EFFECT OF SPATIAL FREQUENCY ADAPTATION ON LOCATION-BASED INHIBITION OF RETURN AS A FUNCTION OF TARGET SPATIAL FREQUENCY

by

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(Under the Direction of James M. Brown)

ABSTRACT

The current study used an inhibition of return (IOR) paradigm to investigate the relationship between spatial attention and the magnocellular (M) and parvocellular (P) pathways. By selectively adapting participants to a particular spatial frequency (1 cpd or 12 cpd), we expected to find differences in IOR values depending on how adaptation influenced visual pathway activity. Simple reaction times (RTs) to target onset were relatively equal across adaptation conditions, with RTs to 12 cpd targets longer than RTs to 1 cpd targets. Target spatial frequency differences in IOR were not found. However, overall IOR was greater in the 1 cpd, relative to the 12 cpd adaptation condition and the control condition. These findings suggest adapting the M-pathway using a low spatial frequency affected IOR more than adapting the P-pathway using a high spatial frequency.

INDEX WORDS: spatial frequency adaptation; inhibition of return; covert attention; magnocellular & parvocellular pathways

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CHAPTER 1

INTRODUCTION

For decades, spatial attention has been manipulated and studied using cuing paradigms. One common type of cuing paradigm is a covert cuing task with an exogenous cue. In a covert cuing task, cues draw attention to different locations in space without overt eye movements. The non-informative, exogenous cue captures attention involuntarily and provides no information about the location of the target. The target has an equal chance of appearing at a cued or uncued location. The current study used a covert cuing task with an exogenous cue. As one might expect, when a cue draws attention to the location of a target in advance, responses are typically faster (i.e., the cue facilitates responding). When a target appears at an uncued location, responses are slower, reflecting the added time to reorient attention away from the cue before responding to the target (Posner & Cohen, 1984). However, Posner and Cohen (1984) showed that as the time between the cue and target increases, responses to cued locations are no longer facilitated. When the time between the cue and target exceeds about 300 ms, responses are inhibited for targets appearing at cued locations compared to uncued locations. This difference in response times for cued and uncued locations is oftentimes referred to as inhibition of return, or IOR. Location-based IOR is hypothesized to reflect an attentional bias away from previously inspected locations.

Recently studies by Brown and colleagues have used an IOR paradigm to measure the influence of the magnocellular (M) and parvocellular (P) visual streams on attention by manipulating sensory characteristics of stimuli to selectively stimulate one stream over the other. The M and P pathways are the two primary retino-geniculo-striate pathways providing primary initial input to the dorsal “where” stream in the parietal lobe and the ventral “what” stream in the temporal lobe, respectively; although there is evidence the contributions from each pathway are not exclusive (Ogmen, Breitmeyer, & Melvin, 2003; Ungerleider & Haxby, 1994; Vidyasagar, Kulikowski, Lipnicki, & Dreher, 2002). The M/dorsal stream is sensitive to low spatial frequencies and characterized by neurons with large center-surround receptive fields; while the P/ventral stream is sensitive to higher spatial frequencies and characterized by neurons with smaller center-surround receptive fields (Casagrande & Ichida, 2006; Derrington & Lennie, 1984). Guenther and Brown (2007) found P/ventral-biased stimuli elicited greater amounts of IOR, relative to M/dorsal-biased stimuli. In other words, trials with high spatial frequency targets had greater IOR relative to trials with low spatial frequency targets. The purpose of the current study was to investigate the relationship between spatial attention and the visual pathways, by selectively adapting one pathway relative to the other. Adapting a specific spatial frequency channel could alter the response of the M/dorsal or P/ventral pathways, depending on the adapting spatial frequency. Here we used a low and a high spatial frequency adapting stimulus to influence pathway activity and measured the effect on IOR, our attentional construct.

Visual Pathways and IOR

Reorienting attention from one location to another can be influenced by changes in low-level sensory characteristics that bias processing towards the M/dorsal or P/ventral streams (Carrasco, Loula, & Ho, 2006; Guenther & Brown, 2007; Sumner, 2006; Sumner, Nachev, Vora, Husain, & Kennard, 2004; Yeshurun, 2004). Guenther and Brown (2007) manipulated target spatial frequency to selectively stimulate one visual pathway over the other. Targets and cues were Gabor patches of 1 cpd, 4 cpd, or 12 cpd and were presented in pairs of frequencies in three between-subjects conditions to favor either the M/dorsal or P/ventral pathway (i.e., 1 cpd & 12 cpd; 1 cpd & 4 cpd; 4 cpd & 12 cpd). Simple reaction time (RT) to target onset was measured to targets appearing at cued and uncued locations, using a long stimulus onset asynchrony (SOA; 1450 ms) expected to produce IOR. Consistent with previous findings, a sensory effect on RTs due to spatial frequencies was evident. Overall RTs were longer to the 12 cpd target, compared to the 1 cpd and 4 cpd targets, as well as for 4 cpd compared to 1 cpd (e.g., Breitmeyer, 1975; Solberg & Brown, 2002). This sensory effect is thought to reflect the slower response of the P/ventral pathway, indicated by longer RTs as spatial frequencies increase and responses to them become more P/ventral based (Breitmeyer, 1975). Interestingly, they found 12 cpd targets elicited greater differences between cued and uncued location RTs (i.e., 12 cpd targets had greater IOR as compared to the 1 cpd targets), which indicates reorienting attention back to cued locations was inhibited more by stimuli biased toward the P/ventral relative to the M/dorsal pathway.

Sumner and colleagues also measured IOR while manipulating M and P activity. Sumner et al. (2004) directed covert attention to peripheral locations using non-informative cues at an SOA of 400 ms. Half of the cues were changes in brightness, while the other half changes in color. The cues changing in color were designed to only be visible to the short-wavelength-sensitive cones; hence, they were considered invisible to the color deficient M pathway. As the M pathway is thought to be responsible for detecting abrupt visual changes, it was considered necessary to elicit IOR. However, they found the same amount of IOR was elicited in the color change condition as the brightness condition for manual responses, suggesting IOR can be elicited without M pathway contribution. There is some evidence that spatial attention at cued, or attended, locations facilitates P/ventral activity, while M/dorsal activity is inhibited (Yeshurun &

Levy, 2003). Since the M/dorsal pathway is not necessary to produce IOR, it could additionally support the idea that spatial attention inhibits M/dorsal activity at cued locations.

Spatial Frequency Adaptation and Covert Attention

Another way to manipulate the contribution of M/dorsal and P/ventral activity and spatial covert attention is through the use of selective adaptation to spatial frequencies. Spatial frequency adaptation, the prolonged exposure to a particular spatial frequency, causes a reduction in contrast sensitivity for the same spatial frequency in the same orientation. This reduction affects nearby spatial frequencies within approximately 1-2 octaves (i.e., one octave is about twice, or half, the original spatial frequency), and to a lesser extent, stimuli within a 15° orientation (Blakemore & Campbell, 1969; De Valois, Albrecht, & Thorell, 1982).

Carrasco and colleagues used an exogenous cuing paradigm, while selectively adapting participants to specific spatial frequency gratings, to test whether transient attention improves spatial resolution. Transient attention, also known as exogenous attention, is the involuntary stimulus driven component of attention, which typically captures attention for a brief duration in about 120 ms after the cue (Carrasco et al., 2006; Carrasco & Yeshurun, 2009). Carrasco et al. (2006) presented an exogenous cue in which one of sixteen possible target locations was cued, or a neutral cue in which all sixteen locations were cued. Subjects adapted to either a high (8 cpd) or a low (1 cpd) spatial frequency grating prior to the cuing task. The targets, which could also be 1 cpd or 8 cpd, appeared on a textured background of vertical lines and the subject’s task was to report whether the targets were tilted to the left or to the right.

They found adaptation to a high spatial frequency, compared to a low spatial frequency, improved accuracy for the task at central retinal locations. Typically performance for cued trials is lower than neutral trials at central retinal locations (known as the *central performance drop),* and higher for cued trials in the periphery compared to the neutral trials. This performance drop is thought to reflect a discrepancy between the scale of a texture and spatial filter size, which affects spatial resolution at central and peripheral locations. For example, smaller texture scales are processed better in central locations where spatial filters are also smaller; therefore, presentation of a larger texture scale at central locations would not be processed appropriately due to the size of the spatial filter. In this study, adapting to a high spatial frequency (8 cpd) grating, improved accuracy for cued and neutral trials at central locations, removing the central performance drop; whereas adapting to a low spatial frequency (1 cpd) grating, resembled the baseline condition, maintaining the central performance drop with improved performance for cued trials in the periphery. Carrasco and colleagues suggest transient covert attention raises sensitivity to higher spatial frequencies by altering spatial filter size, which in turn affects spatial resolution. In other words, transient covert attention improves spatial resolution for higher spatial frequencies relative to low spatial frequencies, additionally supporting the hypothesis that spatial attention facilitates P/ventral activity at attended locations.

Recently, Yeshurun (2009) also used spatial frequency adaptation to influence M/dorsal and P/ventral activity and investigate transient attention. She cued one of two possible locations or presented a neutral cue indicating all four possible locations were cued, while adapting participants to either a low (0.25 cpd) or a high (8 cpd) spatial frequency Gabor patch at an orientation of 45° or 135°. The target, presented in a two-interval-forced-choice task, was always the same spatial frequency as the adapting stimulus, but could appear either in the same or opposite orientation as the adapting stimulus. When subjects adapted to 8 cpd, accuracy levels dropped for targets in the same orientation, relative to the opposite orientation, as expected. This adaptation effect (opposite orientation accuracy > same orientation accuracy) was more pronounced for cued relative to neutral locations. When subjects adapted to 0.25 cpd, accuracy was relatively equal for targets of the same and opposite orientation for cued locations; whereas for neutral locations, accuracy levels were impaired for same orientation targets, relative to opposite orientation targets. This indicates a greater decrease in accuracy for stimuli of the same orientation at cued locations during high spatial frequency adaptation and relatively no change in accuracy for stimuli of the same orientation at cued locations during low spatial frequency adaptation. Yeshurun suggests transient attention favors P/ventral activity at cued/attended locations, which leads to an inhibitory effect on the M/dorsal system. Therefore, transient attention would increase adaptation to high spatial frequencies at cued locations and reduce, or eliminate, adaptation to low spatial frequencies.

The studies by Carrasco, Yeshurun, and colleagues show adapting to spatial frequencies to study visual pathway activity and exogenous cuing is not a novel concept. However, the IOR paradigm used in the present study does not necessarily manipulate transient attention as they define it. At long SOAs, the total duration between the first stimulus (i.e., cue) and the response exceeds the approximate 120 ms attentional capture elicited by the cue in a transient attention task (Carrasco et al., 2006). While we cannot assume our experiment is manipulating transient attention, one could argue the abrupt onset of each intermediary stimulus (i.e., blinking refixation cross, target, etc.) could elicit a transient response on its own (e.g., Breitmeyer, 1975; Tolhurst, 1975). Carrasco and colleagues use an orientation discrimination task, amongst other non-RT tasks, to measure the effect of transient attention on the visual pathways. How and if each transient response would affect RTs in an IOR paradigm was unknown.

To the author’s knowledge, this is the first adaptation study to examine the relationship between M/dorsal and P/ventral activity and exogenous cuing, while recording RTs in an IOR paradigm. Previous research has shown simple RTs for adapted stimuli were greater for adapted high spatial frequencies than for adapted low spatial frequencies, when adapting to a high contrast grating (80%) and testing at low contrasts (Menees, 1998). This adaptation effect (post-adapt RT – pre-adapt RT) was greatest for stimuli most similar to the adapting stimulus (i.e., within an octave of the adapting spatial frequency and with a contrast value 0.3 log units above unadapted contrast threshold). As the contrast of the testing grating increased (0.5 or 0.7 log units above), RTs increased as well, but to a much lesser extent. Although perceived contrast of a grating appears lower after adaptation (Blakemore & Campbell, 1969) and RTs increase as contrast decreases (Harwerth & Levi, 1978; Plainis & Murray, 2000), Menees suggests a high contrast test stimulus might have no influence on RTs since it would still be easily detectable. Pilot data by Menees suggests the adaptation effect might decrease to zero as test contrast is increased to much higher levels (50% and 75%).

Present experiment

The primary goal of this study was to determine whether adaptation could influence covert attention, while measuring RTs to suprathreshold stimuli. Following a similar procedure as Guenther and Brown (2007), targets and cues were 1 cpd or 12 cpd. The adapting spatial frequencies were also either 1 cpd (*Adapt 1*) or 12 cpd (*Adapt 12*), with a control condition (*No adapt*) used to assess the effects of adaptation. Two main factors were expected to contribute to the outcome: sensory and attentional. One can think of a sensory effect as a low-level change brought on by some intrinsic property of the stimulus and an attentional effect as a by-product of manipulating visual spatial attention via the covert cuing paradigm used here. Sensory effects should be most evident in RT differences and attentional effects should be most evident by differences between cued and uncued RTs (i.e., IOR).

Depending on whether the adapting and target spatial frequencies were the same (e.g., participant views 12 cpd adapting stimulus and responds to a 12 cpd target, or vice versa) or different from each other (e.g., participant views 12 cpd adapting stimulus and responds to a 1 cpd target, or vice versa), we expected varying sensory outcomes (see Figure 1). When the adapting and target spatial frequencies were the same, the sensory effects of adaptation would be most evident. RTs to targets of the same spatial frequency as the adapting screen were expected to increase, in relation to the No adapt condition, with longer RTs for the 12 cpd targets and shorter RTs for the 1 cpd targets. This would create even longer RTs for adapted high spatial frequencies and adapted low spatial frequencies relative to their unadapted counterparts, similar to the Menees (1998) study. However, if Menees is correct in assuming high contrast stimuli will still be equally detectable, the use of high contrast stimuli in this study might lead to no change in RTs for adapted spatial frequencies. When the adapting and target spatial frequencies were different, the effects of sensory adaptation should be at a minimum, and minimal reduction in the response to the target is expected. Therefore, from a sensory standpoint we expected RTs to be of similar duration to the No adapt condition, with longer RTs for the 12 cpd targets and shorter RTs for the 1 cpd targets.

Depending on whether the visual pathways become activated or become deactivated through adaptation, we expected different attentional effects (see Figure 1). For instance, it is possible the presence of a 12 cpd adapting screen (Adapt 12) will activate the P/ventral pathway. It could be considered that such an activation would create a bias toward P/ventral responding. By continuously activating the P/ventral pathway with a 12 cpd adapting stimulus, IOR may increase, similar to previous studies, which have shown greater IOR to P/ventral-biased stimuli. In the case of the 1 cpd adapting screen (Adapt 1), it is possible the M/dorsal pathway will be activated, creating an M/dorsal-biased condition and possibly leading to a reduction of IOR, similar to previous studies. However, if repeated activation of a visual pathway leads to adaptation of it (i.e., a reduction in its ability to respond), the reverse is expected. For instance, continuously activating the P/ventral pathway might lower the pathway's overall ability to respond to the target (especially to 12 cpd), thereby leading to a decrease in IOR; whereas, continuous activation of the M/dorsal pathway might lead to an overall reduction in responding (especially to 1 cpd), leading to an increase in IOR.

In summary, when the target and adapting spatial frequencies are different, very little or no sensory adaptation effects should be evident, which should lead to no changes in RTs, compared to the No adapt condition. However, when target and adapting SFs are the same, we expect to see the greatest sensory adaptation effects, which could lead to longer RTs for the adapted spatial frequencies, compared to the No adapt condition. From an attentional standpoint, we predict IOR would either increase or decrease, depending on whether the visual pathways become activated or deactivated through adaptation.

CHAPTER 2

METHOD

Participants

One hundred nine University of Georgia undergraduate and graduate students participated for course credit: 36 participants in the Adapt 1 condition (20 female), 37 participants in the Adapt 12 condition (20 female), and 36 participants in the No adapt condition (21 female). All participants had normal or corrected-to-normal vision, were right-handed as classified by the Annett Handedness Scale, and had no reported history of Attention Deficit Hyperactive Disorder.

Stimuli and apparatus

Stimuli presentation and data collection were conducted using a PC computer running E-Prime® software with a color monitor operating at 85 Hz (dimensions: 9.5° x 12.6°). Participants viewed the monitor from a distance of 143.2 cm using a chin-rest in a darkened room. Responses were recorded using a standard keyboard.

The adaptation screen was either a 1 cpd or 12 cpd vertical sinusoidal grating, encompassing the full computer screen. Adaptation screen mean luminance was 29.7 cd/m^2. To avoid an afterimage of the adapting screen, participants traced the contours of a white, centrally-located diamond outline (one pixel thick) with their eyes. The diamond had 90° angles and was chosen to prevent additional adaptation to contours of the same orientation as the grating. The diamond subtended 1.2° x 1.2° (luminance: 70.9 cd/m^2). During the control condition, participants traced the outline of the same diamond on top of a blank gray background (mean luminance: 29.7 cd/m^2).

Each trial began with a small black “x” on the center on the screen, subtending 0.3° x 0.3°. Similar to Guenther & Brown (2007), stimuli were presented against a gray background (mean luminance: 29.7 cd/m^2) and cues and targets were Gabor patches subtending 2˚. The patches appeared centered 2.5˚ above or below a centrally-located black fixation cross, subtending 0.4˚ x 0.4˚. The contrast of the 1 cpd and 12 cpd targets were suprathreshold (32.8 % and 62.5%, respectively) and matched for perceived contrast by researchers in the lab.

Procedure

The experiment had a 2 (SF: repeated vs. non-repeated) x 2 (location: cued vs. uncued) x 2 (position: upper vs. lower visual field) x 2 (target spatial frequency: 1 cpd vs. 12 cpd) x 3 (type of adaptation: 1 cpd vs. 12 cpd vs. no-adaptation) mixed design with type of adaptation as the only between-subjects variable. This resulted in three between-subjects conditions and 16 within-subject conditions. Each within-subject condition consisted of 15 trials, divided into two blocks (eight trials per condition in the first block and seven trials per condition in the second block). Trial presentation was randomized within each block. There were 48 catch trials where no target was presented (24 in each block), which produced 288 total trials in this experiment. Prior to the experiment proper, participants were familiarized with the procedure in a practice phase (one trial from each condition plus 4 catch trials).

A two-minute adaptation period preceded each block. Participants slowly traced, by moving their eyes, the outline diamond located on a 1 cpd, 12 cpd, or gray background. At the beginning of each trial a small black “x” appeared at the center of the screen, signaling participants to start the trial. When ready, participants pressed the spacebar with their left hand and an additional 3 s adaptation period occurred to maintain a constant level of adaptation. A fixation cross then appeared at the center of the screen, indicating that it was time to stop making eye movements and fixate on the cross for the remainder of the trial.

One second later, a Gabor patch appeared either above or below fixation for 900 ms. This cue patch could be either 1 cpd or 12 cpd. Two-hundred ms after the cue disappeared, the black fixation cross turned white for 150 ms and then changed back to black. This blinking cross served as a refixation stimulus to ensure participants reoriented attention back to fixation between the cue and target. After an additional 200 ms, another Gabor patch of 1 cpd or 12 cpd appeared, creating an SOA of 1450 ms. The target could appear in the same location as the cue (*location cued*) or in the opposite location of the cue (*location uncued*).

Participants responded to the onset of the target patch by pressing the zero key on the numeric keypad with their right index finger as fast as possible. RTs were measured as the time between target onset and response. If a response was made on a catch trial (no target presented), an error warning was shown at the center of the screen. At the end of each trial, the small “x” reappeared on the screen indicating the beginning of the next trial.

CHAPTER 3

RESULTS

Trimming Process

Participants with high false alarm rates (i.e., responding on > 15% of catch trials) and a high number of excluded trials (i.e., having > 5% of total trials outside the range of $150 < RT < 1100$ ms) were excluded from analysis, which accounted for 56% of the total exclusions. Participants with means in one or more conditions exceeding 2.5 standard deviations above or below the mean RT or mean IOR values were also excluded, which accounted for 44% of the total exclusions. Due to the trimming process, 33% of all participants were excluded, leaving 24 (12 female) in the Adapt 1 condition, 23 (13 female) in the Adapt 12 condition, and 26 (13 female) in the No adapt condition.

RT analyses

A 2 (SF: repeated vs. non-repeated) x 2 (location: cued vs. uncued) x 2 (position: upper vs. lower visual field) x 2 (target spatial frequency: 1 cpd vs. 12 cpd) repeated measures ANOVA on RT values was used for each adaptation condition. All three adaptation conditions had a significant main effect of location [*Adapt 1*: $F(1, 23) = 104.00$, $p < .001$; *Adapt 12*: $F(1, 22) = 29.43$, $p < .001$; *No adapt*: $F(1, 25) = 34.46$, $p < .001$], and target spatial frequency [*Adapt 1*: $F(1, 23) = 34.34$, $p < .001$; *Adapt 12*: $F(1, 22) = 54.53$, $p < .001$; *No adapt*: $F(1, 25) = 66.81$, $p < .001$]. These results indicate cued trial RTs were longer than uncued trial RTs and RTs with 12 cpd targets were longer than trials with 1 cpd targets (See Figure 2). The Adapt 12 and No adapt conditions also had a significant main effect of position, with longer RTs in the lower visual field compared to the upper visual field [*Adapt 12:* $F(1, 22) = 9.38$, $p < .01$; *No adapt:* $F(1, 25) =$

6.05, *p* < .05]. The only significant interaction was position x target spatial frequency in the Adapt 1 condition, *F*(1, 23) = 5.45, *p* < .05, with RTs to 12 cpd targets in the upper visual field (*M* = 391) greater than RTs to 12 cpd targets in lower visual field (*M* = 386) and 1 cpd targets in both the lower (*M* = 364) and upper visual fields (*M* = 358). All other main effects and interactions did not reach significance.

RT analyses across adaptation conditions showed no significant main effect of adaptation condition, *F*(2, 70) = 1.04, *p* > .05, indicating RTs were not different across conditions. However, the interaction of location x adaptation did reach significance, *F*(2, 70) = 3.13, *p* < .05, indicating cued trial RTs were significantly longer than uncued trial RTs in the Adapt 1 condition relative to both the Adapt 12 condition, *t*(45) = 2.22, *p* < .05, and the No adapt condition, *t*(48) = 2.23, *p* < .05. No significant difference was found between the Adapt 12 and No adapt conditions, *t*(47) = -0.04, *p* > .05.

IOR analyses

Although, significant amounts of IOR were found, as indicated by the significant difference in cued and uncued RTs, no significant main effects or interactions were found by adaptation condition. More specifically, contrary to the results found by Guenther and Brown (2007) no target spatial frequency differences in IOR were found within any of the adaptation conditions, particularly the No adapt condition, which is most similar to their study [*Adapt 1*: *F*(1, 23) = 2.28, *p* > .05; *Adapt 12*: *F*(1, 22) = 1.23, *p* > .05; *No adapt*: *F*(1, 25) = 0.66, *p* > .05]. Nevertheless, Figure 3 shows a significant main effect of adaptation on IOR across adaptation conditions, *F*(2, 70) = 3.13, *p* < .05, indicating IOR values were significantly higher for the Adapt 1 condition relative to both the Adapt 12, *t*(45) = 2.22, *p* < .05, and No adapt condition,

$t(48) = 2.23$, $p < .05$. No significant difference was found between the Adapt 12 and No adapt condition, $t(47) = -0.04$, $p > .05$.

According to Figure 4, when the adapting and target spatial frequencies were the same (i.e., 1 cpd target in Adapt 1 compared 12 cpd target in Adapt 12), there were no differences in IOR as a function of target spatial frequency, $t(45) = 1.27$, $p > .05$. However, when IOR to a target of a particular spatial frequency from the same adaptation condition was compared to IOR to the same target spatial frequency of a different adaptation, there were differences. For instance, there was significantly less IOR for participants responding to a 1 cpd target in the Adapt 12 condition relative to participants responding to a 1 cpd target in the Adapt 1 condition, $t(45) = 2.23$, $p < .05$, and there was marginally greater IOR for responses to a 12 cpd target in the Adapt 1 condition relative to responses to a 12 cpd target in the Adapt 12 condition, $t(45) = 1.91$, $p = .06$.

CHAPTER 4

DISCUSSION

Sensory Effects

Consistent with previous results, sensory differences in RT were found for targets: overall RTs for 12 cpd targets were longer than RTs for 1 cpd targets (e.g., Breitmeyer, 1975; Guenther & Brown, 2007; Solberg & Brown, 2002). However, contrary to our prediction, spatial frequency specific sensory effects due to adaptation were not evident, as indicated by similar RTs across adaptation conditions for both targets. At first glance, these results seem inconsistent with the Menees (1998) study, in which longer RTs were found to adapted stimuli compared to unadapted stimuli; however, the use of suprathreshold adapting and testing stimuli could have lessened the effectiveness of the adaptation. Despite the fact that adapting to a high contrast stimulus reduces the perceived contrast of a test stimulus, including suprathreshold stimuli (Blakemore, Muncey, & Ridley, 1973), it is possible the change in perceived contrast was not sufficient to affect reaction times in this paradigm. In other words, the criterion content at which participants were using to judge the presence of the stimulus was already sufficiently surpassed and the reduction in perceived contrast after adaptation did not affect RTs. Menees considered this notion herself and reported pilot data showing null results on RTs as test contrast increased.

Attentional Effects

We predicted attentional effects would manifest in either adaptation or activation of the visual pathways. We found overall IOR to be greater in the Adapt 1 condition relative to the Adapt 12 and No adapt conditions (see Figure 3). This increase in IOR relative to the No adapt condition would suggest an adaptation account of our results for the Adapt 1 condition only. As predicted by the adaptation account, presenting a 1 cpd adapting screen would continuously stimulate the M/dorsal pathway, leading to an overall reduction in pathway responding and an increase in IOR. The question arises, though: Why was adaptation only evident in Adapt 1? The adaptation account predicted an increase in IOR for Adapt 1, but it also predicted a reduction in IOR for Adapt 12 through deactivation of the P/ventral pathway. Why did adaptation affect IOR in Adapt 1, but seemingly not affect IOR in Adapt 12?

One possible reason for the increase in IOR for Adapt 1 could be a result of the adaptation process itself. To avoid an afterimage of the gratings, participants made saccadic eye movements to trace a centrally-located diamond. Whereas the saccades and diamond were consistent in all three conditions, it is possible an interaction occurred between the stimuli in each condition and the added variables. Saccadic eye-movements have been shown to suppress M pathway activity (known as *saccadic suppression*) requiring greater contrast levels for the detection of a low spatial frequency grating, compared to a condition without eye-movements (Burr, Morrone, & Ross, 1994; Ross, Burr, & Morrone, 1996). Additionally, P pathway activity was shown to be relatively unaffected during saccades.

Is it possible suppressing M pathway activity contributed to the difference in IOR for Adapt 1? The visual effects of saccadic suppression are greatest at the beginning of the saccade (Diamond, Ross, & Morrone, 2000) and typically last for about 100-150 ms after the end of the saccade (Johns, Crowley, Chapman, Tucker, & Hocking, 2009). Saccades in this experiment were made prior to the actual IOR task. Between the adaptation screen and the onset of the cue, there was a one-second interval, in which participants were required to cease all eye movements and fixate on a black cross. This time period would have been sufficient to cancel any effects of saccadic suppression on response times and would not be able to explain the difference for the Adapt 1 condition.

Additional evidence against a saccadic suppression explanation comes from Sumner et al.'s (2004) study showing suppression of the M pathway has no effect on the magnitude of IOR in a manual response IOR task, similar to the paradigm used here. Whereas, they did show suppression of the M pathway affects IOR using a saccadic eye movement response, IOR disappeared in those conditions. They suggest differing mechanisms must create IOR, namely, saccadic responses produce IOR as a consequence of executing an eye movement via the retinotectal pathway and manual responses produce IOR through attentional mechanisms in the cortical pathway with additional contribution from the retinotectal pathway. As this study produced an increase in IOR and not a lack of IOR, it is not likely saccadic suppression can explain the given results.

Another possible explanation for the increase in IOR during the Adapt 1 condition could come from the presence of the diamond during the adaptation process. Some participants reported perceiving the Adapt 1 diamond as a three-dimensional object (e.g., "the diamond looked like it was floating in front of a striped background"; "the diamond appeared to be coming out of the screen", etc.). There is some previous evidence indicating that the magnitude of IOR may increase when object-based attention is utilized, in addition to location-based attention (Bourke, Partridge, & Pollux, 2006; Brown, 2009). In object-based attention, attention is focused on an object on the screen, as opposed to a location in space and in the case of object-based IOR, can reflect an attentional bias away from a previously attended object. Whereas, the current study manipulated location-based attention by cuing locations in space using spatial frequency patches, the perception of a 3-D diamond prior to the location-based IOR task in

Adapt 1, could have utilized object-based attention, in turn creating additional inhibition to the diamond regardless of the adapting spatial frequency.

Brown and colleagues presented participants with a 3-D cube during a traditional location-based IOR task to bias processing towards the P/ventral pathway. The P/ventral pathway plays a major role in object processing (Brown, 2009; Ungerleider & Haxby, 1994), and as stated previously, the presentation of P/ventral-biased stimuli tends to increase overall IOR. Whether the cues and targets appeared on or beside the cube, IOR increased by about 10 ms, relative to a condition in which no cube is presented, for both 1 cpd and 12 cpd targets (Brown, 2009). In a condition using 2-D squares, instead of 3-D cubes, IOR values were relatively unchanged from the no-cube condition. Three-dimensional cubes can be thought of as having more "object-like" qualities, as compared to a two-dimensional square. The authors suggest the difference in IOR is due to the additional inhibition created by object-based attention in the 3-D cube condition.

On the other hand, a study by Theeuwes and Pratt (2003) measuring IOR while manipulating depth through binocular disparity did not show differences in IOR between 2-D and 3-D conditions. Cues were produced by a change in brightness in one of four rectangular figure-eight placeholders (e.g., a square box on top of another square box) and targets were produced by removing pieces of one of the figure-eight placeholders, creating a letter "S" or letter "H" (SOA: 883 ms). While RTs were measured, participants had to discriminate between different types of targets in order to respond. Participants had to indicate whether the target appeared as a letter "S" or a letter "H". They showed IOR could be created in three-dimensional space, but found no difference in IOR values between 2-D and 3-D conditions. Conversely, Bourke et al. (2006) found the exact opposite effect. They followed the same experimental paradigm as Theeuwes and Pratt (2003), but connected the rectangular boxes in the foreground with the rectangular boxes in the background to create one cohesive three-dimensional object instead of two separate items. When they cued locations on the cube-like object, they found IOR increased. Bourke et al. suggested the perception of the placeholder as one cohesive three-dimensional object instead of two separate items as in the Theeuwes and Pratt (2003) study, utilized the object-based component of IOR and lead to an increase of IOR. In other words, the stimuli in the Bourke et al. (2006) study can be thought of as having more “object-like” qualities than the stimuli used in the Theeuwes and Pratt (2003) study, similar to the 3-D cubes in the experiments by Brown and colleagues.

To investigate the possibility of object-based three-dimensional effects in our study, we collected pilot data for a follow-up study to determine the predominant perception of the diamond. While we cannot assert the participants from this pilot data had the same perception as those in the original experiment, the studies by Brown and colleagues would suggest the conditions perceived as having 3-D objects should have greater IOR compared to those conditions perceived as having 2-D objects. Eleven out of thirteen participants indicated they perceived the Adapt 1 screen as 3-D, while three out of thirteen participants perceived the Adapt 12 as 3-D and no one perceived the No adapt screen as 3-D. Comparison of all three groups using the Cochran’s Q statistic lead to a significant difference between groups, Q (2, $N = 13$) = 16.17, $p < .001$. Comparison of Adapt 1 versus Adapt 12 also lead to a significant difference between the two groups, Q (1, $N = 13$) = 6.40, $p < .05$. If the perception of the diamond in Adapt 1 during the experiment proper was also perceived as a three-dimensional object more so than in Adapt 12, it might explain the selective increase in IOR for Adapt 1.

Thus far, we have suggested two potential explanations for the current results: the predicted adaptation account and the post-hoc object-based attention explanation. Before we can determine which explanation best accounts for the results, we must address an aspect of the study we have not yet discussed: the lack of a target spatial frequency difference in IOR within the conditions. In particular, the No adapt condition, which contains stimuli most similar to those used in Guenther and Brown (2007), did not show a target spatial frequency difference, as Guenther and Brown did. Perhaps, the No adapt condition was not an adequate comparison for the adaptation conditions.

If we compare the two adaptation conditions to each other instead (see Figure 4), we see that our adaptation did affect the Adapt 12 condition as well, but only marginally. As shown by the striped bars, IOR for 12 cpd targets in Adapt 12 (same spatial frequency) was marginally lower (p = .06) than IOR for 12 cpd targets in Adapt 1 (different spatial frequency). This slight difference suggests 12 cpd adaptation leads to lower IOR for 12 cpd targets, consistent with the adaptation account (e.g., presenting a 12 cpd adapting screen would continuously stimulate the P/ventral pathway, leading to a reduction in responding and a decrease in IOR). In other words, IOR for targets of the same spatial frequency as the adaptation frequency decreased relative to similar targets in a different adaptation condition, when the target spatial frequency was 12 cpd.

When we compare the outcomes of our 1 cpd targets in each adaptation condition, the adaptation account still holds true (e.g., presenting a 1 cpd adapting screen would continuously stimulate the M/dorsal pathway, leading to a reduction in responding and a increase in IOR). IOR for 1 cpd targets in Adapt 1 (same spatial frequency) is significantly greater than for 1 cpd targets in Adapt 12 (different spatial frequency). This indicates IOR for targets of the same spatial frequency as the adaptation increased relative to similar targets in a different adaptation condition, when the target spatial frequency was 1 cpd.

All in all, both explanations are viable with the given data and cannot be distinguished from each other at this stage. Both theories suggest an increase in IOR will happen, but through stimulation of different pathways. The adaptation account suggests the presentation of a 1 cpd adapting screen continuously stimulates the M/dorsal pathway, leading to deactivation of the pathway. Adapting the M/dorsal pathway, thereby, leads to an increase in IOR for the Adapt 1 condition. Marginal differences in IOR for 12 cpd targets in Adapt 12 and 12 cpd targets in Adapt 1 indicate adaptation could have affected the Adapt 12 condition, as well, but was not strong enough to show significant results. Since the P/ventral pathway plays a major role in object processing, the object-based attention explanation suggests the perception of the diamond in Adapt 1 as a three-dimensional object biased processing towards the P/ventral pathway. Previous research has shown stimuli that bias processing towards the P/ventral pathway, lead to an increase in IOR (Brown, 2009). In order to dissociate the explanations from each other, additional experiments will need to be conducted.

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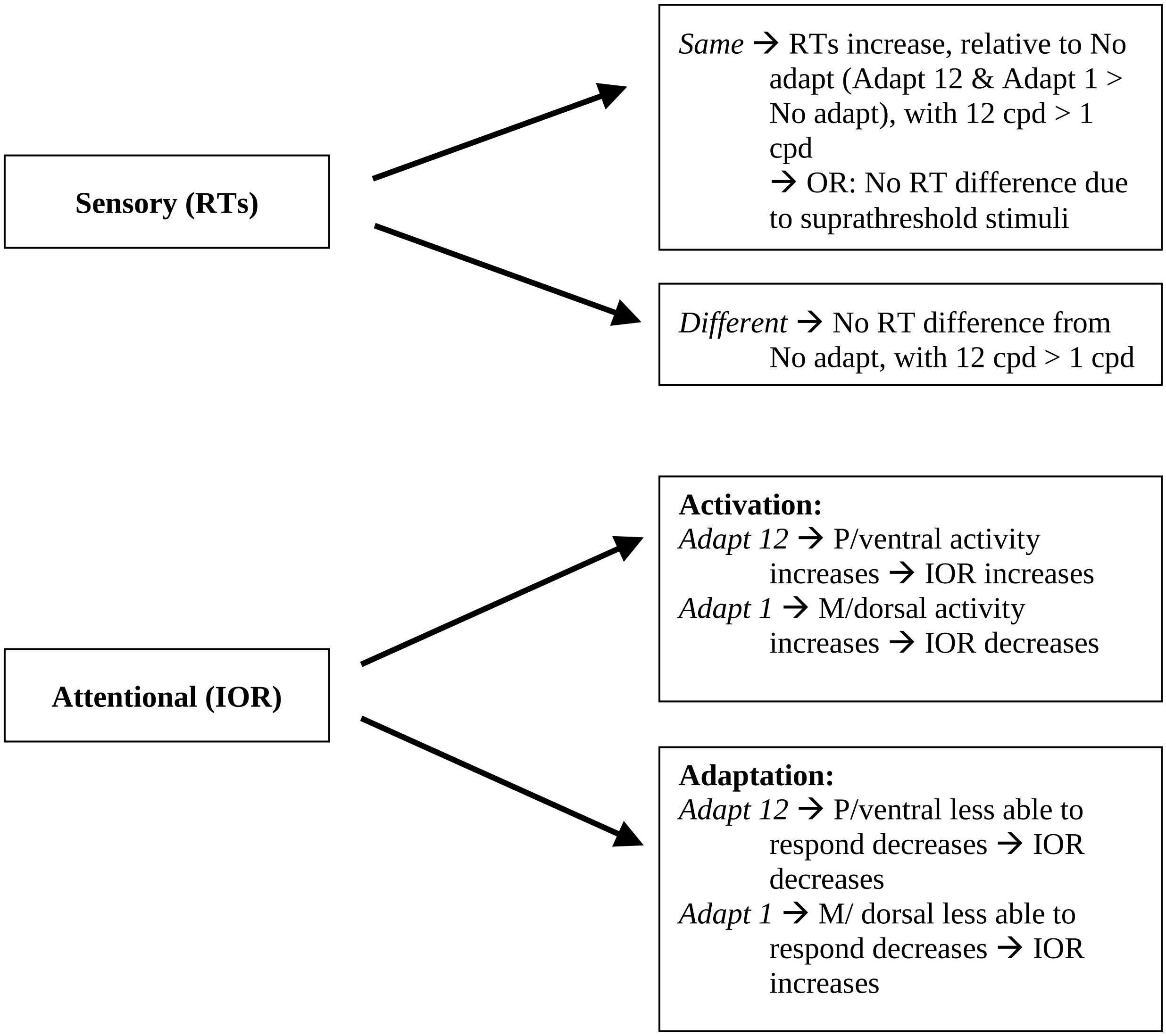

Figure 1: Predicted outcomes of the adaptation manipulations on sensory and attentional components.

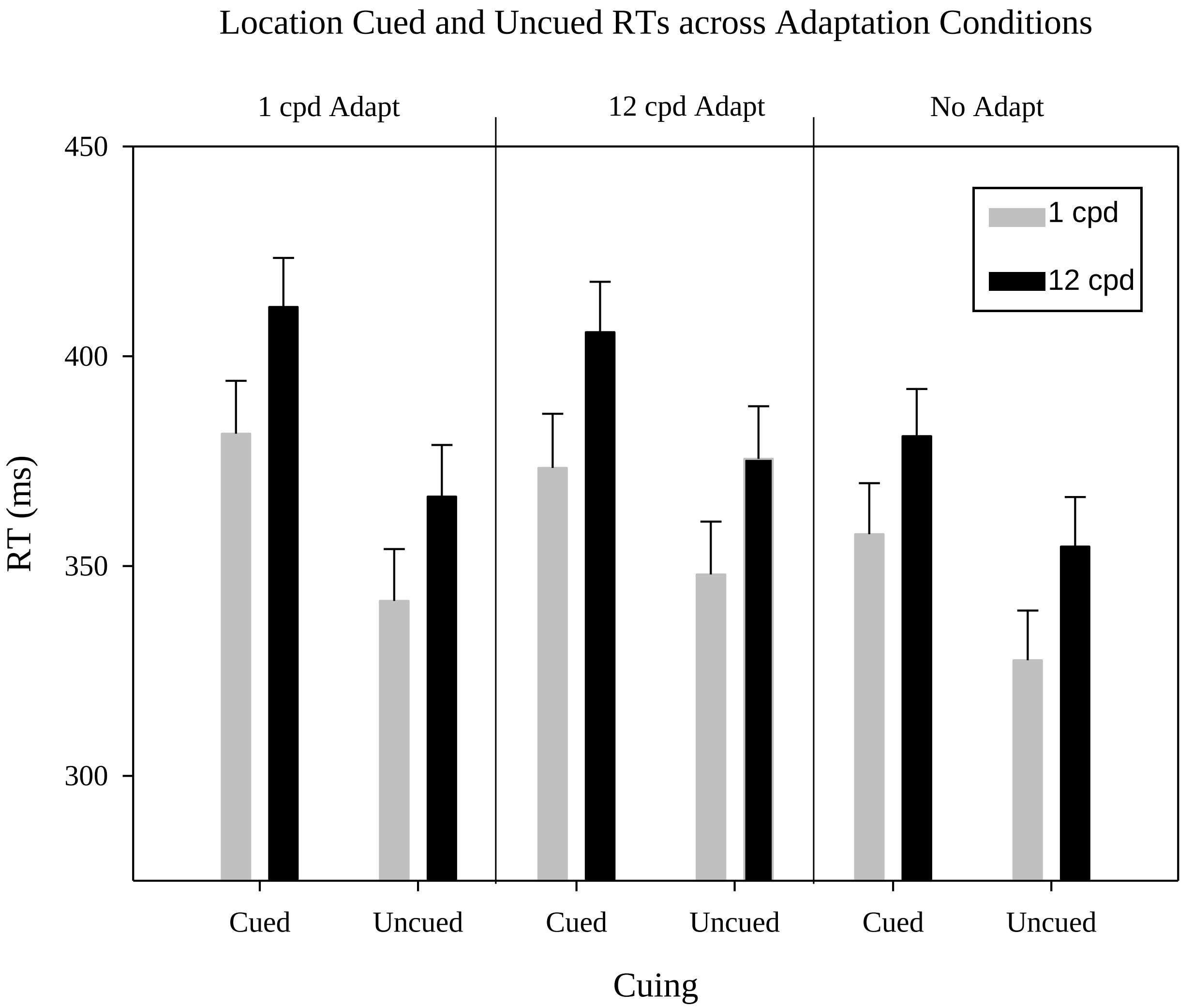

Figure 2: Mean reaction times for cued and uncued trials across adaptation condition as a function of target spatial frequency.

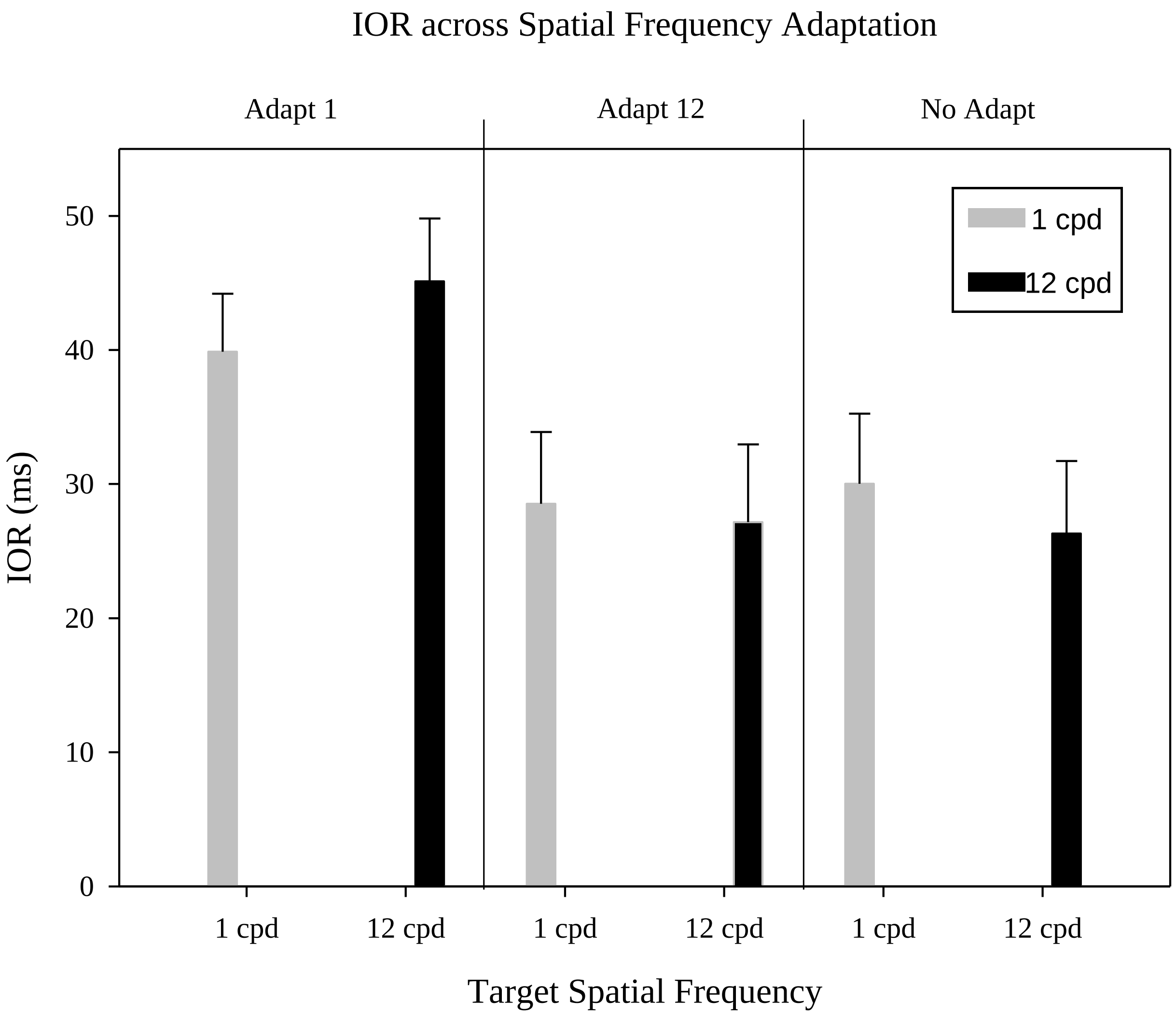

Figure 3: Mean IOR values across adaptation conditions as a function of target spatial frequency

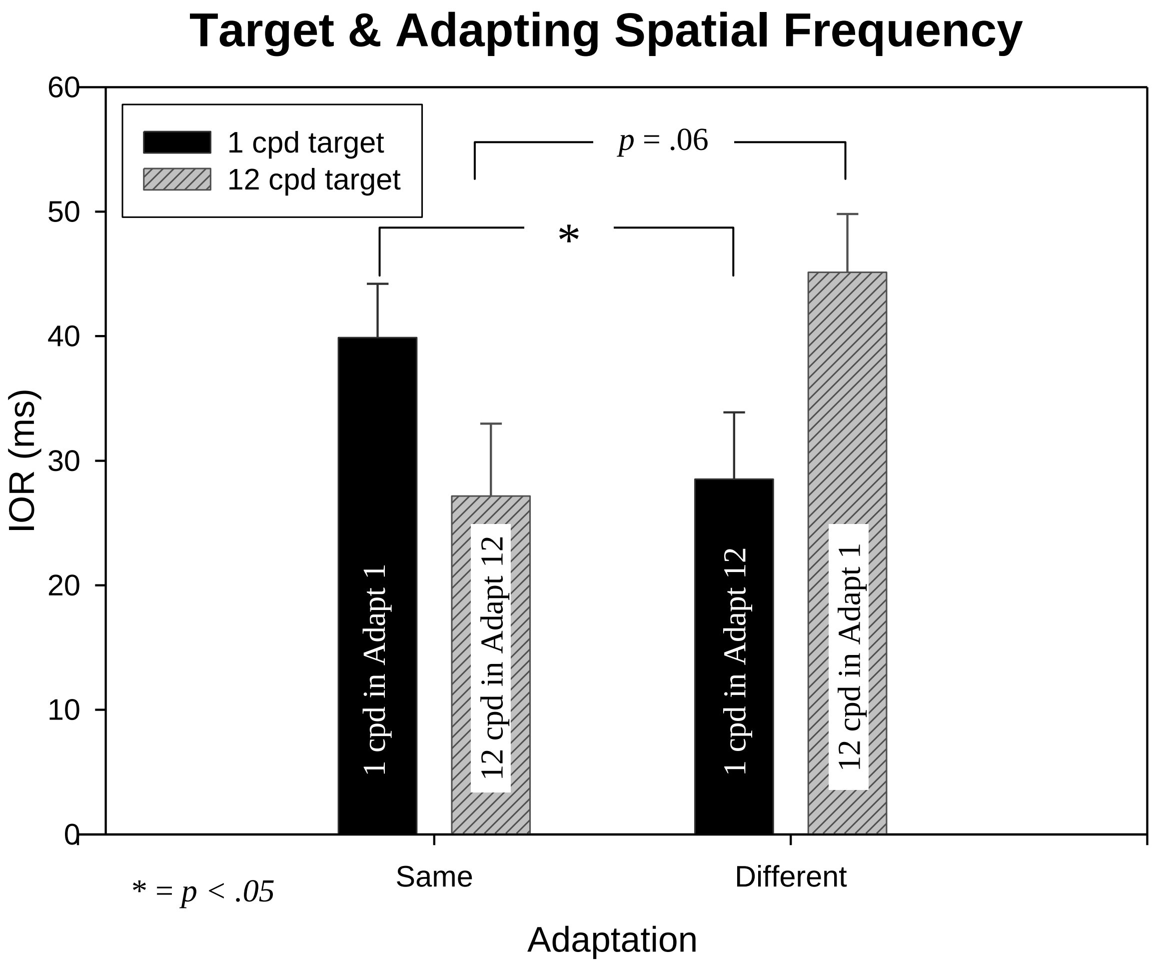

Figure 4: Mean IOR values as a function of target spatial frequency and adapting spatial frequency. Dark, solid bars refer to trials in which the target spatial frequency equaled 1 cpd, whereas the striped bars refer to 12 cpd targets. “Same” indicates target and adapting spatial frequencies are equivalent. “Different” refers to a 1 cpd target in Adapt 12 (left) or a 12 cpd target in Adapt 1 (right).