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BRIEF REPORT

Hand Position Alters Vision by Modulating the Time Course of Spatial Frequency Use

Laurent Caplette
Université de Montréal

Bruno Wicker
Aix-Marseille Université

Frédéric Gosselin and Greg L. West
Université de Montréal

The nervous system gives preferential treatment to objects near the hands that are candidates for action. It is not yet understood how this process is achieved. Here we show evidence for the mechanism that underlies this process having used an experimental technique that maps the use of spatial frequencies (SFs) during object recognition across time. We used this technique to replicate and characterize with greater precision the coarse-to-fine SF sampling observed in previous studies. Then we show that the visual processing of real-world objects near an observer's hands is biased toward the use of low-SF information, around 288 ms. Conversely, high-SF information presented around 113 ms impaired object recognition when objects were presented near the hands. Notably, both of these effects happened relatively late during object recognition and suggest that the modulation of SF use by hand position is at least partly attentional in nature.

Keywords: action-perception, spatial frequencies, magnocellular pathway, hand-position, object recognition

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Human perception and action systems interact to produce very accurate, visually guided movements to accomplish everyday tasks (e.g., reaching and grasping). It is therefore not surprising that action can have a large effect on perceptual processes. Research during the last decade has demonstrated that performance is affected by the type of action being performed and the spatial relationship between an observer's effectors (e.g., hands, tools) and the target object (Bekkering & Neggers, 2002; Fagioli, Hommel, & Schubotz, 2007; Wohlschläger, 2000).

More recently, it has been hypothesized that the effect of hand proximity on vision represents a biasing of visual processing toward pathways responsible for different aspects of visual input (i.e., perception and action; Abrams & Weidler, 2014; Goodhew, Edwards, Ferber, & Pratt, 2015; Goodhew, Fogel, & Pratt, 2014; Gozli, West, & Pratt, 2012). Current models of vision propose that visual processing is divided into two major pathways known as the parvocellular (P) and magnocellular (M) systems, whose separation begins at the retinal level (Derrington & Lennie, 1984; De Valois, Albrecht, & Thorell, 1982; Kaplan & Shapley, 1986; Shapley, 1990), and is responsible for the functional distinction between visual perception and vision for action (Goodale & Milner, 1992). Further, the ventral–perception visual stream has a larger number of projections from the P pathway while the dorsal–action visual stream has a larger number of projections from the M pathway (Livingstone & Hubel, 1988).

Crucially, the M and P pathways preferentially treat separate bands of spatial frequencies (SFs): Low SFs, which provide coarse visual information, are extracted early and processed through the fast-acting M pathway; conversely, high SFs, which provide finer visual information, are extracted later and processed more slowly by the P pathway. This coarse-to-fine SF extraction has been observed behaviorally in numerous studies (e.g., Hughes, Nozawa, & Kitterle, 1996; Hupé et al., 2001; Schyns & Oliva, 1994; Caplette, Wicker, & Gosselin, 2016). Further, this temporal distinction between the processing of low and high SFs is present in both the early visual cortex (Goddard, Carlson, Dermody, & Woolgar, 2016; Jemel, Mimeault, Saint-Amour, Hosein, & Mottron, 2010; Parker & Salzen, 1977) and the frontal cortex (Bar et al., 2006; Goddard et al., 2016).

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Laurent Caplette, Département de psychologie, Université de Montréal; Bruno Wicker, Institut de Neurosciences de la Timone, CNRS UMR 7289, Aix-Marseille Université; Frédéric Gosselin, and Greg L. West, Département de psychologie, Université de Montréal.

Correspondence concerning this article should be addressed to Greg L. West, Department of Psychology, University of Montreal, Pavillon Marie-Victorin, 90 Avenue Vincent d'Indy, Montreal, QC, Canada H2V 2S9. E-mail: gregory.west@umontreal.ca

A growing body of evidence suggests that hand position near a stimulus can bias visual processing toward the action-oriented M pathway, which preferentially treats low SFs, and impair the processing of high-SF information conducted along the perception-oriented P pathway (Abrams & Weidler, 2014; Goodhew et al., 2014; 2015; Gozli et al., 2012). This mechanism is hypothesized to facilitate precise interaction with objects that are candidates for action by up-signaling visual information conducted along the dorsal–action M pathway, and down-signaling perceptual information along the P pathway (see Goodhew et al., 2015, for a review).

At this point, many aspects of the effect of hand position on SF sampling remain unclear, i.e., (a) What specific SF bands during visual processing are differentially affected by hand position? (b) What is the impact of hand position on the visual treatment of ecologically valid objects that people would find in their everyday lives? And notably, (c) at which stage or stages of object recognition does hand position affect SF sampling? To address these research questions, we employed a technique that maps, with unprecedented resolution, the use of SFs contained in everyday objects across time. More specifically, we created dynamic stimuli from still images (e.g., a bench, a pale, a plant, a wrapped gift, a cake), which were presented as 333-ms videos that randomly revealed SF bands (ranging from 0.5 to 128 cycles per image [cpi]) at variable time points (ranging from early to late time points within the video). In Experiment 1, we tested the value and reliability of this method by examining the time course of SF sampling during object recognition with hands in a typical downward position. We expected to find the coarse-to-fine sampling that has been observed in past studies (e.g., Caplette et al., 2016; Hughes et al., 1996; Hupé et al., 2001; Schyns & Oliva, 1994). In a second experiment, with a new set of subjects, we investigated the impact of hand position on this pattern of SF extraction by contrasting conditions in which subjects placed their hands either near or far from the stimulus.

General Method

Materials

The experimental programs ran on Mac Pro (Apple, Inc., Cupertino, CA) computers in the Matlab (Mathworks, Inc., Natick, MA) environment, using functions from the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). All stimuli were presented on Asus VG278H monitors (1,920 × 1,080 pixels at 120 Hz; Fremont, CA), calibrated to allow linear manipulation of luminance. Luminance ranged from 1.6 cd/m^2 to 159 cd/m^2.

Stimuli

Eighty-six grayscale images of everyday man-made objects were selected from the database used in Shenhav et al. (2013) and from Internet searches. Images were 256 × 256 pixels and median object width was 220 pixels. The objects were cropped manually and pasted on a homogenous mid-gray background. The SF spectrum of each image was set to the mean SF spectrum of the images, and mean luminance was equalized across images using the SHINE toolbox (Willenbockel et al., 2010). Resulting images had a root mean-square (RMS) contrast of about 0.20.

On each trial, participants were shown a short video (333 ms) consisting of an object image, with random SFs gradually revealed at random time points (e.g., Video S1; Video S2); that is, on each video frame, there would typically be several SFs shown among all possible SFs, and these would change from frame to frame. To create these dynamic stimuli on each trial, we first randomly generated a matrix of 256 SFs × 40 frames (with SFs ranging from 0.5 to 128 cpi, and each frame lasting 8.33 ms), in which most elements were 0s and a few were 1s. The number of 1s was adjusted on a trial-by-trial basis to maintain performance at 75% correct. We then convolved this *sparse matrix* with a 2D Gaussian kernel (a *bubble;* $\sigma_{SF} = 1.5$ cpi; $\sigma_{time} = 15$ ms). This resulted in the trial's *sampling matrix*: an SF × Time plane with randomly located bubbles. Every column of this sampling matrix was then rotated around its origin to create isotropic, *two-dimensional (2D) random filters*. Finally, these 2D random filters were dot-multiplied by the base image's spectrum and inverse fast-Fourier transformed to create a filtered version of the image for every video frame (see Figure 1 for an illustration of this method). To ensure accurate luminance display, we applied noisy-bit dithering to the final stimuli (Allard & Faubert, 2008).

Procedure

Participants sat in front of a computer monitor, in a dimly lit room. They completed two 500-trial blocks on the first day and two more on the second day. A short break occurred every 50 trials. Each trial was comprised of the following events: a fixation cross (300 ms), a blank screen (200 ms), the video stimulus (333 ms), a fixation cross (300 ms), a blank screen (200 ms), and an object name at the basic level of abstraction that remained on screen either until a response was provided, or for a maximum of 1 s, in which case it was replaced by a blank screen until a response was provided. The number of bubbles was adjusted on a trial-by-trial basis using a gradient-descent algorithm to maintain performance at 75% correct. Subjects were asked to indicate whether the name matched the object as accurately and as rapidly as possible. The basic-level name and the object matched 50% of the time; on the trials in which they didn't match, the name was randomly chosen among the basic-level names of all other objects.

Regression Analysis

Accuracies and response times were transformed into z scores for every object (separately for each condition in Experiment 2) to minimize variability due to differences in object recognizability or familiarity with the object name. Further, z scores were calculated for each 500-trial block to diminish variability due to task learning, and for each subject to minimize residual individual differences in performance. Trials associated with z scores over 3 or below -3 (either in accuracy or response times) were discarded from the regressions (2.23% of trials in Experiment 1; 0.26% of trials in Experiment 2).

To uncover which spatial frequencies in which time frames led to accurate object recognition, we performed multiple least-square linear regressions between accuracies and corresponding sparse matrices, separately for each subject (and each condition, in Experiment 2). The resulting matrices of regression coefficients were then summed across subjects and convolved with a Gaussian kernel ($\sigma_{SF} = 5$ cpi; $\sigma_{time} = 42$ ms); henceforth we shall refer to

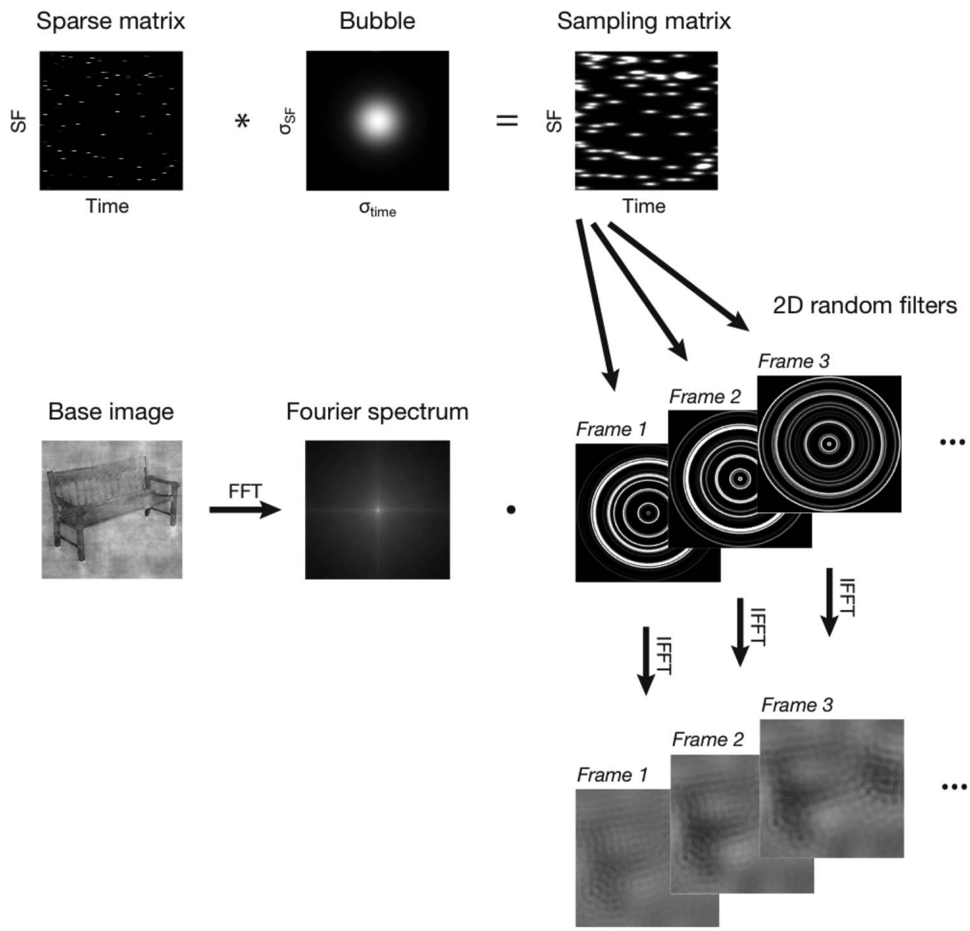

Figure 1. Illustration of the sampling method. On each trial, we randomly generated a matrix of dimensions 256×40 (representing respectively SFs and frames) in which most elements were zeros and a few were ones. We then convolved this sparse matrix with a 2D Gaussian kernel (a "bubble"). This resulted in the trial's sampling matrix, shown here as a plane with a number of randomly located bubbles. Every column of this sampling matrix was then rotated around its origin to create isotropic 2D random filters. Finally, these 2D random filters were dot-multiplied by the base image's spectrum and inverse fast Fourier transformed to create a filtered version of the image for every video frame.

these matrices as classification images. The same procedure was repeated with 500 bootstrapped samples, which were then used to transform the summed regression coefficients into z scores. Finally, we applied a cluster test (Chauvin, Worsley, Schyns, Arguin, & Gosselin, 2005) to the classification images to assess their statistical significance. Given an arbitrary z-score threshold (here, ± 3.5), this test gives a cluster size, k, above which the specified p-value (here, $p < .05$, two-tailed), is satisfied, controlling the family-wise error rate (FWER) while taking into account the correlation in the data.

Experiment 1

In Experiment 1, we tested the value of this new method by examining the time course of SF sampling during object recognition with hands in a typical downward position. We expected to find the classic coarse-to-fine sampling that has been observed in past studies (e.g., Caplette et al., 2016; Hughes et al., 1996; Hupé et al., 2001; Schyns & Oliva, 1994).

Method

On the campus of the University of Montreal, 23 right-handed adult participants (10 men; mean age = 22.14; SD = 1.85) were recruited. Subjects had normal or corrected-to-normal vision, and did not suffer from any visual or reading disability. The study was approved by the ethics board of the University of Montreal's Faculty of Arts and Sciences. Written consent from all participants was obtained after the procedure had been fully explained, and a monetary compensation was provided upon completion of the experiment. During the task, chin rests were used to maintain viewing distance at 76 cm; images subtended 6×6 degrees of visual angle.

Results and Discussion

Participants responded correctly on an average of 75.02% of the trials and required an average of 84.32 bubbles to do so. The mean response time was 719 ms. The z-scored group-classification im-

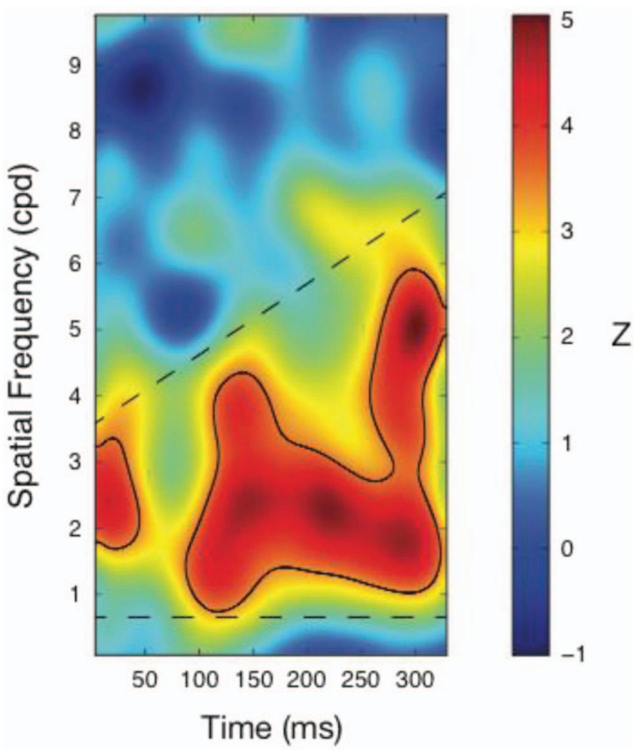

Figure 2. Classification image depicting the correlations between SF-time pixels and accurate object recognition. Pixels enclosed by solid lines are significant ($p < .05$, two-tailed, FWER-corrected). Dashed lines represent the best fitting linear SF sampling model (see text for details).

age is illustrated in Figure 2. We included the SFs from 0.08 to 9.83 cycles per degree (cpd; equivalent in this experiment to 0.5 to 59 cpi) in our analyses, because they have been consistently identified as contributing to accurate object recognition (e.g., Caplette, West, Gomot, Gosselin, & Wicker, 2014; Caplette et al., 2016; Gold, Bennett, & Sekuler, 1999). The z scores indicate the correlation between the presentation of a given SF on a given time frame and accuracy; white curves indicate significant clusters ($p <$ .05, two-tailed, FWER-corrected). This analysis revealed a first earlier significant cluster that peaked at 2.25 cpd and 13 ms ($z_{max} = 4.49$, $k = 148$) and led to accurate object recognition. A second later, significant cluster peaking at 5.08 cpd and 304 ms ($z_{max} = 5.05$, $k = 1{,}240$) also led to accurate object recognition.

To reduce the dimensionality of the results and characterize them more concisely, we fitted a linear model on the classification image. The model consisted of a surface defined by the inequalities $a_1 + b_1 t < f < a_2 + b_2 t$, where f stands for spatial frequency (cpd), t stands for time (s), and a_1, a_2, b_1, and b_2 are free parameters. The model was fitted using the Nelder–Mead simplex method. The best fitting model ($R^2 = 0.67$) displayed a clear coarse-to-fine pattern, such that the highest SFs sampled were steadily increasing across time ($a_2 = 3.68$ cpd; $b_2 = 10.32$ cpd/s) and such that, perhaps more surprisingly, the lowest SFs sampled were the same throughout the video ($a_1 = 0.69$ cpd; $b_1 = 0.00$ cpd/s; see Figure 2).

In summary, the observed time course of SF sampling matches a coarse-to-fine model, thus confirming what has been observed in previous studies. Further, our method characterized this sampling pattern with greater precision than previous methods and showed that low SFs continue to be used in the latest time frames (see also Caplette et al., 2016). Together, these results demonstrate the value and the reliability of our method.

Experiment 2

In Experiment 2, we employed the technique that was validated in Experiment 1 to investigate with unprecedented precision how hand position (i.e., when hands are near or far from the stimulus) modulates the time course of SF sampling. We expected to replicate, with everyday objects, the finding that the proximity of the hands to the stimulus enhances the extraction of low SFs and/or impairs the extraction of high SFs reported in the literature. Furthermore, we believed that the high-SF resolution of our method would allow us to detect the precise SFs affected by hand position, and that its high temporal resolution would allow us to discover the precise moments during object recognition that hand position would influence SF processing.

Method

On the campus of the University of Montreal, 28 right-handed adult participants (17 women; mean age = 22.1, $SD = 2.19$) were recruited. Subjects had normal or corrected to normal vision, and did not suffer from any visual or reading disability. The study was approved by the ethics board of the University of Montreal's Faculty of Arts and Sciences. Written consent from all participants was obtained after the procedure had been fully explained, and a monetary compensation was provided upon completion of the experiment.

During the task, chin rests were used to maintain viewing distance at 35 cm; images subtended 13 × 13 degrees of visual angle. It is important to note, half the trials were performed with a key press (hands–distal condition), and half were performed with two mice attached to either side of the monitor (hands–proximal condition; see Gozli et al., 2012). Participants' elbows were resting on the table while in the hands–proximal condition so that no physical effort had to be exerted. Conditions were alternated in blocks of 50 trials (the first condition was counterbalanced among participants).

Results and Discussion

Participants responded correctly on an average of 73.13% of the trials in the hands–proximal condition, and of 74.10% in the hands–distal condition, $t(27) = 0.96$, $p > .25$; they required an average of 66.26 bubbles in the hands–proximal condition, and of 66.93 bubbles in the hands–distal condition, $t(27) = 0.84$, $p > .25$. In agreement with a previous study (Reed, Grubb, & Steele, 2006), the mean response time was shorter in the hands–proximal condition compared to the hands–distal condition (633 ms vs. 747 ms; $t(27) = 4.26$, $p < .001$).

Figure 3 illustrates the z scored group classification images for the two conditions and the contrast between them. Z scores indicate the correlation between accuracy and the presentation of a given SF on a given time frame; white curves indicate significant clusters ($p < .05$, two-tailed, FWER-corrected). In the hands–proximal condition, a first cluster that peaked at 1.27 cpd and 88

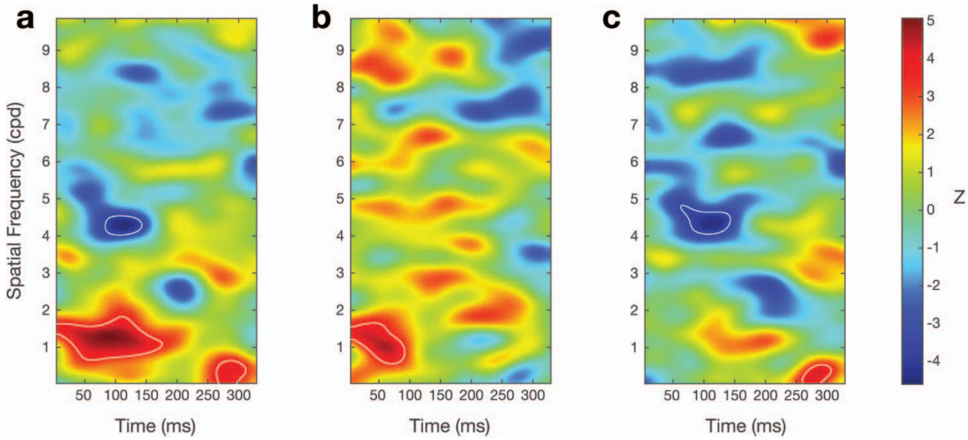

Figure 3. Group classification images depicting the correlations between SF-time pixels and accurate object recognition: (a) hands–proximal condition; (b) hands–distal condition; (c) hands–proximal condition − hands–distal condition. Pixel clusters enclosed by white lines are significant ($p < .05$, two-tailed, FWER-corrected).

ms ($z_{max} = 5.08$, $k = 391$) and a second cluster that peaked at 0.35 cpd and 296 ms ($z_{max} = 4.17$, $k = 78$) led to accurate object recognition, while a third cluster that peaked at 4.31 cpd and 113 ms ($z_{max} = 4.60$, $k = 81$) led to inaccurate object recognition. In the hands–distal condition, a unique cluster that peaked at 1.15 cpd and 46 ms ($z_{max} = 4.63$, $k = 191$) led to statistically significant accurate object recognition. This is very similar to the early SF-sampling pattern observed in Experiment 1.

In the contrast between these two conditions, one cluster that peaked at 0.27 cpd and 288 ms ($z_{max} = 4.26$, $k = 51$) led to more accurate recognition in the hands–proximal condition than in the hands–distal condition, whereas a second cluster that peaked at 4.42 cpd and 104 ms ($z_{max} = 4.46$, $k = 124$) led to more accurate recognition in the hands–distal condition than the hands–proximal condition.

Given the fact that each object was repeated 23 times, on average, during the course of the experiment (although always with different SFs revealed at different moments), we tested whether there was some learning effect. To do that, we contrasted classification images derived from the first and last blocks of trials. We did not find any significant difference; however, this result should be interpreted carefully, given the poor signal-to-noise ratio in our data.

In summary, we showed that the sampling of relatively high SFs peaking at 4.42 cpd was impaired and that the sampling of relatively low SFs peaking at 0.27 cpd was enhanced when objects were near the hands. Most important, by evaluating the time course of SF sampling when hands were near target objects, we showed that the bias toward low SF processing occurred in the latest time frames at around 288 ms, whereas the decreased sensitivity to high SFs occurred around 104 ms.

General Discussion

The main goal of the present study was to investigate how the time course of SF sampling is altered when objects are presented near the hands. On each trial, subjects had to recognize an object from a brief video sampling random SFs on random frames; we then reverse-correlated the revealed SFs and time frames with response accuracy. This technique allowed us to map the time course of SF sampling with unprecedented precision.

We first put our method to the test by examining the time course of SF sampling in a basic object-recognition task. As expected, we observed the classic coarse-to-fine sampling reported in the literature (Caplette et al., 2016; Hughes et al., 1996; Hupé et al., 2001; Schyns & Oliva, 1994). However, our method allowed us to characterize this coarse-to-fine sampling with much greater precision than previous methods, notably indicating that low SFs are used continuously. These results demonstrate the value and the reliability of our method.

In our second experiment, we tackled our main research question: How exactly does hand position alter SF sampling? We replicated the finding—and extended it to everyday objects—that the prioritization of objects near the hands is driven by an increased use of relatively low SFs and a decreased use of relatively high SFs when hands were proximal to the target object. What is important to note is our high-resolution technique provided the increased resolution to reveal that this effect is driven specifically by low SFs peaking at 0.27 cpd and high SFs peaking at 4.42 cpd. These results are consistent with a biasing of processing toward magnocellular pathways when hands are near the stimuli.

Most important to note: This technique gave us a novel opportunity to examine the time course of SF use as a function of hand position. In both hands–proximal and –distal conditions, low SFs in early stages of object recognition (peaking at 46 ms and 88 ms) contributed to accurate object recognition, and high SFs presented around 113 ms led to decreased accuracy in the hands–proximal condition. In later stages of object recognition (around 288 ms), low SFs contributed significantly more to accurate object identification in the hands–proximal condition than in the hands–distal condition.

The time course of the effect of hand position on SF sampling informs us about underlying object-recognition mechanisms. The discovery that hand position modulates SF sampling in later time frames (>100 ms) suggests that the effect is attentional rather than purely perceptual. The fact that hand position modulates the use of high SFs seen around 113 ms and low SFs seen around 288 ms in the videos implies that this information is processed by the brain later than these latencies. This is relatively late by object-recognition standards: the first bottom-up object processing sweep is believed to extend up to about 100 ms after stimulus onset (Lamme & Roelfsema, 2000). Thus, the effect of hand position on SF processing appears to have a top-down component, which involves attentional selection of visual information. Some researchers have already proposed that space near the hands is attentionally prioritized (Abrams, Davoli, Du, Knapp, & Paull, 2008; Reed et al., 2006; Reed, Betz, Garza, & Roberts, 2010); our findings furthermore elucidate that specific SFs are prioritized or inhibited in the near-hands space. This finding reconciles attentional and magnocellular accounts of the hands effect: Attention acts on specific SFs by biasing processing toward the magnocellular or parvocellular pathway (attention can exert its influence as early as the LGN; e.g., O'Connor, Fukui, Pinsk, & Kastner, 2002; McAlonan, Cavanaugh, & Wurtz, 2008). Faster processing in near-hands space (e.g., Reed et al., 2006) might be due to this biasing toward the magnocellular pathway, which conducts information at a faster rate (see Gozli et al., 2012).

Further, the recently discovered interaction between the attentional demands of a given task and the SFs modulated by hand position also supports the hypothesis that the effect of hands on SF use is attentional (Goodhew & Clarke, 2016). Future studies using this new, dynamic stimulus-presentation method could help confirm this conclusion. For example, both the attentional demands and hand position could be manipulated (as in Goodhew & Clarke, 2016), and the similarity of the time frames of the effects of both factors could be assessed. In a related way, we could also evaluate the time course of SF use in a condition that emphasizes top-down processing, and in another that emphasizes bottom-up processing (e.g., through priming the object identity or not before the stimulus). By verifying if the hand-position effect can be explained by the effect of either condition, we could disentangle these two explanations; in addition, this would provide a powerful test of popular object-recognition models (e.g., Bar, 2003; Bullier, 2001).

In conclusion, our results demonstrate that the visual system biases processing in magnocellular and parvocellular pathways according to hand position at a late processing stage. Using the method introduced in this paper, future studies can examine how the hand–position phenomenon interacts with different attentional demands.

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