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Keywords: magnocellular pathway, spatial frequency, face perception, reach trajectories

1.0 Introduction

Perception of biologically relevant information from the environment is an essential feature of the primate sensory system. Humans are efficient and quick in detecting briefly viewed biological visual stimuli, in particular, faces. In contrast to non-face objects, face perception is known to be carried out in a more configural manner, i.e, the information from the face is processed as an undifferentiated whole, at a single glance, beyond just the sum of the parts or the interrelations of the parts (Young, Hellawell & Hay, 1987; Tanaka & Farah, 1993; Maurer, Le Grand, & Mondloch, 2002).

Different aspects of facial information processing have been associated with distinct ranges of spatial frequencies. For instance, configural processing may stem from low level sensory and perception mechanisms, particularly through low spatial frequency (LSF) information, whereas high spatial frequency (HSF) conveys more local featural information about the stimulus (Shulman, Sullivan, Gish & Sakoda, 1986; Hughes, Nozawa, & Kitterle, 1996; Han, Yund & Woods, 2001). The coarse-scale blurred features of LSF image may capture the diagnostic information needed for configural processing while fine-tuned details through HSF facilitates information regarding finer details of the stimuli.

Research on spatial frequency and visual processing has also established that LSF information is carried mainly via magnocellular channels that are structured for faster transduction of visual signals to the subcortical and cortical regions (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Bar, 2003). Fine-grained high spatial frequency (HSF) information, on the other hand, has a comparatively slower transmission via the parvocellular channels

(Livingstone & Hubel, 1988; Bullier, 2001). Magnocellular neurons project predominantly to the dorsal visual stream for information regarding motion and spatial location, while the recognition of object identity is processed along the ventral cortical pathway, mainly subserved by parvocellular channels (Felleman & Van Essen, 1991; Orban, Van Essen &Vanduffel, 2004). Finer details regarding the object's color, shape, inner feature and textures are carried chiefly through the slower parvocellular system, while the magnocellular system carries achromatic and global shape information (Kaplan & Shapley, 1986; Macé, Thorpe & Fabre-Thorpe, 2005). Parvo-outputs are thus predominant at higher spatial frequencies while Magno-outputs dominate at low spatial frequencies (Tobimatsu, Tomoda & Kato, 1995).

The magnocellular system facilitates rapid detection of object identity and location despite poor spatial resolution. Research findings illustrate that top-down modulations (predominantly through the LSF channels) bias the output of the bottom-up sensory input thereby facilitating rapid global processing (Kveraga, Boshyan & Bar, 2007; Kveraga, Ghuman & Bar, 2007). The global predictions obtained from the blurred LSF image are then progressively integrated with the HSF information in subsequent processes along the inferior temporal regions of the cortex. This reduces the computational demands on the system and improves efficient recognition.

Laycock, Crewther and Crewther (2007) have proposed a 'magnocellular advantage' model of visual perception wherein an initial rapid feedforward sweep through the dorsal stream activates parietal and frontal areas that further feeds back into the primary visual cortex.

103 However, despite several neuroimaging and neurophysiology reports, direct evidence for the role
104 of the magnocellular system in the early stages of face perception remains to be established.
105
106 Here, to examine the magnocellular contribution to face perception, we used a simple
107 technique to selectively suppress the magnocellular system. We exploited the property of the
108 magnocellular pathway's inhibitory response to red light (due to the long wavelength of red
109 light). Early on, Wiesel and Hubel (1966) reported inhibition of magnocellular channels by red
110 light, followed by several other research reports in recent times (Okubo & Nicholls, 2005;
111 Bedwell, Miller, Brown, Yanasak, 2006; West, Anderson, Bedwell & Pratt, 2010). Red light
112 causes tonic suppression of the excitatory activity of (type IV) cells of the magnocellular
113 pathway. This specific property of magnocellular suppression due to red color has been
114 demonstrated in both animal and human studies throughout the visual stream including the
115 retinal ganglion cells (de Monasterio, 1978), the lateral geniculate nucleus (Dreher, Fukada,
116 Rodieck, 1976) and the striate cortex (Livingstone & Hubel, 1984). Human behavioral studies
117 have reported reduced performance on magnocellular pathway-dependent tasks in the presence
118 of a red background (Breitmeyer & Breier, 1994; Chapman, Hoag & Giaschi, 2004; Bedwell,
119 Brown & Orem, 2008) on a variety of tasks such as reading performance (Chase, Ashourzadeh,
120 Kelly, Monfette & Kinsey, 2003), depth perception (Brown & Koch, 2000) and global motion
121 (Breitmeyer & Williams, 1990). An fMRI study reported decreased activity in the V5/MT region
122 (that receives substantial magnocellular input) with red as opposed to a neutral background
123 (Bedwell, Miller, Brown & Yanasak, 2006).
124

125 By manipulating the background color, we designed the study to examine the
126 contribution of the magnocellular pathway when processing LSF-HSF face hybrids. In the
127 experimental task (described in detail in the methods section), there is greater emphasis on M-
128 pathway input (i.e., identifying location, whether left or right) of the target rather than mere
129 identification. Since the LSF interference is reliant on adequate magnocellular pathway
130 functioning and the color red suppresses such functioning, we hypothesize that the LSF
131 component will have less effect on the trajectories with a red background compared to a grey
132 one.
133
134 In addition, to maximize the difference between the LSF and HSF components of the
135 LSF-HSF face hybrids, we shall present the stimuli at foveal and peripheral locations. The
136 density distribution of magnocellular channels is known to be much higher at periphery (Silveira
137 & Perry, 1991) and so it is likely that LSF interference at peripheral locations (see Awasthi,
138 Friedman & Williams, 2011a for more details) can help tease apart the differential engagement
139 of the two channels. Since we hypothesize that red light shall impair magnocellular functioning,
140 the effect on trajectories is likely to be less pronounced at peripheral locations with a red
141 background compared to a grey one.
142
143 We use a relatively novel behavioral measure that provides rich information regarding
144 perceptual decision making in real-time. Recent research reports (Gold & Shadlen, 2001; Spivey
145 & Dale, 2006; Freeman & Ambady, 2011) have demonstrated that motor responses are generated
146 in parallel with partial (incomplete) perceptual information that is continuously updated by
147 perceptual-cognitive processing over time. Continuous tracking of hand movements during the

148 reaching task can reveal otherwise hidden, underlying parallel processes in real- time (Song &
149 Nakayama, 2009). Tracking of hand movements are reported to provide unusually high-fidelity,
150 real-time access to fine-grained traces of the perceptual phenomena that are otherwise not
151 captured by discrete traditional measures (Resulaj, Kiani, Wolpert & Shadlen, 2009). Using a
152 discrete measure (such as a button press reaction time response), we cannot disentangle with
153 certainty and precision the early versus late processing of LSF and HSF in responding to the
154 hybrids. Analyzing the shapes of the trajectories and separating the early versus late components
155 of reaching movements allow early access to the state of the decision making process while the
156 subjects reach to the targets.
157
158 There is a growing body of research that models how manual action exposes the real-time
159 unfolding of underlying cognitive processing (Song & Nakayama, 2009; Resulaj et al 2009). In
160 our study, the reaching trajectories can potentially tease apart magno versus parvo inputs because
161 in addition to the top-down recognition (of pointing to the target sex), the subjects are required to
162 identify the location of target (whether left or right). In doing so, the trajectory they take (as the
163 information in hybrids progressively unfolds) provides a window into the magnocellular
164 afferents that project onto the dorsal stream structures important for reaching. Amongst a wide
165 variety of measures that are used to examine the trajectories of movement (Awasthi, 2012), we
166 use path offset/curvature area and movement onset times in this study as these are well suited to
167 provide valuable information based on task requirements and study design.
168
169
170 **2.0 Method**

171

172 **2.1 Ethics Statement**

173 The ethical aspects of this study were approved by the Human Research Ethics Committee
174 (HREC) of Macquarie University.

175

176 **2.2 Stimuli, Design and Procedure**

177 Similar to the previous experiments (described in Awasthi, Friedman & Williams, 2011a;
178 2011b), male and female face images were Fourier transformed and multiplied by low-pass and
179 high-pass Gaussian filters to preserve low (<8 cpf) and high SF (>25 cpf) information in each
180 image. The images were equated for luminance and contrast energy using Shine toolbox before
181 filtering and were then superimposed to make LSF-HSF hybrid images (see Figure 1). Both the
182 grey (RGB values of 75, 75, 75) and red background (RGB values of 255, 0, 0) had equal
183 luminance. Presentation software (Neurobehavioral Systems) was used to present the stimuli.
184 The stimuli had a mean height and width of 5.7° visual angle at foveal presentation and were
185 presented 21.7° from fixation for peripheral presentation.

186

187 Four combinations of hybrid images were used in the experiment. A four-factor within-
188 subjects design was used, the factors being Eccentricity (periphery, fovea), Target Location (left,
189 right), Target Congruity (congruent, incongruent) and Distractor Conflict (present, absent). All
190 factors were fully crossed, yielding sixteen experimental conditions. Congruity was defined as
191 the sex of the HSF face being the same as that of the LSF face in a hybrid. Thus, MM and FF
192 were congruent whereas FM and MF were incongruent conditions. For instance, in the hybrid
193 image **FF**, the first letter (**F**) of the hybrid indicates the sex of the LSF face (**Fem**ale) and the

second letter (**F**) indicates the sex of the HSF face (**F**). For hybrid **FM**, the LSF face is **F**emale and the HSF face is **M**ale (Figure 1a).

(Insert Figure 1 somewhere here)

For each subject, the target sex was assigned at the beginning of the experiment for the entire session (e.g., Female). The task involved pointing to the target (e.g., female face) on the touch screen. At viewing distance, the HSF face was salient (most visible) and was the target for all trials throughout the experiment. In congruent target trials, both the LSF and HSF components of the hybrid face were the same sex (e.g., both Female; FF) while for the incongruent target trials, the LSF component was of the opposite sex (e.g., Male; MF). To maximize the LSF interference effect, we also manipulated whether the face on the other side of the target location held a target-matched LSF distractor (e.g., an LSF female) or not (e.g., no LSF female). There was no HSF distractor. Two hybrid faces were presented at the left and right side of the fixation cross (for foveal presentation) and at far periphery (for peripheral presentation) (Figure 1b). Subjects were instructed to begin the task with eyes on the fixation. After the initial liftoff, they could move their eyes freely.

2.3 Subjects

Right-handed subjects were recruited from the Macquarie University community who volunteered their participation. All subjects reported normal or corrected-to-normal vision and gave written, informed consent before participation. 15 subjects (seven females, mean age: 25.2 years, SD=4.3) participated in the task.

2.4 Procedure

Subjects sat in a quiet, dark room at a table with a LCD touch screen (70 × 39 cm, 1360 × 768 pixels, 60Hz) positioned approximately 70 cm in front of them. Two small infrared light emitting diode (LED) markers were attached to the right index fingertip of the subject. The starting position (a button) was aligned with the body midline, approximately 20 cm in front of the subjects. Each trial began with subjects placing their right index finger on the centrally located starting button in front of the touchscreen. Hand movements were tracked with an Optotrak Certus Motion Capture System (Northern Digital Inc.) at a 200 Hz sampling rate. The tracking system was calibrated at the beginning of each experiment.

In both the grey background and the red background conditions, two hybrids were presented *peripherally* and *centrally* in alternate blocks. The peripheral and central presentation of hybrids is equivalent in terms of stimuli and the procedure, except that in the central condition, two hybrids were present on either side of fixation. Subjects performed the red and grey sessions on consecutive days in a counterbalanced manner. They were assigned Male or Female as the target sex (also counter-balanced across subjects). They were instructed to maintain fixation on a cross at the center of the screen (that appeared for 1000 ms) before reaching out and pointing to the target. Subjects had to begin their reaching response within 350 ms of target onset but their final responses (either left or right) were not speeded, with sufficient (cutoff 1.5 seconds) time for the finger to change direction or correct its course. Trials were aborted when started too early (before the target onset) or too late (after 350 ms). For all responses, feedback was provided onscreen. After a block of training with 40 trials, 16 blocks of 40 trials each were carried out with adequate breaks in between. Only the correct response trials

240 were used for further data analysis. The subjects had a mean accuracy rate of 93.34 % (SD=3.69)
241 for the grey background and 94.11% (SD=3.21) for the red background.
242
243 We used cubic splines for data smoothing and interpolation when markers were occluded
244 (for less than 10% of the trajectory in a trial). Movement data was analyzed using Matlab (The
245 Mathworks, Inc). We calculated the maximum deviation from a straight-line path from start to
246 end of the movements. We then defined maximum curvature as the ratio of this deviation to the
247 length of the straight-line path (Atkeson & Hollerbach, 1985; Smit & Van Gisbergen, 1990). The
248 average maximum curvature was computed for all subjects and used as the dependent variable.
249
250 **2.5 Curvature Results**
251 The curvature in the trajectory is taken as a measure of uncertainty in the decision
252 making process. The mean trajectories (pooled for all subjects) are shown in Figure 2. The
253 differences in the trajectories were initially quantified by comparing the maximum curvature.
254 When subjects select a target and do not change their mind (i.e., when the LSF and HSF
255 components unambiguously correspond to one target), they reach directly to the target, and the
256 curvature is low. When there are competing sources of information (i.e., the LSF and HSF are
257 incongruent, or there is an LSF distractor on the other side), this uncertainty in the decision
258 making process is reflected through greater curvature. Repeated measures ANOVA with
259 background color (grey, red), eccentricity (periphery, fovea), target congruity (congruent,
260 incongruent), distractor conflict (present, absent) and target location (left, right) was carried out.
261 (Insert Figure 2 somewhere here)
262

263 Eccentricity, target congruity, distractor conflict and target location significantly
264 influenced the curvature as shown by the significant main effect of eccentricity $F(1, 14) = 5.00$,
265 $p<0.05$, target congruity $F(1, 14) = 199.50$, $p<0.001$, distractor conflict $F(1, 14) = 70.92$,
266 $p<0.001$, and location $F(1, 14) = 14.73$, $p<0.001$. The main effect of background color also
267 approached significance $F(1, 14) = 4.56$, $p=0.051$ with pairwise comparisons showing larger
268 curvature for grey (mean=0.283) than red (mean=0.237) background.
269
270 Mean curvature across eccentricity was significantly larger in red background conditions
271 than in the grey background conditions as shown by a significant interaction between
272 background color and eccentricity $F(1, 14) = 5.00$, $p=0.042$. Post-hoc (Tukey HSD) analysis
273 showed that difference between peripheral and foveal presentations were significantly greater in
274 red (M= 0.2) than at the grey (M=0) background at $p<0.01$.
275
276 Mean curvature due to target congruity was significantly larger in peripheral
277 presentations (M= 0.22) than in the foveal presentations (M=0.30) as shown by a significant
278 interaction between eccentricity and target congruity $F(1, 14) = 14.24$, $p=0.002$. Post-hoc
279 (Tukey HSD) analysis showed that target congruity differences were significantly larger at
280 periphery (0.08) than at the fovea (0.06) at $p<0.001$. Further results show that congruity
281 differences at fovea for grey background (M= 0.27) were significantly larger than for the red
282 background (M=0.20) but not for the periphery, shown by a three-way interaction between
283 background color X eccentricity X target congruity $F(1, 14) = 14.24$, $p=0.002$. Post-hoc (Tukey
284 HSD) analysis showed that target congruity differences at fovea were significantly larger for
285 grey (mean difference= 0.06; $p<0.01$) than for red background. Tests of violations of sphericity

were performed on the data.

4.0 Discussion

In this study, we examined the role of LSF and HSF in a face categorization task at fovea and periphery. To infer the role of the magnocellular visual pathway, a novel technique was used wherein the reaching performance against a red background (believed to suppress the magnocellular pathway) was compared to that against a neutral grey background. Results from curvature measure demonstrate the differential role of grey and red background in sex categorization task, likely indicating the magnocellular suppression. Previous research has implicated the possible role of the magnocellular pathway in rapid detection and categorization of achromatic stimuli (Delorme, Richard & Fabre-Thorpe, 1999). For example, Michimata, Okubo and Mugishima (1999) showed that red background impairs the perception of a global visual pattern believed to rely on LSF processing. Other studies have also shown reduced flicker sensitivity when presented on a red background (Stromeyer, Cole & Kronauer, 1987). West, Anderson, Bedwell and Pratt (2010) also demonstrated that the perception of fearful faces is suppressed under red diffused light, lending support to the idea of global precedence through the magnocellular pathway.

Early information in LSF faces is carried through the magnocellular pathway and this information may be crucial for quick start times required in the fast categorization task used here. Spatial frequency and stimulus location (peripheral versus foveal presentation) significantly influence the categorization task as shown in the curvature measure.

Skottun (2004) has argued that red light also attenuates the parvocellular red–green color-opponent cells. In contrast, studies have demonstrated that color-contrast detection by red-green opponent cones is confined to foveal vision and is known to fall steeply across the periphery (Mullen & Kingdom, 2002; Mullen, Sakurai & Chu, 2005). It is probable that the red background interacts with the parvocellular pathway as well, mechanisms of which remain to be investigated.

Across all the red diffuse light literature, there is no standard measure of luminance; instead there is a standard of keeping equiluminance across all conditions. It may be the case that researchers who use high luminance may see a greater effect of inhibition of the M-pathway than those who use lower luminance. However, researchers have been able to find the effects of red diffuse light with both high luminance (Chapman, Hoag & Giaschi, 2004), and low luminance (Mullen, Kingdom, 2002). Research by Breitmeyer has shown that dark adaptation was useful to observe the inhibitory effects of red diffuse light (Breitmeyer & Breier, 1994; Breitmeyer & Williams, 1990) by providing the required bias towards the M-pathway.

In our previous studies using the same experimental setup (Awasthi et al 2011a; b), we demonstrated significantly larger peripheral interference by LSF information while reaching for HSF targets. In concordance with our previous findings and the research showing higher density distribution of magnocellular channels at periphery, the LSF interference in the current study reflects the differential engagement of the magnocellular pathway in grey versus red background. In yet another study using red glasses for experimental manipulation, Williams, Grierson and

Carnahan (2011) demonstrated that diffused red light suppresses magnocellular activity thereby significantly disrupting visual threat processing.

Deficits in global identification of faces (as seen in prosopagnosia) and other developmental conditions might have a magnocellular contribution (Grinter, Maybery & Badcock, 2010). It is likely that magnocellular dysfunction, if present in face recognition deficits, concerns more integrated processes at levels where information from parvocellular and magnocellular channels interact. In line with Laycock et al.'s magnocellular deficit proposal, we recently reported delayed integration of low and high spatial frequency information in developmental prosopagnosia (Awasthi et al 2012). This integration failure could be due to an attention-perception mechanism that favors parvocellular over magnocellular channels reflecting a tradeoff between segregation and integration of information (Yeshurun, 2004) that ultimately reflects in impaired face processing. The deficient responsiveness of the magnocellular channels has been reported in schizophrenia (Martinez et al., 2008) as well as in other developmental conditions (Laycock et al., 2007), subsequently influencing higher level perceptual processing.

Findings from our study provide strong support for the role of the magnocellular pathway in face perception. The contextual associations between stimuli in the environment activate predictive early guesses, available through partial, blurred, yet rapidly available information about the stimulus identity. It is noteworthy though that non-face object may also utilize this magnocellular advantage. However, much experimental data on the topic remains to be generated to generalize the advantage to certain or all object classes. Fenske, Aminoff, Gronau and Bar (2006) demonstrate the top- down facilitation that is triggered by both the early

355 information about an object, as well as by contextual associations between an object and other
356 objects in the vicinity within which it is typically recognized. As the magnocellular pathway is
357 predominantly attuned to low spatial frequency (LSF) information, Bar's proposed model
358 predicts that the early, quick and dirty LSF information processing is projected to the orbito-
359 frontal cortex, which in turn selects potential matches based on the global, LSF-based properties
360 of the bottom-up input. Predictions to identity fine-tuned features of the stimulus global
361 properties (obtained initially from the blurred LSF image) are then projected to the high spatial
362 frequency dominated object recognition areas along the inferior temporal regions of the cortex. A
363 rapid projection via the magnocellular pathway plays a crucial role in this facilitation, resulting
364 in rapid recognition of biologically salient stimuli such as faces. Taken together, it may be more
365 appropriate to describe the predictions generated by the low and high SF as phases evolving over
366 time, rather than as separate bouts of visual information (although using separate pathways) each
367 one adding further to the perceptual processing. The magnocellular system helps in deciphering
368 the overall three-dimensional organization, position and movement of visual objects in the
369 environment. Selective engagement of the magnocellular system provides a framework for
370 expedient prioritization of biologically salient stimuli that compete for attention and action.
371

Figure legends

Figure 1 (a) Stimuli: LSF-HSF hybrid images used in the experiments. To see the LSF content, squint, blink, or step back from the figure (b) Experimental setup showing the touchscreen where two hybrid images were presented peripherally and centrally in alternate blocks. Subjects start each trial at the grey button on the table to reach out and touch the respective black target box on the screen.

Figure 2 (a) Mean trajectories for grey background (b) Mean trajectories for red background.

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520

Figure 1(on next page)

Figure1

(a) Stimuli: LSF-HSF hybrid images used in the experiments. To see the LSF content, squint, blink, or step back from the figure (b) Experimental setup showing the touchscreen where two hybrid images were presented peripherally and centrally in alternate blocks. Subjects start each trial at the grey button on the table to reach out and touch the respective black target box on the screen.

a

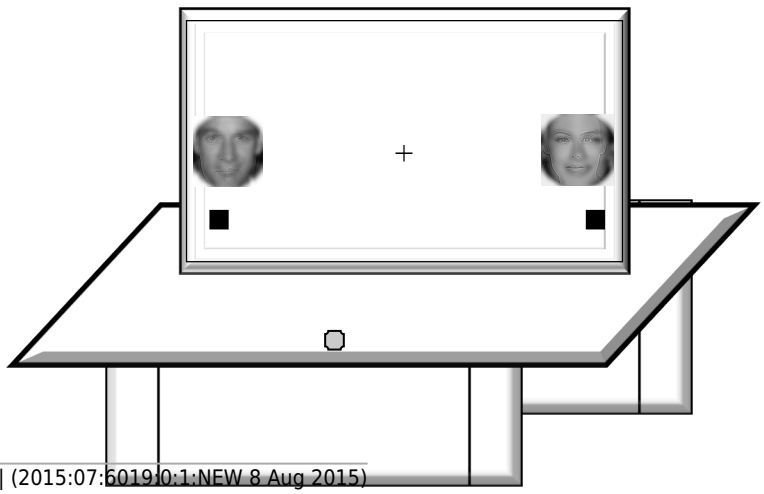
LSF **F**emale- HSF **F**emale (**FF**)

LSF **M**ale- HSF **M**ale (**MM**)

LSF **M**ale- HSF **F**emale (**MF**)

LSF **F**emale- HSF **M**ale (**FM**)

b



2

Figure2

(a) Mean trajectories for grey background (b) Mean trajectories for red background.