) and can

influence both the interpretation of concurrent events (Joseph & Nakayama, 1999; Sekuler & Palmer, 1992) as well as subsequent behavior (Gerbino & Salmaso, 1987). Similarly, studies on full occlusion show that information about object shape, color, velocity, and motion direction can be maintained across periods of occlusion (Flombaum, Scholl, & Santos, 2009; Hollingworth & Franconeri, 2009; Moore, Stephens, & Hein, 2010; Saiki, 2003). This information can be used to track and identify objects across episodes of occlusion (Hollingworth & Franconeri, 2009; Von Hofsten et al., 2007; Scholl & Pylyshyn, 1999), as well as predict events occurring during occlusion (Baillargeon, 1986; Benguigui, Ripoll, & Broderick, 2003; Von Hofsten et al., 2007). Furthermore, it has been shown that an object under occlusion can be the target of object-based attention, suggesting that the representation contains information about feature binding that occurred before occlusion (Behrmann, Zemel, & Mozer, 1998; Moore, Yantis, & Vaughan, 1998). On a neural level, the representation of occluded objects resembles that of visible, non-occluded objects. Several studies have reported a wide network of activity in visual areas of the brain that overlaps with activity found when objects are not occluded. This network includes both visual areas involved in the processing of higher order stimulus information such as object shape (Kourtzi & Kanwischer 2001; Kovács, Vogels, & Orban,

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1995), object identity (Hulme & Zeki, 2007), and relative location (Graziano, Hu, & Gross, 1997), as well as retinotopically mapped areas involved in the processing of basic features of the visual scene (Ban et al., 2013; Rauschenberger, Liu, Slotnick, & Yantis, 2006).

Together, these studies suggest that the representation of occluded objects incorporates a wide range of features, derived from the period that the object was still visible. These features are represented by visual areas of the brain that also represent these features during perception of the visible object (Ban et al., 2013). Furthermore, these representations seem to be object-like in nature (Behrmann et al., 1998) enabling us to understand events that occur during occlusion as well as to categorize objects on reappearance (Baillargeon, 1986; Scholl & Pylyshyn, 1999).

Most studies on occlusion have focused on the static visual properties of an object (e.g. color or shape). However, in many natural situations image properties such as shape, luminance, and location change over time. For example, when a tennis ball temporarily disappears behind a wall, its location continues to change during occlusion. Additionally, if the ball is spinning, its visual features also change along its trajectory. Representing these feature changes and the rate at which they occur could aid in the interpretation of events occurring during occlusion as well as facilitate the identification of objects upon reappearing. For example, a change in velocity or spin would suggest that the object interacted with another object while under occlusion. Up until now, only the change of location over time (motion) has been studied (Olson, Gatenby, Leung, Skudlarski, & Gore, 2004; Von Hofsten et al., 2007; Ban et al., 2013). These studies have shown that both location and speed are represented during occlusion. For example, Olson et al. (2004) reported that activity in human MT/V5 for occluded motion was similar to that observed during visible motion, suggesting that area MT/V5 continues to represent the velocity and direction of the object during its occlusion. In addition, a study by Ban et al. (2013) showed that the retinotopic representation of the position of an occluded object in areas V1 and V2 is updated over the course of the occlusion period. This suggests that the temporal derivative of position – velocity – is used to extrapolate the predicted position of the object during occlusion. It is unknown however, whether dynamic changes other than motion, such as those occurring for the spinning ball, also continue to be represented during occlusion.

Here we present two experiments in which we investigate whether dynamic changes in the visual features of an object are represented during occlusion. To this end, we investigated whether the temporal frequency content of a luminance-modulated (i.e. flickering) object is represented during occlusion. We used a well-known temporal illusion - temporal frequency induced time dilation – in which the perceived duration of an event increases as a result of an increase in its temporal frequency content (Kanai, Paffen, Hogendoorn, & Verstraten, 2006; Ortega & López, 2008). By combining this property of duration perception with a situation in which the object becomes occluded, we can investigate whether the dynamic properties of an object are represented during occlusion. We hypothesized that if the temporal frequency content of an occluded object is represented during occlusion, it should lead to patterns of time dilation similar to those observed during normal, visible presentation.

2. Experiment 1

We presented participants with a duration reproduction task in which participants replicated the duration of a stimulus that was either static or luminance-modulated at different temporal frequencies. On each trial the stimulus was paired with the presentation of an occluder that moved either in front or behind the stimulus, and then returned to its starting position after a short delay. As a result the stimulus either remained visible or became temporarily occluded. If the temporal frequency content of the stimulus is represented during occlusion we should observe longer reproduction for higher temporal frequency modulations, both for the non-occluded and occluded stimuli.

To assure that participants are aware of the onset, offset, and temporal frequency content of the stimulus, a brief pre- and post- occlusion presentation of the stimulus is needed. These presentations could lead to time dilation, making it difficult to interpret any time dilation found for occluded stimuli. To solve this issue, we added a control condition, in which the stimulus remained visible but the luminance-modulation was faded out and back in over the period in which the occlusion event occurred. This extinction condition simulates the pre- and post- occlusion presentation of temporal frequency content in the occluded condition, without presentation of the deletion (and accretion) cues that would lead to maintenance of the temporal frequency content of the stimulus. As such any effect of initial presentation should occur for non-occluded, occluded and extinction stimuli. On the other hand, any effect of the representation of temporal frequency during occlusion should only be observed for occluded stimuli and not for stimuli with fading luminance-modulation.

To summarize, if temporal frequency is represented during occlusion we should observe time dilation both when the stimulus remains visible as well as when it becomes occluded. Additionally, time dilation for the occluded stimuli should be larger than any time dilation observed in the extinction condition.

2.1. Material and methods

2.1.1. Participants

A total of 20 healthy adults participated in this study (7 male; mean age = 22.5, SD = 3.41). All participants had normal or corrected-to-normal vision and normal stereoscopic vision. They received monetary reward or course credits as compensation for their participation and were naïve as to the purpose of the experiment. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the local ethics committee. All participants were informed that they could stop their participation at any time and that the data would be processed anonymously. After agreeing with these terms all participants signed a written informed consent form.

2.1.2. Apparatus and stimuli

Stimuli were presented on two linearized 24-inch LCD monitors (screen resolution at 1920 × 1080 pixels, 60 Hz refresh rate) controlled by single Windows workstation (Windows 10) running MATLAB 2010A (MathWorks, Inc.) and the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). Both screens were viewed dichoptically through a mirror setup. Throughout the experiment images from the right screen were projected to the right eye and images from the left screen to the left eye. The total distance between the participant and each of the screens was ∼85 cm. From this distance the full screen subtended 35.38° × 20.08° of visual angle. Head movements were restrained using a chinrest.

All stimuli were presented on both monitors and were presented on a grey background (62.5 cd/m^2). To facilitate binocular fusion between the two images all presentation was accompanied by a square, pink-noise frame (96.79% Michelson contrast) that started 11.2° × 11.4° from the center of the screen and subtended 2.8° × 2.8° of visual angle.

2.1.3. Procedure

Each trial started with a white central fixation cross (322 cd/m^2; 0.57° × 0.57°) and a grey-black textured occluder (4.1° × 2.28°; black: 0.33 cd/m^2, grey: 30.3 cd/m^2) presented 2.85° above the fixation cross (Fig. 1). The perceived depth of the occluder relative to the frame was manipulated by creating disparity between the occluder on the left and right screen (+/−0.12°), causing the occluder to be perceived as either in front or behind the frame. To facilitate binocular fusion and the perception of depth, vertical edges were added to the occluder in the form of a smaller grey rectangle, starting at 2.6° × 0.78° from the center of the occluder location and subtending 1.50° × 1.50°. After 250 ms the fixation cross was replaced with a test stimulus consisting of a white circle (diameter: 1.9°) that was either static (214 cd/m^2) or luminance-modulated at a temporal frequency of 5 or 10 Hz. Luminance modulation was sinusoidal with a peak contrast of 50.12% (Michelson contrast). After a short delay from the onset of the test stimulus (33, 67, 100 ms) the occluder started to move downwards with a speed of 13.68°/s until its center aligned with the center of the screen after 217 ms. Depending on the condition, this resulted in the occluder moving either in front (Occluded condition) or behind (Non-Occluded & Extinction conditions) of the stimulus, in line with the depth cue derived from the occluder location relative to the frame. The occluder then maintained its position for 466–533 ms, 766–833 ms, or 1066–1133 ms depending on the duration of the test stimulus. Following this period, the occluder moved up to its original position (at 13.68°/s) and remained on the screen. In the Extinction condition the amplitude of the luminance modulation of the test stimulus faded out and back in with a linear profile. The goal of this fading was to mimic the disappearance of the temporal frequency content in the Occlusion condition.
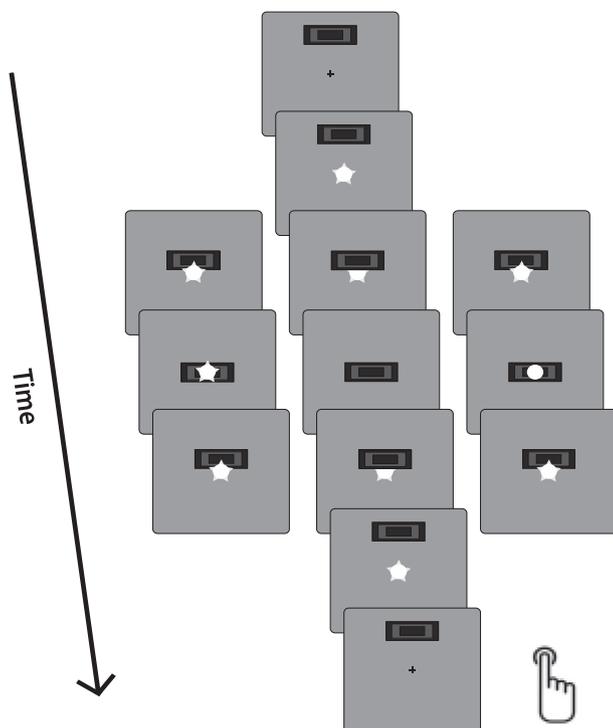
Fig. 1. Overview of the procedure. Participants reproduced the duration of a test stimulus by pressing and holding a key. The test stimuli were presented in three different occlusion conditions (Non-Occluded, Occluded, and Extinction: shown from left to right). Depending on the condition, the occluder either moved behind the test stimulus (Non-Occluded and Extinction) or in front of the test stimulus (Occlusion). In the Extinction condition, luminance modulation faded in and out across the period when stimulus and occluder overlapped.

The decrease in amplitude started when the occluder first touched the stimulus, 67 ms after motion onset, and ended when the stimulus and occluder completely overlapped 200 ms after motion onset. Similarly, the luminance modulation was reintroduced over a period of 133 ms starting with the reappearance of the stimulus. The participants' task was to reproduce the duration of the test stimulus by pressing and holding down the right-arrow key. After reproduction the next trial was initiated by pressing spacebar.

Participants were tested in a 3 × 3 × 3 within-subject factorial design. The three factors were Duration (1000, 1300, or 1600 ms), Occlusion (Non-Occluded, Occluded, Extinction), and Temporal Frequency (Static, 5 Hz, or 10 Hz luminance modulation). Participants completed two blocks consisting of either a combination of Non-Occluded and Occluded trials or a combination of Non-Occluded and Extinction trials. Blocked presentation assures that occluded presentations are assumed to reflect an occluded presentation of the Non-Occluded trials – were the temporal frequency modulation persists – and not an occluded presentation of the Extinction trials. The order of the two types of blocks was counterbalanced across conditions. For each block, all combinations of factors were counterbalanced and assigned randomly across trials. Within each block every combination of factors was repeated 30 times, resulting in a total of 540 trials per block and a grand total of 1080 trials across the entire experiment. During each block participants were given three self-timed breaks spread evenly across the experiment. Both experimental blocks lasted about 45 min and were separated by a 15-min break.

2.2. Results

For each participant and each unique combination of conditions, individual trials with responses more than two standard deviations away from the mean were removed from further analysis. This resulted in the removal of a total of 902 trials (4.18%). We then calculated the average reproduced duration for each condition for each participant (see Fig. 2). The resulting data were analyzed using a 3 × 3 × 3 repeated measures ANOVA, with Reproduction Duration as the dependent measure and Duration (1000, 1300, 1600 ms), Temporal Frequency (Static, 5 Hz, and 10 Hz), and Occlusion (Non-Occluded, Occluded, Extinction) as factors. For all results Greenhouse-Geisser corrections were used if Mauchly's test of sphericity showed that the assumption of sphericity was violated. For all post-hoc comparisons using t-tests reported in the manuscript, p-values were adjusted for multiple comparisons using the Holm-Bonferroni correction method (Holm, 1979). The corrected p-values are reported for ease of interpretation, alpha is at 0.05 for all statistical tests. The error bars in all images reflect within-subject standard errors, calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008).

We observed a main effect of Duration ($F(1.04,19.73) = 57.42$, $p < 0.001$, $\eta^2 = 0.751$). Pairwise comparisons revealed that this effect was due to an increase in reproduction durations over the three measured test durations ($p < 0.001$ for all comparisons) indicating that participants' responses were sensitive to the presented duration. We also observed a main effect of Temporal Frequency, $F(1.22,23.24) = 36.06$, $p < 0.001$, $\eta^2 = 0.66$. Subsequent paired sample t-tests for the main effect of Temporal Frequency revealed that participants reproduced shorter durations in the Static condition compared to both the 5 Hz ($t(19) = -5.07$, $p = 0.007$) and 10 Hz conditions ($t(19) = -8.44$, $p = 0.007$). Additionally, reproductions in the 5 Hz condition were shorter than those in the 10 Hz condition ($t(19) = -3.37$, $p = 0.007$). Additionally, we observed a main effect for Occlusion ($F(1.46,27.73) = 7.14$, $p = 0.006$, $\eta^2 = 0.27$). Subsequent paired sample t-tests revealed that this effect was characterized by significantly longer reproductions in the Non-Occluded
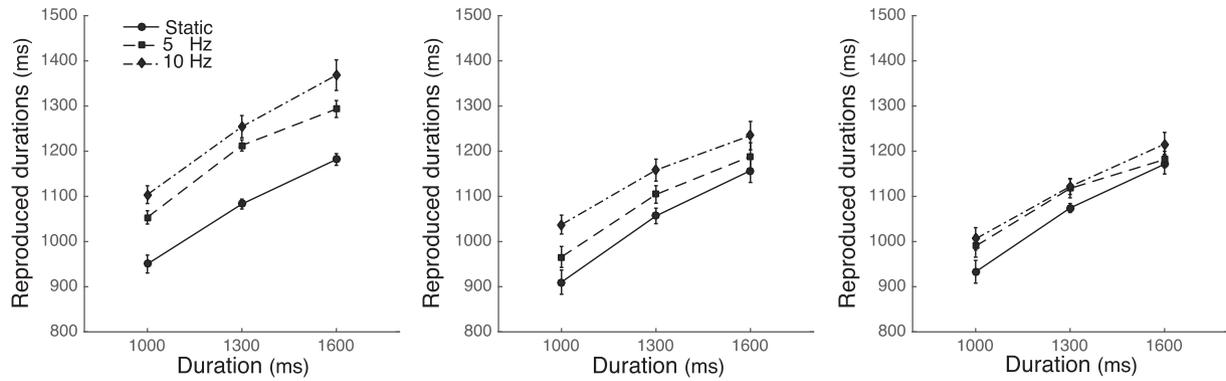
Fig. 2. Average Reproductions plotted as a function of the presented durations for each Temporal Frequency. Separate plots for each of the Occlusion conditions, left to right: Non-Occluded, Occluded, Extinction. Error bars reflect within-subject standard errors.

condition compared to both the Occlusion and Extinction conditions ($t(19) = 3.27$, $p = 0.007$ and $t(19) = 3.28$, $p = 0.007$, respectively). There was no significant difference between the Occlusion and Extinction conditions ($t(19) = 0.01$, p = 0.995). Finally, we observed a significant interaction between Duration and Temporal Frequency ($F(2.51,47.66) = 10.42$, $p < 0.001$, $\eta^2 = 0.35$). There were no other significant interactions: Duration * Temporal Frequency ($F(2.85,54.01) = 1.87$, $p = 0.148$, $\eta^2 = 0.09$), Duration * Occlusion ($F(2.57,48.81) = 1.35$, $p = 0.271$, $\eta^2 = 0.07$), and Duration * Temporal Frequency * Occlusion ($F(8,152) = 1.84$, $p = 0.074$, $\eta^2 = 0.09$).

To understand the observed interaction between Temporal Frequency and Occlusion we compared the magnitude of time dilation between each of the Occlusion conditions. By doing so we can assess whether, and how, the observed time dilation differed between each of the occlusion conditions. We expected a larger effect of temporal frequency content in the Non-Occluded condition compared to both the Occlusion and the Extinction conditions. More importantly, if information about the temporal frequency content of the test stimulus is maintained during occlusion we expect the observed time dilation to be larger for the Occluded condition compared to the Extinction condition. Because there was no significant interaction that included the factor Duration we first averaged our data across the different test durations. We then subtracted the average reproductions for the Static condition from the average reproductions for both the 5 Hz and 10 Hz conditions for each of the occlusion conditions. The resulting difference scores reflect the amount of time dilation occurring in the 5 Hz and 10 Hz conditions for each of the occlusion conditions (Fig. 3).

Next we conducted a 2×3 repeated-measures ANOVA with Magnitude of Time Dilation as the dependent variable and Temporal Frequency (5 Hz, 10 Hz) and Occlusion (Non-Occluded, Occlusion, Extinction) as factors. This analysis revealed a main effect of Temporal Frequency ($F(1,19) = 18.47$, $p < 0.001$, $\eta^2 = 0.49$), indicating that there was more time dilation in the 10 Hz condition compared to the 5 Hz condition. Next, we observed a main effect of Occlusion ($F(2,38) = 12.21$, $p < 0.001$, $\eta^2 = 0.39$), which shows that the amount of time dilation was different between the three Occlusion conditions. We analyzed this difference by conducting pairwise comparisons, revealing that the amount of time dilation was significantly higher in the Non-Occluded condition, compared to both the Occluded ($t(19) = 3.61$, $p = 0.004$) and Extinction conditions ($t(19) = 4.38$, $p = 0.001$). No significant difference was observed between the Occluded and Extinction conditions ($t(19) = 1.45$, $p = 0.16$). However, we did observe a significant interaction effect between Temporal Frequency and Occlusion condition ($F(2,38) = 5.22$, $p = 0.01$, $\eta^2 = 0.22$). This significant interaction seemed to reflect a larger
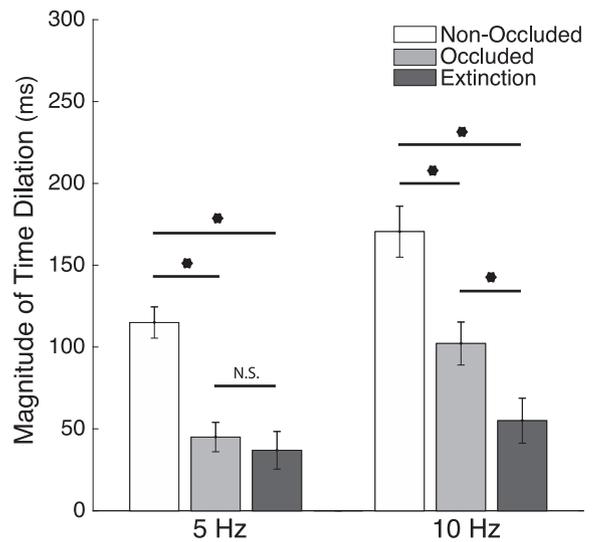
Fig. 3. Magnitude of Time dilation, plotted separately for each Temporal Frequency (5 Hz, 10 Hz), for each of the Occlusion conditions (Non-Occluded, Occluded, Extinction). Diamonds indicate significant deviation tested at an alpha of 0.05 (corrected for multiple comparisons). Error bars reflect within-subject standard errors.

difference between the different occlusion presentations in the 10 Hz condition compared to the 5 Hz condition (Fig. 3). To investigate this apparent difference in the magnitude of time dilation in the 5 Hz and 10 Hz conditions, we conducted two separate repeated-measures ANOVAs with Magnitude of Time Dilation as the dependent variable and Occlusion (Non-Occluded, Occluded, Extinction) as a factor. For the 5 Hz condition we found a main effect of Occlusion ($F(2,19) = 12.09$, $p < 0.001$, $\eta^2 = 0.39$). Subsequent paired sample t-tests revealed that this effect reflected a significant difference between the Non-Occluded and Occlusion and Extinction conditions, $t(19) = 4.81$, $p < 0.001$ and $t(19) = 4.07$, $p < 0.001$ respectively. There was no significant difference between the Occlusion and Extinction conditions ($t(19) = 0.44$, $p = 0.665$). For the 10 Hz condition we again found a main effect of Occlusion ($F(2,19) = 11.19$, $p < 0.001$, $\eta^2 = 0.37$). Subsequent paired sample t-tests revealed that this effect reflected a significant difference between the Non-Occluded and the Occlusion and Extinction conditions, $t(19) = 2.70$, $p < 0.028$ and $t(19) = 4.40$, $p < 0.001$ respectively. More importantly, there was a significant difference between the Occlusion and Extinction conditions ($t(19) = 2.15$, $p = 0.044$), with more time dilation during occlusion presentations compared to the extinction presentations.

2.3. Discussion

We found that the presentation of luminance-modulated stimuli (5, 10 Hz) led to longer reproductions compared to static stimuli and that this effect was larger for the high temporal frequency stimuli (10 Hz) compared to the lower temporal frequency stimuli (5 Hz). In other words, the participants judged the duration of the stimulus as being longer with increased temporal frequency content. This replicates the results of earlier studies in which increases in temporal frequency content cause dilation of perceived duration (Kanai et al., 2006; Ortega & López, 2008). Subsequent analysis showed that significant time dilation occurred in each of the three occlusion conditions (Non-Occluded, Occluded, Extinction). More importantly, we compared the magnitude of time dilation between each of the Occlusion conditions. We found significantly larger time dilation for non-occluded presentations compared to the occluded and extinction presentations, for both the 5 Hz and 10 Hz presentations. Crucial to answering our question, we observed larger time dilation in the Occluded condition compared to the Extinction condition, but only for the 10 Hz luminance-modulated stimuli. In the 5 Hz condition, no significant difference between Occlusion and Extinction conditions was observed. These results show that the observed time dilation for the occluded presentations did not results from the pre- and post- occlusion presentation of the stimulus and instead reflected the continued representation of temporal frequency content during periods of occlusion.

3. Experiment 2

Experiment 1 provides the first evidence for the representation of dynamic features during occlusion. In this experiment, we used the Extinction condition as a control for any time dilation that resulted from the pre- and post- occlusion presentation of the modulated stimulus. This Extinction condition was constructed to mimic the decrease in temporal frequency content that occurs during occlusion, without the deletion and accretion cues that accompany occlusion. As a result, the way in which the temporal frequency content is erased differs between the two conditions. In the Occluded condition the temporal frequency content of the stimulus is removed as the edge of the occluder moves over the stimulus. In the Extinction condition however, this loss of temporal frequency content occurs gradually across the entire stimulus. This difference in the way in which the stimulus loses its temporal frequency content might result in a difference between the points in time at which the stimulus is perceived as losing its temporal frequency content. Furthermore, differences in the temporal frequency and contrast profiles of stimuli have been shown to cause changes in the perceived duration of an event (Bruno & Johnston, 2010; Matthews, 2011; Bruno, Ayhan, & Johnston, 2012; Bruno, Ayhan, & Johnston, 2015). While the modulations used in these studies do not match the conditions presented here, they underscore the sensitivity of duration perception to differences in low-level visual properties. As a result, we cannot be sure that differences in the way by which temporal frequency content was erased in both conditions contribute to the differences we found in the reproduced durations.

To address this concern, we designed a second experiment in which we compared two occlusion events that were visually identical but differed in the expected temporal frequency content of the stimulus during occlusion. Earlier work on object permanence and inhibition of return (IOR) has shown that manipulating expectations about occluded stimuli can lead to changes in preferential looking behavior (Spelke, Kestenbaum, Simons, & Wein, 1995) and IOR (Jefferies, Wright, & Lollo, 2005). These studies demonstrate that expectations can change observers' representations of occluded objects. By manipulating participants' expectations about the temporal frequency content of stimuli during occlusion, we can probe the representation of temporal frequency without changing the visual properties of the presentations.

Similar to experiment 1 we presented participants with a duration reproduction task in which they reproduced the duration of stimuli that either remained visible or became occluded after a short delay. We manipulated participants' expectations about the temporal frequency content of the stimulus during occlusion by changing the context in which the occlusion event occurred. Each block of trials contained a single type of stimulus: a static stimulus (Static), a stimulus modulated at 10 Hz (Continuous), or a stimulus whose 10 Hz modulation was temporarily extinguished (Disrupted). The goal of this blocked design was to support the expectation that the occluded stimulus had the same properties as the non-occluded stimulus presented in the same block. As a result participants should have different expectations for the properties of the stimulus while it is under occlusion. For the Continuous modulation blocks, the continuously modulated stimulus for the non-occluded trials will provide evidence that the stimulus continues to flicker while disappearing behind the occluder. In the Disrupted modulation blocks, however, the non-occluded trials will provide evidence that the stimulus will cease to flicker once it is occluded. To strengthen this expectation of the stimulus' properties during occluded, we added induction trials at the start of each block in which the occluder moved in front of the stimulus but was semi-transparent. This allowed participants to observe the stimulus while it was being 'occluded', strengthening the assumption of a common fate for non-occluded and occluded stimuli.

Crucially, the disruption of the temporal frequency modulation always occurred after the occluder had fully moved in front or behind the stimulus. As a result, the occlusion event for the continuous and disrupted stimuli is visually identical, differing only in the expected temporal frequency of the stimulus during the occlusion event. We hypothesized that if temporal frequency is represented during occlusion, we should find more time dilation for occlusion events presented in the context of continued modulation, compared to those presented in the context of disrupted modulation.

3.1. Methods

3.1.1. Participants

21 Healthy participants completed this experiment (7 male; mean age = 23.24, SD = 3.63). All participants had normal or corrected-to-normal vision and normal stereoscopic vision. All participants gave written informed consent before participating and received monetary reward as compensation. The experiment was conducted in line with the principles expressed in the Declaration of Helsinki and received approval by the local ethics committee.

3.1.2. Apparatus and stimuli

All materials were identical to those used in Experiment 1. The visual properties of all stimuli were also identical to those used in Experiment 1; any differences are reported in the procedure.

3.1.3. Procedure

The procedure was similar to that of the first experiment. Each trial started with the presentation of a white central fixation cross, noise frame, and a grey-black textured occluder presented above fixation. This occluder was either opaque (Non-Occluded, Occluded) or semi-transparent (Induction). After 250 ms the fixation cross was replaced with a white circle with a duration sampled from a uniform distribution ranging between 1000 and 1600 ms. This test stimulus was either static, continuously

modulated at 10 Hz, or modulated with a temporary disruption. This disruption occurred in line with the occlusion event, always starting and ending when the occluder fully overlapped with the stimulus. To avoid strong transients, the disruption always started and ended on the average luminance of the stimulus. This resulted in three temporal frequency profiles: Static, Continuous, and Disrupted. After a short delay (33, 67, 100 ms) the occluder moved downward (13.68°/s) going either in front (Occluded, Induction) or behind (Non-Occluded) the stimulus. After 217 ms the center of the occluder was aligned with the center of the screen. After the occluder had stopped moving, it maintained its position for 466–1133 ms depending on the duration of the stimulus and the starting delay. Following this period, the occluder moved up to its original position (at 13.68°/s) and remained on the screen. Participants reproduced the presented duration by pressing and holding the right arrow key. A new trial was initiated by pressing the spacebar.

Participants were tested in a 2×3 within-subject factorial design. The two factors were Occlusion (Non-Occluded, Occluded), and Temporal Frequency (Static, Continuous, Disrupted). Participants completed six blocks, with each block consisting of a single Temporal Frequency presentation and both occlusion conditions. The order of these blocks was counterbalanced across participants. Within each bock all combinations of the occlusion representations were counterbalanced and randomized across trials. Each blocked started with 25 repetitions of the two occlusion conditions (Non-Occluded, Occluded) as well as 25 Induction trials, followed by a further 50 repetitions of only the Non-Occluded and Occluded conditions. This resulted in a total of 50 trials for each unique combination between Induction trials and Temporal Frequency, and 150 trials for each unique combination with the Non-Occluded and Occluded conditions across the entire experiment. In total, participants completed 1050 trials spread over two 45-min sessions interrupted by a 15-min break.

3.2. Results & discussion

Because we presented randomly sampled durations between 1000 and 1600 ms, we first needed to calculate the reproduction error for each individual trial. To do this we calculated the ratio between the duration reproduced by the participants and the presented duration on each trial. Similar to the first experiment we then removed all individual trials with reproduction ratios two standard deviations larger or smaller than the mean for each condition, for each individual participant. This procedure resulted in the removal of 817 trials (3.71%). Next, we calculated the average reproduction ratio for each condition (Fig. 4).

The resulting data were analyzed in a 2×3 repeated-measures ANOVA with Reproduction Ratios as the dependent variable and Occlusion (Non-Occluded, Occluded) and Temporal frequency (Static, Continuous, Disrupted) as factors. As in Experiment 1 Greenhouse-Geisser corrections were used when the assumption of sphericity was violated. All post-hoc comparisons using t-tests were adjusted for multiple comparisons using the Holm-Bonferroni correction method (Holm, 1979). Corrected p-values are reported. Error bars in all images reflect within-subject standard errors, calculated using per-subject normalization of the data (Cousineau, 2005; Morey, 2008). Data for Induction trials were not analyzed here because we only collected one third of the data collected for the other Occlusion conditions, and because the results were not of our primary interest. A separate ANOVA was conduced for the Induction trials, which showed similar results to the data reported for the Non-Occluded condition.

We observed a main effect for Occlusion $(F(1,20) = 6.41, p < 0.020, \eta^2 = 0.24)$ reflecting longer reproductions for the Non-Occluded compared to the Occluded stimuli. We also observed a
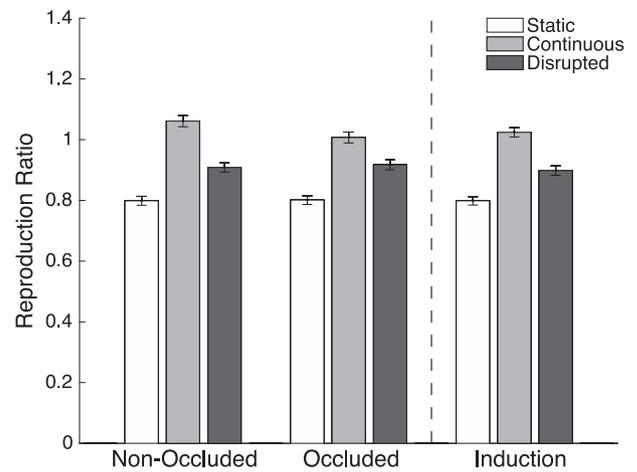

Fig. 4. Average Reproduction Ratios, plotted separately for each Occlusion (Non-Occluded, Occluded, Induction) and Temporal frequency condition (Static, Continuous, Disrupted). Induction data were provided for transparency but are not analyzed in the manuscript. A reproduction ratio of 1 reflects veridical reproductions, with lower values reflecting underestimation and higher values reflecting overestimation. Error bars reflect within-subject standard errors.

main effect of Temporal Frequency $(F(2,40) = 29.638, p < 0.001, \eta^2 = 0.597)$. Pairwise comparisons revealed that this main effect reflected shorter reproductions in the Static condition compared to both the Continuous and Disrupted conditions $(t(20) = -7.70, p < 0.001$ and $t(20) = -3.82, p < 0.001$, respectively). Furthermore, reproductions were longer in the Continuous condition compared to the Disrupted condition $(t(20) = 3.88, p < 0.001)$. Finally, we observed a significant interaction between Occlusion and Temporal frequency $(F(2,40) = 34.46, p < 0.001, \eta^2 = 0.633)$.

To better understand the interaction between Occlusion and Temporal Frequency we conducted a second analysis comparing the time dilation found for the Continuous and Disrupted conditions. We first calculated the percentage of time dilation for each Occlusion condition, for each participant (Fig. 5). These data were then subjected to a 2×2 repeated-measures ANOVA with Time Dilation (%) as the dependent variable and Temporal frequency (Continuous, Disrupted) and Occlusion (Non-Occluded, Occluded) as factors. Results showed main effects for Temporal Frequency $(F(1,20) = 10.83, p = 0.004, \eta^2 = 0.351)$ and Occlusion $(F(1,20) = 10.69, p < 0.004, \eta^2 = 0.348)$. There was also a significant interaction
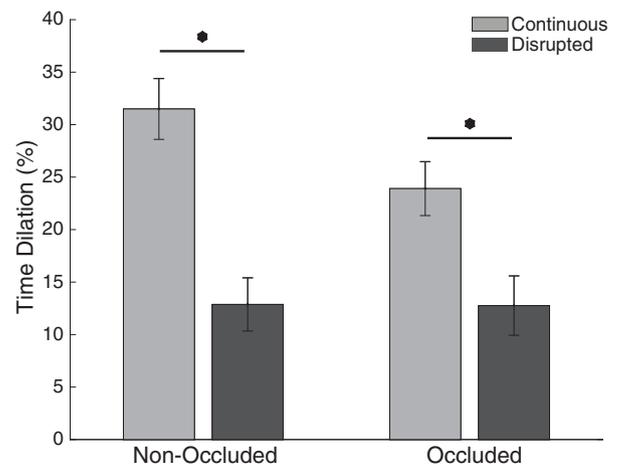
Fig. 5. Average Time Dilation (%) for the Continuous and Disrupted presentations, plotted separately for each Occlusion condition (Non-Occluded, Occluded). Diamonds indicate significant deviation tested at an alpha of 0.05. Error bars reflect within-subject standard errors.
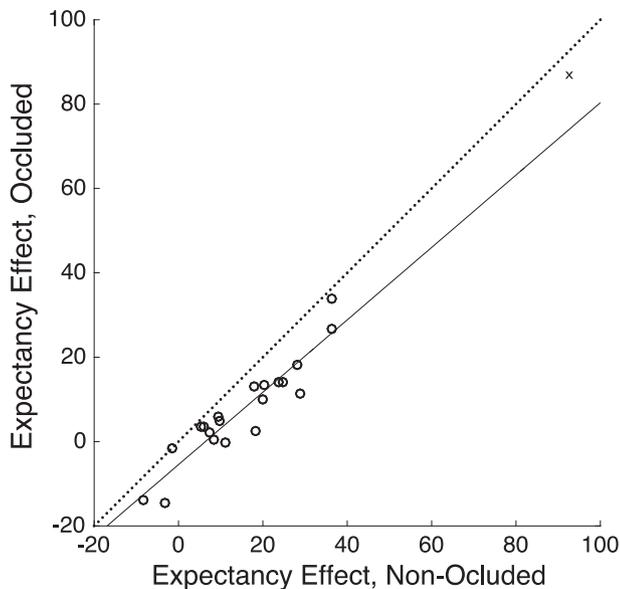
Fig. 6. Scatterplot plotting the percentage of Time dilation that results from the difference in expected temporal frequency (Expectancy effect, %), for the Non-Occluded (x-axis) and Occluded (y-axis) conditions. Each open circle represents an individual participant. The x indicates an outlier (deviation >2*std), which was not included in the analysis. The dotted line indicates the regression line while the solid line represents the unity line.

between Temporal Frequency and Occlusion ($F(2,40) = 58.34$, $p < 0.001$, $\eta^2 = 0.745$) which seems to reflect a smaller difference between the Continuous and Disrupted conditions for the Occluded condition, compared to the Non-Occluded condition. To further interpret this interaction we conducted two separate paired sample t-tests, one for each Occlusion condition. For the Non-Occluded condition we found larger time dilation for the Continuous condition compared to the Disrupted condition ($t(20) = 4.08$, $p < 0.001$). More importantly, for the Occluded condition we found the same result with larger time dilation in the Continuous condition compared to the Disrupted condition ($t(20) = 2.46$, $p = 0.023$). Since the Occluded version of the Continuous and Disrupted conditions were visually identical, this difference can only be explained by a difference in the representation of the stimulus during occlusion as a result of the different context in which they were presented. To further support the claim that these results reflect a difference in expected temporal frequency, we conducted a correlational analysis of the difference in Time Dilation between the Continuous and Disrupted conditions for the Non-occluded and Occluded conditions. We first calculated the difference in percentage of time dilation between the Continuous and Disrupted conditions. The resulting difference score reflects the time dilation that can only be explained by the difference in expected temporal frequency. We then correlated this Expectancy Effect for the Non-Occluded and Occluded conditions and found a strong correlation ($r = 0.93$, $p < 0.001$; Fig. 6). This correlation supports the idea that participants' representation of the occluded stimulus is based on their non-occluded counterpart. Together, these results demonstrate that dynamic stimulus properties can be represented during occlusion, and that this representation can be modulated by expectations about the stimulus during the occlusion event.

4. General discussion

In this study we investigated whether dynamic stimulus information is represented during occlusion. To answer this question we used a well-known temporal illusion (temporal frequency

induced time dilation) in which the perceived duration of a stimulus increases with an increase in temporal frequency content. We combined this illusion with a situation of stimulus occlusion to probe the representation of temporal frequency during occlusion. We hypothesized that if temporal frequency content is represented during occlusion it should affect judgments of duration made for temporarily occluded stimuli. To test this hypothesis we conducted two experiments.

In the first experiment, participants reproduced the duration of a stimulus that was either static or luminance-modulated (5 Hz, 10 Hz). During each presentation the stimulus either remained visible (Non-Occluded) or became temporarily occluded (Occluded). In a third, control condition (Extinction), the stimulus remained visible but its luminance modulation temporarily faded out, mimicking the loss of temporal frequency information in the occluded condition. This allowed us to dissociate between time dilation as a results of pre- and post- occlusion presentation of the stimulus and time dilation occurring during the period of occlusion. We observed clear time dilation, with longer reproductions for the luminance-modulated stimuli (5 & 10 Hz) compared to the static stimuli. Moreover, this effect was larger for the 10 Hz modulation compared to the 5 Hz modulation. Furthermore, time dilation occurred in all three occlusion conditions, with the effect being larger for the Non-Occluded condition compared to the Occlusion and Extinction conditions. More importantly, time dilation was larger in the Occluded condition compared to the Extinction condition. This was true only for the 10 Hz luminance modulation, with no difference being observed for the 5 Hz modulation. This result indicates that the time dilation in the Occluded condition cannot be fully explained by the pre- and post- occlusion presentation of the stimulus. Instead, it argues for a representation of temporal frequency content during periods of occlusion.

In a second experiment we manipulated the expected temporal frequency of stimuli during occlusion by presenting occlusion events in different contexts of non-occluded presentations. These contexts consisted of blocked presentations of stimuli that were either static, continuously modulated at 10 Hz, or modulated at 10 Hz with a temporary disruption occurring in line with the occlusion event. The goal of these blocked presentations was to strengthen the assumption that the occluded stimulus had the same visual properties as its non-occluded counterpart. Since the disruption of temporal frequency content occurred during the occlusion of the stimulus, the continuous and disrupted modulations were visually identical when the stimulus became occluded. This allowed us to compare reproductions for occlusion events that were visually identical, but differed in the expected temporal frequency content of the stimulus during occlusion. We observed time dilation for the continuously modulated and disrupted stimuli, both when they were occluded as well as when they remained visible. We also observed larger time dilation for stimuli that were continuously modulated compared to the disrupted stimuli. This was true for the non-occluded presentations, which differed in their visual properties, but also for the occluded presentations, which were visually identical. Because the occluded presentations were visually identical, these observed difference between continuously modulated and disrupted stimuli cannot be explained by pre- and post- occlusion presentations of the stimulus. Together, these results demonstrate that dynamic stimulus properties can be represented during occlusion, and that this representation can be modulated by expectations about the stimulus during the occlusion event. Correlation analysis showed a strong correlation between time dilation for the non-occluded and occluded presentations, further supporting the notion that participants' representation of the occluded stimuli had similar properties as their non-occluded counterparts.

Our study provides the first evidence that dynamic stimulus properties other than changes in location are represented during occlusion. This shows that the representation of an occluded object can incorporate a wide range of information that has been accumulated over time and argues for a veridical representation of the visual features of the occluded object. The effect of temporal frequency on duration estimation during occlusion occurred even though the temporal frequency content of the stimulus was irrelevant for the completion of the task. This shows that dynamic properties of the stimulus can be represented automatically without any focused effort to maintain the information, similar to the results reported in earlier studies (Ban et al., 2013; Murray et al., 2006). Overall, these findings support the idea that observer maintain a rich, object-like representations of objects under occlusion based on the visual properties encoded during perception of the object before occlusion. Similar perception-like representations have been proposed and verified to underlie visual imagery (Bartolomeo, 2002; Johnson & Johnson, 2014), and visual working memory (Harrison & Tong, 2009). In general, findings from these domains support the view that internal representations of objects or events in the visual modality rely on a process of reactivation in visual areas that is highly similar to the activation observed during actual perception.

One possible concern about the results of Experiment 1 stems from the crucial comparison between the Occlusion and Extinction conditions. The goal of the Extinction condition was to mimic the loss in temporal frequency content, without the use of deletion and accretion cues that normally accompany occlusion events. This leads to a qualitative difference in the disappearance of the temporal frequency content between the two conditions. For the Occlusion condition the stimulus loses and gains contrast energy as a function of the spatial location of the occluder. For the Extinction condition the contrast energy fades linearly across the entire stimulus in the same time it takes the occluder to fully occlude the stimulus. These differences in the way temporal frequency content is removed could affect the perceived duration of the two events differently, compromising our comparison between the two conditions. When discussing these differences in the loss of temporal frequency content, it is important to stress that they pertain to the contrast energy of the stimulus that signals the temporal frequency, and not the temporal frequency itself. Several studies have shown that changes in temporal frequency content and speed can affect the perceive duration of an event (Bruno et al., 2012; Bruno et al. 2015; Matthews 2011). However, in our experiment the temporal frequency changes from 10/5 Hz to static in both the Occluded and Extinction conditions. As such, these types of effects do not confound the data presented here. What does differ between these two conditions is the way in which the contrast energy of the stimulus decreases. Bruno and Johnston (2010) have shown that changes in contrast can lead to changes in the perceived duration of events. More specifically, they showed that a few seconds of adaptation to a high contrast stimulus with a temporal frequency of 10 Hz or higher resulted in compression of a subsequent interval compared to adaptation to a lower contrast. Since our stimulus loses contrast energy during occlusion/extinction, similar compression of the occluded interval could occur. Given the qualitative difference between the two conditions, this compression could differ between the two occlusion conditions. However, it is unclear in what condition contrast adaptation would be higher, making it difficult to predict which interval would be compressed more. Moreover, since these compression effects are relatively small, ranging within the 10–20 ms range for 10 Hz presentations after more than a second of adaptation, it is unlikely to explain the ∼50 ms difference in time dilation reported here. A second possible issue with the difference in decrease of the contrast energy of the stimulus is that it could lead

to a difference in the time point at which evidence for the presence of a 5/10 Hz signal falls below threshold. Plotting the total stimulus contrast as a function of time shows a linear pattern for the Extinction presentation and a pattern that approaches linearity for the Occlusion presentation (with slight deviations due to the stimulus being a circle, see Supplementary materials: Fig. S1). Given the similar global spatiotemporal profiles of the two conditions and the relatively short occlusion period (133 ms, ∼0.65/1.3 cycles for the 5/10 Hz presentations), it seems unlikely that the time point at which the stimulus is viewed as no longer flickering is very different between the Occlusion and Extinction conditions. As a result, any difference in the total on-period of the temporal frequency signal should be relatively small and will not lead to any substantial shifts in the perceived duration of the pre- and post-occlusion segments of the Occlusion condition compared to the Extinction condition. Any differences that do occur are unlikely to account for the twofold increase in the magnitude of the duration illusion observed between the Occluded (102 ms, 60% remaining of the illusion found for non-occluded presentation) and Extinction (56 ms, 33% remaining of the illusion found for non-occluded presentation) presentations in the 10 Hz conditions. This conclusion is further supported by the fact that the effect of temporal frequency content on duration tends to plateau for longer durations. The initial presentation of the temporal frequency signal causes the largest amount of dilation, with only a small, non-linear added dilation effect resulting from an increase in the duration of the event (Kanai et al., 2006). To conclude, while the Occluded and Extinction condition differ in their visual properties, these differences are unlikely to explain the reported difference between the Occlusion and Extinction conditions.

In Experiment 1, we did not find evidence for the representation of temporal frequency content during occlusion for stimuli modulated at 5 Hz. One possible explanation for this result is the smaller time dilation effect for the non-occluded presentations of the 5 Hz stimuli. Less time dilation for non-occluded stimuli predicts smaller amounts of time dilation in the occluded and extinction presentations, which could result in smaller differences between the two conditions that can no longer be detected in the noise of participants' performance. Alternatively, the lack of time dilation for 5 Hz modulation could be explained by the lower sensitivity to 5 Hz stimulation compared to 10 Hz stimulation. Earlier work has shown that human observers are most sensitive to temporal frequencies ranging between 8 and 12 Hz (Kelly, 1961; Shady, MacLeod, & Fisher, 2004). This difference in the encoding of the information could results in a weaker representation of the temporal frequency information, explaining the lack of an effect in the 5 Hz condition. Finally, it has been documented that higher contrast in temporal frequency content between stimuli capture attention (Cass, Van der Burg, & Alais, 2011). In our experiment the difference in temporal frequency content between the stimulus and the static background is much larger in the 10 Hz condition than it is in the 5 Hz condition. Similar to the previous point, such a difference could lead to less effective encoding of the temporal frequency content of the stimulus, resulting in a smaller/no effect for stimuli with a lower temporal frequency content. Within the current design it is not possible to validate or dissociate any of these explanations.

Previous experimental work examining the relative contribution of spatio-temporal versus feature information has shown that both can be used to establish object correspondence during occlusion events (Flombaum et al., 2009; Hollingworth & Franconeri, 2009; Moore et al., 2010). However, tracking combinations of feature and location information seems to be an effortful process with a limited capacity (Cohen, Pinto, Howe, & Horowitz, 2011; Saiki, 2003). As a result, it seems that spatiotemporal information is often prioritized over feature information even when both are

available. (Flombaum et al., 2009; Kimchi & Pirkner, 2014; Scholl, 2007). Furthermore, the extent to which each of these types of information is used seems to depend on the informativeness and reliability of each source of information (Hein & Moore, 2012; Papenmeier, Meyerhoff, Jahn, & Huff, 2013). In the current study, the location of the stimulus was constant throughout the experiment. This lack of change in the spatial location of the stimulus decreases the relevance of this information and lowers the need for integration of spatio-temporal and feature information. It is unclear how the addition of locational change would influence the representation of the dynamic feature properties of an object. Most likely, a similar prioritization of spatio-temporal information will be observed. Alternatively, the temporal component of feature change could increase the informativeness of an objects features resulting in increased prioritization of the feature information. Investigating this interaction could further inform theories about the importance of the temporal components of feature and location information in the prioritization of spatio-temporal information.

This study focused on temporal frequency as a dynamic object property. However, information about dynamic properties like temporal frequency and speed are derived from other sources of visual information. In our study, temporal frequency content is derived from the rate of luminance change over time. However, other changes – such as changes in color under conditions of equiluminance – also convey temporal frequency information. This raises an interesting question about the way by which temporal frequency information is represented during occlusion. One possibility is that the information is represented in neurons encoding the actual changes in luminance. Luminance and contrast sensitive neurons in lower level visual areas have been shown to possess selectivity for a wide range of temporal frequencies (Foster, Gaska, Nagler, & Pollen, 1985; Singh, Smith, & Greenlee, 2000) and as such can represent both the changes in luminance as well as the resulting temporal frequency. However, since temporal frequency selective neurons are present throughout the visual cortex (D'Souza, Auer, Strasburger, Frahm, & Lee, 2011; Fawcett, Barnes, Hillebrand, & Singh, 2004; McKeeff, Remus, & Tong, 2007; Singh et al., 2000) it is also possible that this information is represented in other visual areas, independent of the signal that defines the temporal frequency content. Previous work has already shown that information about motion is represented as both locational changes over time (Ban et al., 2013) as well as its velocity derived from this locational change (Olson et al., 2004), showcasing this possible distinction. Whether a similar redundancy occurs for the representation of dynamic stimulus properties such as temporal frequency remains an interesting topic for future study.

Acknowledgments

Appendix A. Supplementary data 1

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.visres.2017.05.012.

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