

Brief article

Hand position alters vision by biasing processing through different visual pathways

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ARTICLE INFO

Article history:

Received 21 July 2011

Revised 13 April 2012

Accepted 27 April 2012

Available online 24 May 2012

Keywords:

Near-hand vision

Action–perception interface

Perihand space

Magnocellular

Parvocellular

Visual pathways

ABSTRACT

The present study investigated the mechanisms responsible for the difference between visual processing of stimuli near and far from the observer's hands. The idea that objects near the hands are immediate candidates for action led us to hypothesize that vision near the hands would be biased toward the action-oriented magnocellular visual pathway that supports processing with high temporal resolution but low spatial resolution. Conversely, objects away from the hands are not immediate candidates for action and, therefore, would benefit from a bias toward the perception-oriented parvocellular visual pathway that supports processing with high spatial resolution but low temporal resolution. We tested this hypothesis based on the psychophysical characteristics of the two pathways. Namely, we presented subjects with two tasks: a temporal-gap detection task which required the high temporal acuity of the magnocellular pathway and a spatial-gap detection task that required the spatial acuity of the parvocellular pathway. Consistent with our prediction, we found better performance on the temporal-gap detection task and worse performance on the spatial-gap detection task when stimuli were presented near the hands compared to when they were far from the hands. These findings suggest that altered visual processing near the hands may be due to changes in the contribution of the two visual pathways.

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1. Introduction

Perception and action share a close and reciprocal relationship. The effect of visual perception on action is obvious; in our everyday activities, reaching, grasping, or pointing to items is much easier when those items are visible. The effect of action on visual perception is more subtle, and it is only in the last decade or so that an experimental literature showing the sensitivity of vision to action has emerged. Not only does the type of action affect perception (e.g., Bekkering & Neggers, 2002; Fagioli, Hommel, & Schubotz, 2007; Wohlschläger, 2000), but the spatial relationship between the observer's effectors (e.g., hands, tools) and perceived objects also alters vision. In-

deed, there is evidence that attentional mechanisms give priority to objects in the space near the hands (Abrams, Davoli, Du, Knapp, & Paull, 2008; Reed, Grubb, & Steele, 2006). For example, Reed et al. (2006) used an attentional cueing experiment, in which subjects responded with a keypress to the onset of a peripheral target (left or right) appearing after a cue (a frame around one of the two target locations, predicting target location with 70% accuracy). While performing this task, the subjects placed one hand next to one of the two possible target locations (left or right). Results showed that targets appearing near the hands received faster responses than those appearing on the opposite side, consistent with a higher attentional prioritization of the near-hand space (also see Hari & Joutsmäki, 1996; Kao & Goodale, 2009).

What other consequences, aside from the selective prioritization, can result from presenting visual information near the hands? Investigating this, several recent studies

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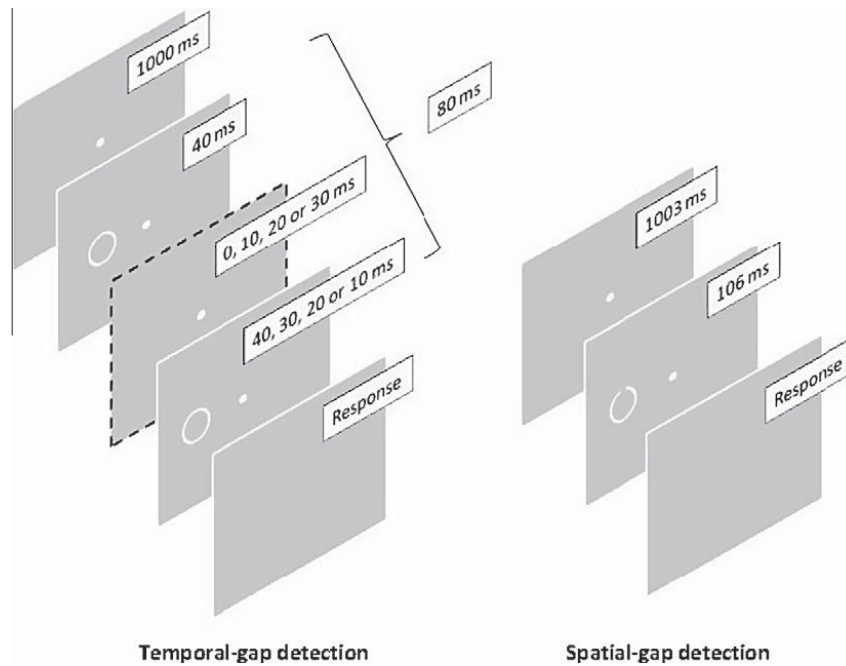


Fig. 1. The progression of events on a trial during the temporal- (left panel) and the spatial-gap (right panel) detection tasks. The display framed in dashed lines represents the temporal gap (50% of trials) that varied in duration without changing the total exposure duration (80 ms).

examined how performance on visual tasks changes depending on whether the responding hands are positioned on a table in front of the observer (as typically used in most perception and cognition experiments) or are positioned on both sides of the display monitor (thus placing the displayed information between the two hands; see Fig. 2). A study by Abrams et al. (2008) found that having both hands near the displayed information resulted in smaller inhibition of return in a spatial cueing task, a slower visual search, and a larger attentional blink in a rapid serial visual presentation task. To account for these findings, Abrams et al. (2008) suggested that since vision for items that can be potentially grasped and manipulated might benefit from a more extensive perceptual analysis, attentional disengagement is delayed for near-hand stimuli compared to items far from the hands. The idea of delayed attentional disengagement near the hands seems

consistent with the earlier proposal of selective prioritization (Reed et al., 2006) while also carrying the intuitive idea that proximal objects (i.e., candidates for action) may require relatively prolonged visual processing.

More recent findings, such as enhanced performance on change detection tasks near the hands (Tseng & Bridgeman, 2011) and interference with semantic processing of words and sentences (Davoli, Du, Montana, Garverick, & Abrams, 2010), seem to pose challenge for an account based on attentional prioritization or delayed disengagement of attention. Change detection, in particular, involves processing multi-item displays in which delayed disengagement from individual items could be detrimental to performance. Describing the seemingly disparate findings of facilitation and decline in visual tasks in the near-hand space, Davoli et al. (2010) speculated that performance in tasks involving spatial processing might benefit from



Fig. 2. Position of the hand in relation to the display monitor in the hand distal (left panel) and hand proximal (right panel) conditions.

hand-proximity, whereas performance in tasks involving semantic processing (and, perhaps visual identification; Abrams et al., 2008) might decline. What mediates the enhanced spatial processing is unclear. Turning to the literature, the attentional prioritization hypothesis, which posits that attentional resources may be more readily allocated to the space near the observer's body parts (Reed et al., 2006), provides one possible mechanism. But three observations point against the view that attentional prioritization mediates the effect of hand-proximity. First, if the allocation of attention is biased toward the near-hand space, then hand-proximity should interact with other factors known to orient visual attention (e.g., exogenous peripheral cues). The two effects, however, have been shown to be additive (Reed, Betz, Garza, & Roberts, 2010; Reed et al., 2006; see also Brown, Doole, & Malfait, 2011), suggesting that separate mechanisms underlie the effect of hand-proximity than those underlying allocation of attention in space. Second, the speeded processing resulting from hand-proximity is still observed even when subjects know the location of an upcoming target, without the spatial uncertainty inherent to the attentional cueing paradigm (Kao & Goodale, 2009). The third observation, from Cosman and Vecera (2010), is that hand-proximity can influence figure-ground segregation, a process thought to occur earlier than selective attention (Qiu, Sugihara & von der Heydt, 2007). Thus, attentional prioritization seems unlikely to be the mechanism responsible for the effects of hand-proximity on vision.

Here, we propose a hypothesis to explain the hand-proximity effect that is grounded in the fact that vision consists of multiple parallel processing streams each devoted to different aspects of the visual input. This view leads to the possibility that the proximity of a visual target to the hands might have different effects on these processing streams. Of particular interest are the two major visual pathways known as the parvocellular (P) and magnocellular (M) systems, which are segregated starting at the retinal ganglion cells through the lateral geniculate nuclei (LGN), providing input to largely distinct areas of the visual cortex V1 and V2 (Derrington & Lennie, 1984; Kaplan & Shapley, 1986; Livingstone & Hubel, 1988; Shapley, 1990). Although, the two pathways are much less segregated in higher levels of the visual cortex (see Ferrera, Nealy, & Maunsell, 1992), the majority of the P and M pathways are thought to take part, respectively, in the ventral and dorsal visual streams (Livingstone & Hubel, 1988; Ungerleider & Mishkin, 1982). The anatomical distinction between the P and M cells, therefore, translates roughly into the functional distinction between visual perception and vision for action (Goodale & Milner, 1992). Based on this distinction, we hypothesized that placing the hands near an object might bias visual processing toward a higher contribution of the M system as the system prepares to act on the objects in sight. By contrast, placing the hands away from an object might give relative priority to perception, biasing information processing toward the P system.

To test this hypothesis, we took advantage of the high spatial acuity and high temporal acuity that are known as psychophysical correlates of the P and M pathway, respectively. This assumption goes back, in part, to the pio-

neering studies on the M and P cells that examined the two cell types in the LGN of monkeys, showing that M cells have receptive field centers 2–3 times larger than those of the P cells, which yield the low spatial acuity of processing along the M pathway (Derrington & Lennie, 1984; Livingstone & Hubel, 1988). Additionally, M cells were also found to be much more responsive to small luminance contrasts and were easily saturated, while P cells had lower sensitivity to luminance contrasts and not easily saturated (Derrington & Lennie, 1984). By temporarily saturating the M cells with a sudden increase in background luminance, Pokorny and Smith (1997) discovered a psychophysical method for examining processing characteristics in the P pathway alone, and by presenting low-contrast luminance stimuli after a period of adaptation to background luminance they reported a similar method for examining the M pathway in isolation. Based on the Pokorny and Smith's paradigm, further studies estimated the differences in spatial resolution along the two pathways in human observers. According to their estimate, M cells' low spatial acuity is best suited for spatial frequencies around 1–2 cycles per degree (cpd) of visual angle, whereas P cells' high spatial acuity is suited for spatial frequencies above 4 cpd (Leonova, Pokorny, & Smith, 2003; McAnany & Alexander, 2008).

Aside from the difference in spatial acuity, the speed with which signals travel through the M and P pathways is different. The M pathway consists of cells with larger axon diameters (i.e., better conductance) and less neuronal convergence than cells in the P pathway (Maunsell et al., 1999). The less neuronal convergence in the M pathway allows for summation of signals across relatively smaller intervals of time, which yields higher temporal acuity in the M pathway. Pokorny and Smith's (1997) study estimated the temporal summation of signals for the P pathway to be above 150 ms and below 50 ms for the M pathway. As a result, M pathway is best suited for processing transient stimuli and rapid changes.

In addition to different spatial and temporal acuity of the two pathways, a final assumption we made concerns the inhibitory interaction between the P and M pathways. It is thought that biasing activity toward one of the pathways can bias activity away from the other pathway (Bocanegra & Zeelenberg, 2011; Yeshurun, 2004; Yeshurun & Levy, 2003). Such pattern of bias has been recently reported by Bocanegra and Zeelenberg (2009, 2011) who investigated the changes in visual processing that result from seeing fearful faces. The authors used two complimentary visual detection tasks that differently relied on the contributions of the M and P pathways. One task demanded high temporal acuity (relying on the M pathway) by requiring detection of a short temporal discontinuity in stimulus presentation, while the other task demanded high spatial acuity (relying on the P pathway) by requiring detection of a small spatial (featural) discontinuity (see Fig. 1). Prior to the presentation of each test stimulus, subjects were presented with task-irrelevant fearful human faces, which were thought to activate the "fight or flight" M pathway. When compared to trials with neutral faces, it was found that fearful faces resulted in an enhanced detection of temporal gaps but interfered with detection of spatial gaps (Bocanegra & Zeelenberg, 2011).

In the present study, we tested the potentially different influence of hand-proximity to visual targets on information processing along the M and P pathways by using similar complimentary detection tasks (i.e., a temporal- and a spatial-gap detection) while both hands were either positioned on both sides of the display monitor (proximal) or in front of the display monitor (distal). Our prediction was that the proximal condition (due to higher contribution of the M pathway) will enhance detection of temporal gaps, while the distal condition (due to higher contribution of the P pathway) will show better performance on detection of spatial gaps.

2. Method

2.1. Subjects

Twenty-seven undergraduate students at University of Toronto participated in the experiments. All subjects reported normal or corrected-to-normal vision and gave their informed consent prior to participating.

2.2. Apparatus and procedure

The experiments were run in Matlab (MathWorks, Natick, MA) using the psychophysics toolbox (Brainard, 1997; Pelli, 1997; version 3.0.8). Visual stimuli were displayed on CRT monitors set at different resolutions and refresh rates for the two experiments (temporal-gap detection task: 800×600 and 100 Hz; spatial-gap detection task: 1600×1200 and 85 Hz). The viewing distance from the screen was fixed at 40 cm by a chin/head-rest. Visual stimuli were presented in white (~ 48 cd/m²) against a gray background (~ 11 cd/m²).

Subjects began each trial by looking at the central fixation point (radius = 0.1°). After a fixed time interval (1000 ms for the temporal-gap and 1003 ms for the spatial-gap detection tasks), a circle (radius = 0.4°) was presented 4° (center to center) to the left or right of the fixation (see Fig. 1). In the temporal-gap detection task, the circle was either continuously present (no gap) or interrupted by a temporal gap that could vary in duration (10, 20, or 30 ms). Regardless of the trial type (gaps vs. no-gap), the time between the first onset and the final offset of the circle was always 80 ms (see Fig. 1). The duration of the temporal gap was meant to match the characteristic temporal summation across intervals shorter than 50 ms, while the temporal summation of the P pathway which occurs over intervals of 150–200 ms renders this pathway insensitive to this task (Pokorny & Smith, 1997; Smith & Pokorny, 2003).

In the spatial-gap detection task, each circle was present for 106 ms and was either a full circle (no gap) or had a spatial gap at the top that could vary in size (0.1, 0.26, or 0.35 radians; corresponding to $.025^\circ$, $.066^\circ$, and $.089^\circ$ of visual angle). This range of spatial gap was chosen based on the characteristic high spatial acuity of the P pathway, while the low spatial acuity of the M pathway (most suited to detecting spatial gaps larger than 0.25°)

would render it insensitive to this task (Leonova et al., 2003; McAnany & Alexander, 2008).

In both tasks, subjects reported whether they perceived a gap in the stimulus or not after the circle had disappeared. For the spatial-gap detection task, this meant detection of a featural discontinuity (i.e., lack of closure) above the circle, whereas for the temporal-gap detection task it meant detecting a temporal discontinuity (i.e., a flicker) in the stimulus presentation. A clear screen was displayed until a response was performed. In the proximal hand condition, subjects' hands were placed on both sides of the screen, each being $\sim 24^\circ$ of visual angle away from the center of display (Fig. 2). Responses, in the hand-proximal condition were made by pressing one of two keys on computer mice attached to the sides of the computer screen (right-hand mouse click for *gap*; left-hand click for *no-gap*). In the distal hand condition, subjects' hands were on the table in front of them. Responses in the hand-distal condition were made by pressing one of two keys on the keyboard to report the trial type ("*/?*" key for *gap*; "*z*" key for *no-gap*).

2.3. Design

Each subject performed both the temporal- and the spatial-gap detection tasks, beginning with 80 practice trials (40 trials in the proximal hand conditions) followed by 840 experimental trials. Every 105 trials, subjects switched between the proximal and distal hands conditions (after a short break), resulting in 420 trials in each of the conditions. Within each hand condition, an equal number of gap and no-gap trials were present, with the 'gap trials' were divided equally into trials with different gap sizes. The sequence in which subjects performed the temporal- and spatial-gap detection tasks and the hand condition they started with were both counterbalanced across the subjects. Performance was analyzed based on the signal detection index, d' (calculated as $z(\text{hits}) - z(\text{false alarms})$; Macmillan & Creelman, 1991).

3. Results

After excluding the trials in which a response was made within the first 100 ms after the stimulus presentation (<1% of trials), the data was submitted to a 2×2 repeated measures analysis of variance (ANOVA), with factors of task type (spatial vs. temporal) and hand condition (proximal vs. distal), and d' as the dependent measure (see Fig. 3). The ANOVA revealed a significant effect of task [$F(1, 26) = 23.7$, $MSE = .381$, $p < .001$, $\eta_p^2 = .478$], with performance better on the temporal-gap detection ($d' = 2.72 \pm .16$) compared to the spatial-gap detection task ($d' = 2.14 \pm .15$). There was no main effect of hand position [$F(1, 26) < 1$]. Most importantly, a significant interaction between hand position and task was revealed [$F(1, 26) = 8.60$, $MSE = .100$, $p < .01$, $\eta_p^2 = .249$]. Follow-up two-tailed paired-samples t -tests shows that placing the hands near the visual stimuli resulted in better performance on the temporal-gap detection (distal 2.65, proximal 2.80; $t(26) = 2.17$, $SE = .07$, $p < .05$) while having

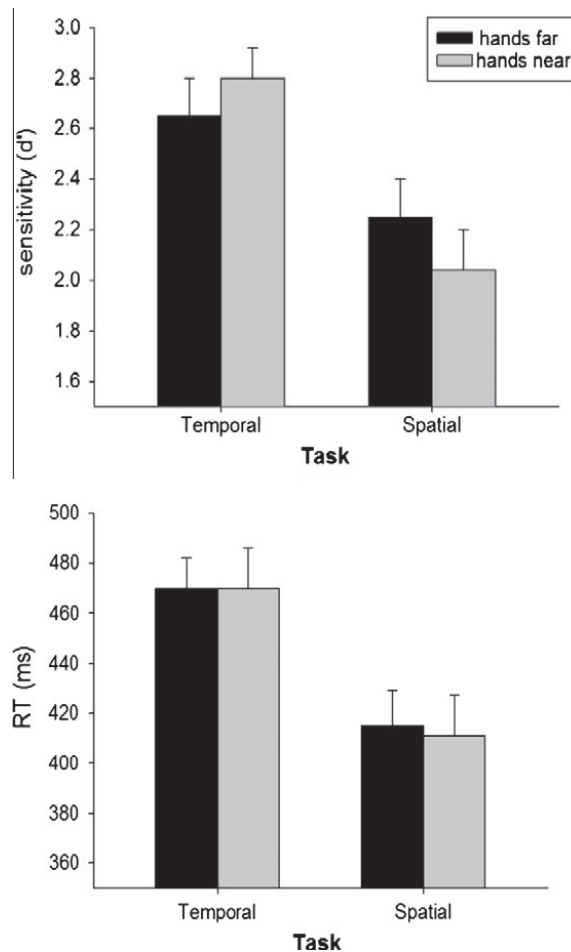


Fig. 3. Changes in visual sensitivity (d' ; top panel) and response time (bottom panel) in the temporal- and the spatial-gap detection tasks as a function of hand position (near vs. far). Error bars represent 95% within-subject confidence intervals.

the hands on the keyboard resulted in better performance in the spatial-gap detection task (proximal 2.04, distal 2.25; $t(26) = 2.03$, $SE = .10$, $p = .052$).

Separate ANOVAs were also conducted for hit rates and false alarm. For hit rates, main effects of both task type and hand position reached significance. Hit rates were higher on the temporal-gap detection task (89%) compared to the spatial-gap detection task (75%) across both hand conditions [$F(1, 26) = 46.7$, $MSE = .010$, $p < .001$, $\eta_p^2 = .642$], and hit rates were higher when the hands were far from the stimuli (83%) compared to when they were near the stimuli (81%) in both tasks [$F(1, 26) = 15.27$, $MSE = .001$, $p < .001$, $\eta_p^2 = .370$]. The hand by task interaction also reached significance [$F(1, 26) = 6.70$, $MSE = .001$, $p < .05$, $\eta_p^2 = .205$]. Two-tailed pair-sampled t -tests showed positioning the hand near the stimuli did not affect hit rates in the temporal-gap detection task [$t(26) = 1.83$, $SE = .028$, $p > .05$] though it reduced hit rates in the spatial-gap detection task from 77% to 73% [$t(26) = 3.57$, $SE = .06$, $p < .01$].

For false alarms, no main effect of hand position or task type was found ($F_s < 1$). The hand \times task interaction was significant [$F(1, 26) = 5.61$, $MSE = .002$, $p < .05$, $\eta_p^2 = .177$]. Two-tailed pair-sampled t -tests showed that placing the hands near the stimuli reduced false alarms from 12.4%

to 9.4% in the temporal-gap detection task [$t(26) = 2.19$, $SE = .013$, $p < .05$] but did not affect false alarms in the spatial-gap detection task ($t < 1$).

To ensure the above interactions between task and hand-proximity were not a product of a speed-accuracy trade-off, we submitted mean response time (RT) data from the correct trials to a similar 2×2 ANOVA (see the bottom panel of Fig. 3), after excluding responses 2.5 SD above and below the total average (3% of trials). This analysis revealed only a main effect of task [$F(1, 26) = 18.3$, $MSE = 4.81 \times 10^3$, $p < .001$, $\eta_p^2 = .414$]. Responses were, on average, slower on the temporal-gap detection task ($M \pm SE = 470 \pm 17$ ms) compared to the spatial-gap detection task (413 ± 10 ms). No main effect of hands or a 2-way interaction were found for the RT data ($F_s < 1$). Taken together, the d' and RT data do not conclusively indicate whether one of the two tasks was inherently more difficult than the other. Although d' was on average higher in the temporal-gap detection task, performance was considerably slower in this task.

4. Discussion

The present study investigated the mechanisms responsible for altered visual processing near the hands (Abrams et al., 2008; Davoli et al., 2010; Reed et al., 2006, 2010). Based on the idea that objects near the hands are immediate candidates for action, we hypothesized that vision near the hands would be biased toward the action-oriented magnocellular (M) visual pathway that supports processing with high temporal resolution but low spatial resolution. Conversely, objects away from the hands are not immediate candidates for action and, therefore, would benefit from the perception-oriented parvocellular (P) visual pathway that supports processing with high spatial resolution but low temporal resolution. Consistent with this hypothesis, hand-proximal condition led to better performance on the temporal-gap detection and worse performance on the spatial-gap detection task, compared to the hand-distal condition. These findings suggest that altered visual processing near the hands is caused by the differential activation of the two visual pathways.

The present finding brings a new perspective on previous findings of altered visual processing near the hands. Critically, as soon as the differential effects of hand-proximity on processes along the M and P pathways is considered, the characteristics of the visual stimuli becomes of great importance. For instance, earlier studies that argued for a facilitated attentional prioritization near the hands used attentional orienting tasks with targets that consisted of a change of luminance (Reed et al., 2006, 2010; Thura, Boussaoud, & Meunier, 2008). We propose that facilitated processing of luminance detection targets, via the luminance sensitive M pathway, is the mechanism underlying the facilitated responses to targets (Reed et al., 2006, 2010). That is why even when subjects know the position of the luminance detection target with certainty prior to onset (i.e., no spatial orienting) hand-proximity can still speed processing (Kao & Goodale, 2009).

Also consistent with the hypothesis that hand-proximity increases the activation of the M pathway is the recent findings of Cosman and Vecera (2010) on the modulation of figure-ground segregation as a function of hand-proximity. In their study, the portion of the stimulus that was near the hand was more likely to be perceived as the figure, whereas the portion of the stimulus far from the hand was more likely to be perceived as the ground. The M channel has long been thought to support figure-ground segregation using inequalities of the display luminance (see Livingstone & Hubel, 1988). Indeed, color differences in equiluminant displays lead to figure-ground ambiguity (Koffka, 1935, cited by Livingstone & Hubel, 1988). If hand-proximity increases the M channel's contribution in processing the proximal stimulus, then it would simulate a luminance inequality. That is, the hand-near (or, more generally, action-relevant) portion of the display has a higher effective luminance compared to the hand-far portions of the display. This notion is compatible with faster detection of a luminance change in the hand-proximal space (Reed et al., 2006), and with higher sensitivity to luminance distractors in the space of potential (pointing) action, compared to the space of mere viewing (Welsh & Pratt, 2008). Thus, we propose that the bias toward perceiving the near-hand object as the figure, rather than the ground, indicates the higher contribution of the M pathway to visual processing of items near the hands.

Similarly, the distinction between the two visual pathways can explain the performance decline in the hand-proximal condition whenever the P pathway is required for target processing. This is particularly the case for tasks requiring perceptual acuity or semantic categorization (e.g., Abrams et al., 2008; Davoli et al., 2010). The relatively lower sensitivity of the M neurons to spatially dense stimuli can account for the performance decline on tasks involving identification of one target item among other alphanumeric distractors (Abrams et al., 2008; Davoli & Abrams, 2009). Furthermore, since semantic processing of words has been shown to be sensitive to the grouping of the constituent letters (Reynolds, Kwan, & Smilek, 2011), the reduced contribution of the P neurons responsible for spatial grouping of letters and words (O'Brien et al., 2002) may be responsible for the decline in semantic processing of words and sentences in the hand-proximal space (Davoli et al., 2010).

Interestingly, the changes in d' across our two tasks was based on different underlying patterns of change in hit rate and false alarms. These differences may be interpreted based on the characteristics of the M and P pathways. Let us consider the pattern of improvement in each task. First, placing the hands near the display enhanced performance in temporal-gap detection by reducing false alarms. Second, placing the hands far from the display enhanced performance in spatial-gap detection by increasing hit rate. Our speculation is that when signal detection relies on the M pathway, conscious access to the presence of the signal is weaker than when signal detection relies on the P pathway. If this assumption affects setting the temporal-gap detection criterion, then false alarms would be more likely than misses (i.e., "the signal might be present, without my conscious access"). By contrast, when detection re-

lies on the P pathway, conscious access to the signal would be relatively stronger. If this assumption affects setting the spatial-gap detection criterion, then misses would be more likely than false alarms (i.e., "without my conscious access, the signal is probably absent"). The idea of differential conscious access across the two pathways is also consistent with the significantly slower responses in the temporal-gap detection, compared to the spatial-gap detection. Further research is needed to test this possibility.

The question remains as to how hand proximity to a target can increase the contribution of the M pathway to target processing. The answer likely has to do with the hand-centered localization of near-hand visual targets, as this allows for more precise actions toward the target (Brown, Morrissey, & Goodale, 2009). Although this hand-centered localization relies on the neuronal populations in the parietal and premotor cortex (e.g., Chang, Papadimitriou, & Snyder, 2009; Graziano & Gross, 1998) it is dependent on the same raw visual input coming from the early visual areas (though see Brown, Krolczak, Demonet, & Goodale, 2008). Therefore, it is possible that more weight, via feedback connections that modulate input from the early visual areas (Callaway, 1998), is given to the pathway that carries the location information and feeds the parietal regions for the hand-centered sensorimotor transformation (i.e., the magnocellular neurons).

In the present study we manipulated the proximity of both hands to the visual display, as opposed to using a single-hand manipulation. This choice was partly based on the findings of Tseng and Bridgeman (2010) who showed the effect of hand-proximity is primarily driven by the simultaneous positioning of both hands. Interestingly, each hand alone produced a much weaker effect (dominant hand) or no effect (non-dominant hand). The authors suggested that the superadditive effect of positioning of both hands might be due to the overlearned nature of bimanual engagement with tasks (e.g., typing, washing dishes, opening a can). Other studies, including those by Abrams et al. (2008) and Davoli et al. (2010), used both hands to find their effects on visual processing with hand proximity because people typically hold items they intend to process in both hands (e.g., holding a page we are reading). In addition, using both hands avoids the issues associated with selectively attending to one hemifield over the other. Thus, examining the effects of proximity with both hands is the appropriate manipulation for the question at hand.

In summary, we argue that the changes in visual processing observed as a consequence of hand-proximity arise from distinct and opposite effects on the activation of the M and P pathways. The findings of the present study, taken together with those by Bocanegra and Zeelenberg (2011), provide strong support for the view that the visual system is sensitive to the specific behavioral context and that subtle changes can affect the extent to which aspects of visual stimuli are weighted (Davoli et al., 2010; O'Regan & Noë, 2001). The mutually inhibiting relationship between the two pathways underlies the trade-off between the two types of processing. Specifically, the action-oriented space near the hands seem to bias the visual system toward a relatively more pronounced activation of the M pathway, which then facilitates processing stimulus requiring high

temporal resolution but hinders processing stimulus requiring high spatial resolution.

Acknowledgements

We thank Josh Moskowitz for his help in collecting the data. This project was supported by a discovery grant from the Natural Sciences and Engineering Council of Canada (NSERC) to J.P. and an NSERC postgraduate scholarship to D.G.

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