Supporting Online Material for

Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices

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Materials and Methods

Two male rhesus monkeys, weighing 6 kg each, were used. All procedures followed the guidelines of the MIT Committee on Animal Care and NIH. Animals were implanted under general anesthesia with a titanium headpost to immobilize the head and titanium recording chambers for recording. Chambers were stereotaxically placed over frontal and parietal cortices (in the same hemisphere) using structural MRI scans. Novel software was developed in Matlab that produced three-dimensional models of each animal’s skull and brain in stereotaxic coordinates. This allowed accurate placement of electrode penetrations.

Absolute timing of neural activity can vary between tasks and with the statistical criterion used. Thus, our main interest was in the relative timing differences between areas. Simultaneous recording from multiple electrodes aids in detecting them because it reduces the influence of extraneous variables such as differences in performance across sessions. We used epoxy coated tungsten electrodes for recording as well as for microstimulation. Electrodes were lowered using a custom built microdrive assembly that lowered electrodes in pairs from a single screw. The microdrive assembly was designed to allow for a high density of electrodes in order to maximize the number of simultaneously recorded neurons and field potentials. The electrodes were acutely lowered through an intact dura at the beginning of every recording session and allowed to settle for a minimum of 2 hours before recording. This ensured stable isolation of single
units over the session. After recording the electrodes were retracted and the microdrive assembly was removed from the well.

Spiking activity and local field potentials were recorded across a maximum of 50 channels simultaneously. Both spiking activity and local field potentials were referenced to ground (rather than to one of the electrodes). This eliminated the possibility that coherence was due to the reference itself having temporal structure. However, ground referencing induces a characteristic, condition independent, drop-off in coherence with frequency (see Fig. 3). The signal from each electrode was divided into spiking activity and a local field potential by filtering between 154 Hz and 8.8 kHz for spikes and between 3.3 and 88 Hz for the local field potential. Single units were sorted from the raw spiking activity signal off-line, using a combination of principal component analysis of waveform traces along with other properties of the recorded waveforms (amplitude, trough/peak latency, etc). An infrared based eye-tracking system monitored eye position at 240 Hz. All analysis code was written in Matlab or C.

**Behavioral Task**

The trial was initiated when the animal fixated a point at the center of the screen. Fixation was required within a 3.2 degree window (+/- 1.6 degrees centered on the fixation point). After a short fixation period (500 ms), the animal was presented with a sample, colored, oriented bar for 1000 ms, centered on fixation. The sample stimulus was removed and the monkey then maintained central fixation over a 500 ms memory delay, which ended with presentation of a visual search array. The array elements were
identical in size and shape to the sample and appeared four degrees from fixation. One of
the array items matched the sample in both color and orientation (the target). Monkeys
needed to make a direct, linear, saccade from central fixation to the target and hold their
gaze at the target for 150 ms to receive an apple juice reward. Any deviations from the
correct saccade path, including saccades to non-target stimuli, were recorded as errors
and not rewarded.

The colored, oriented bars were 0.16 degrees of visual angle in width and 1.6
degrees in height. Nine target stimuli were constructed each day from all possible
combinations of three orientations and three different colors. The orientations and colors
were chosen such that the differences between search items was consistent in both
orientation and color space (stepping was fixed on a given day, but could range from 15
to 25 degrees in orientation and 2 to 5% change in hue). The number of search array
items was varied from 2 to 4 for psychophysical experiments that tested reaction time as
a function of array size. Four search array items were used for neurophysiological
recording experiments. Array items appeared at positions 45, 135, 225, and 315 degrees
from the vertical meridian (see Fig. 1). In pop-out, the non-targets (distractors) differed
from the target by 90 degrees and were all the same color, which was opposite the target
color on the color circle. In visual search, distractors differed from the target by either
color or orientation alone. The difference in color and orientation between the target
stimulus and distractors was the same as the difference between target stimuli. This
allowed a target stimulus on one trial to be a distractor stimulus on the next.
The search and pop-out tasks were interleaved in blocks of approximately 35 trials each. The animals performed a minimum of 720 correct trials during recording sessions, ensuring at least 10 trials for each of the 9 possible targets (3 colors by 3 orientations) at each location and for each task. Data is presented from 24 recording sessions (10 in monkey S, 14 from monkey W).

Due to the large number of simultaneously recorded neurons across all three areas there was no optimization of the stimulus parameters for recording. Likewise, neurons were not pre-selected for responsiveness. Rather, we randomly selected neurons for recording as best we could. Although this may yield neural responses that are below their potential maximum, this factor is consistent across all three regions and across behavioral tasks, and therefore cannot result in the observed effects on timing of selectivity or inter-areal synchrony.

**Recording locations**

A total of 50 electrodes were implanted into parietal and frontal cortex simultaneously, up to 25 in each anatomical area. A total of 802 neurons were recorded across all three anatomical regions in two monkeys (274 from the lateral intraparietal area, LIP, 272 neurons from lateral prefrontal cortex, LPFC, and 243 neurons from the frontal eye fields, FEF; 280 neurons were recorded from monkey S and 522 neurons from monkey W).
The lateral intraparietal region (LIP) recording well was placed at approximately 7 mm AP from the interaural plane and was placed using structural MRIs. To identify LIP neurophysiologically, we trained the animals on a delayed saccade task. During central fixation, a brief spot of light was flashed in the periphery. After a memory delay, the fixation point was extinguished and the animal made a saccade to the remembered location of the light spot. This has been used to isolate LIP from surrounding regions, as it is the only region in the parietal cortex that shows selectivity for target location during the memory delay(1). The animals performed the delayed saccade task at the beginning of every recording session. Electrodes were only considered to be within LIP for that session if a neuron isolated from that electrode showed memory delay activity selective for the remembered location.

The frontal recording well was placed at approximately 23 mm AP from the interaural plane. Microstimulation was used to demarcate the frontal eye fields from dorsolateral prefrontal cortex. Stimulation was delivered as a 200 ms train of bi-phasic pulses with a width 400 µs and an inter-pulse frequency of 330 Hz using the same electrodes used for recording. Current level was started at 150 µA and reduced to find the threshold at which an eye movement vector was elicited 50% of the time. Only sites that had thresholds of stimulation amplitudes less than 50 µA were classified as belonging to the frontal eye fields(2). Anterior sites were classified as belonging to the LPFC. In general, stimulation at LPFC sites did not elicit eye movements even at the highest current amplitude tested (150 µA).
For all of the analysis presented in this manuscript, we required each neuron to be recorded for a minimum of 30 trials for each target location. This yielded 249 LIP neurons, 248 LPFC neurons, and 225 FEF neurons that had enough trials during the pop-out condition. During the search condition 247 LIP neurons, 251 LPFC neurons, and 225 FEF neurons met this criterion. Similar results were obtained from each animal alone, so they are combined for presentation.

**Single Unit Selectivity**

The factor of interest was the location of the target in the search array; it was randomized from trial to trial and thus unknown to the monkey before the array appeared. Neural information about the target location thus reflected the allocation of attention to it. By contrast, the monkeys had prior knowledge of the identity of the target before the array appeared; the sample stimulus instructed it.

We assessed single unit selectivity to the target location by a mutual information statistic.(3) The mutual information statistic reflects how well one can predict the target location based on the firing rate of a given neuron (example LIP and LPFC neurons are shown in Fig. S2). Note that these analyses capture differences in firing rate distributions between target locations, not their overall activation. A neuron could, for example, show a short latency visual response to the onset of the stimulus array but not carry information about target location until later, if at all. Approximately 1/3 of all randomly recorded
neurons in each area showed selectivity for the target location during either the pop-out or visual search tasks (86 neurons in LIP, 85 in FEF, and 98 in LPFC).

To determine whether and when the observed level of mutual information was significantly different from chance, we used a randomization test. The association between neural activity and target locations was randomly shuffled and the amount of mutual information was recalculated. By repeating this process 4999 times, a null distribution was constructed which was then compared to the actual observed mutual information.

The timecourse of mutual information was calculated in non-overlapping windows of 25 ms. Significance was determined within each bin, with the observed amount of information being denoted as significant only if it exceeded 95% of the null distribution (p < 0.05 in each bin). The point at which an individual neuron began to significantly reflect the target location was defined as the time point at which significant information was found for two consecutive bins (chance level = 0.05^2 or 2.5*10^{-3}).

Given the time to first significance for each individual neuron, we constructed a distribution of those times for a given anatomical area, as shown in Fig. 2A and B. The distribution of when individual neurons in each area first showed significant information for the target location appeared to be multimodal. In order to quantify the number and location of modes we fit models with a mixture of one, two, or three Gaussians to the data. We used the Bayesian Information Criterion(4) to determine how well each model
fit the observed data. The BIC is a combination of the residuals between the model and
data and the number of free parameters in the model, correcting for the advantage of
more complex models. The model with the lowest BIC is the model that has the best fit
to the data without over-parameterization. As is shown in Table S1 we found that a
bimodal distribution fit the best for the observed data in all three anatomical regions
during both search and pop-out. The resultant $R^2$ of the fits (Table S2) all show a large
proportion of the variance in the observed data was captured by the mixture of Gaussians.
The bimodal fit estimated both the mean and variance of the distributions. The deviation
about each parameter was estimated using the Fisher Information and was used to both
calculate a confidence interval for each parameter and to test for significant differences
between areas (t-test).

As noted in the main text, curves fit to the distribution of first significance in the
pop-out condition (Fig 2A) showed an early population of LIP neurons centered at 162
ms before the saccade (95% confidence interval or CI: 200 ms – 124 ms). Early
populations in LPFC and FEF followed at 77 ms (95% CI: 84 ms – 70 ms) and 40 ms
(95% CI: 56 ms – 23 ms) before the saccade, respectively (LIP < LPFC, $p = 2*10^{-8}$; LIP
< FEF, $p = 2*10^{-14}$; LPFC < FEF, $p = 2*10^{-7}$; all comparisons by t-test). The
distributions of the neurons that found the target after the saccade was overlapping in all
three areas and centered at approximately 100 ms after saccade.

Similar to the pop-out condition, curves were fit to the distributions from the
search condition (Fig 2B) and showed the reverse ordering. Estimates of the early
populations showed that FEF and LPFC preceded LIP: FEF and LPFC had early modes at 46 ms (95% confidence interval: 75 – 17 ms) and 19 ms (25 - 13 ms) before the saccade, respectively, followed by LIP at 19 ms (8 – 30 ms) after the saccade (FEF < LIP, p = 8*10^{-13}; LPFC < LIP, p = 6*10^{-8}; all comparisons by t-test). The distributions of neurons that found the target after the saccade were overlapping and centered at approximately 100 ms after saccade.

In order to determine when a neural population as a whole began to represent the target location, we compared the observed cumulative distribution to the distribution that is expected by chance (see Fig. S3 for raw cumulative histograms and chance distribution). Given our significance criterion of two consecutive bins of p < 0.05, we calculated the average number of neurons expected to reflect the target location by chance in each 25 ms time bin, along with the standard deviation about that mean. As each comparison was conducted independently for each 25 ms step, the number of comparisons increases with time. But as a neuron can only ‘first’ show selectivity once, the chance level does not increase linearly. Therefore, a Monte-Carlo analysis was used to estimate the number of significant neurons in each time bin by chance. Use of a binomial distribution yielded similar results to the Monte-Carlo analysis. By subtracting the average number of neurons expected by chance from the observed distribution, and normalizing by the standard deviation, we constructed a z-score for the entire population (Fig. 2C and D). This corrected for multiple comparisons across time bins and gave us a specific time at which the entire observed population carried significant information about the target location. Differences between anatomical areas were tested for
significance through a randomization method. We randomly assigned units to different anatomical areas and re-calculated the difference between when each population reached significance. This allowed us to construct a null distribution and determine the p-value for the observed difference in time to significance for the anatomical areas.

**Aligning Data on Array Onset versus Saccade Initiation**

When trials were aligned on visual array onset for both the pop-out and search conditions, the ordering of selectivity across areas was the same as when trials were aligned on saccade (Figure S4). For the pop-out condition, while the distribution was more variable due to the variability in reaction time, LIP showed selectivity for the target location approximately 50 ms after array onset, followed by LPFC and then FEF (after 120 and 220 ms, respectively). All these differences were also significant (LIP < PFC, p = 0.038; LIP < FEF, p = 0.013; PFC < FEF, p = 0.001; randomization tests, see previous methods). When aligning search trials on visual array onset, LPFC and FEF carried significant information at 250 ms after array onset, significantly preceding selectivity in LIP, which began at 320 ms after onset (Fig. 2F, p = 0.044 and p = 0.047, respectively, by randomization test). The overall longer neural latency to find the target during search (approximately 250 ms after array onset) compared to pop-out (between 50 and 100 ms after array onset) parallels the differences in RT for the two conditions (Fig. 1B).

**Correlation of Neural Activity with Behavior**

A number of studies have shown a relationship between neural activity in the frontal and parietal cortices and behavior during focal attention tasks(5-9). Here, we also
found that single unit activity within each area correlated with how quickly the animal found the target. We examined the correlation between neural activity and reaction time in a sliding window manner similar to neural selectivity for target location. Each recorded neuron that met the requirements to be included in the selectivity analysis was tested for significant correlation (p < 0.05) in 25 ms windows, stepped 25 ms over the trial. A total of 6 steps were used, limiting the analysis to the first 150 ms after visual array onset. Only trials for the neuron’s preferred target location were used (assessed by the greatest firing rate over a 200 ms peri-saccadic window). This was done in order to control for saccade metrics and any location-reaction time correlations.

During the pop-out task all three areas had a significant number of neurons with significant correlation between neural activity and reaction time in at least one of the 6 windows. LIP had 23 significantly correlated neurons (9%, p = 0.01), LPFC had 35 (14%, p = 7*10^{-8}), and FEF had 31 (14%, p = 7*10^{-7}). However, during the search condition, while both LPFC and FEF still had a significant number of selective neurons (25, p = 2.4*10^{-3}, and 37, p = 3.3*10^{-10}, respectively) there was not a significant number of selective neurons in LIP (only 16, p > 0.5). This parallels our findings on when these areas found the target location: while all 3 regions showed selectivity for the target before the saccade during pop-out, only LPFC and FEF carried target information before the saccade in the search task. Furthermore, by demonstrating a correlation between single unit activity and the speed of the behavioral response this confirms that our regions of interest were directly involved in the task and supports the results on their roles in attention.
Coherence Statistic

In order to measure the synchrony between local field potentials, we used the coherence statistic. Coherence is a measure of the co-spectrum between two signals, and is normalized for the power in each signal alone. By normalizing, it allows coherence values to be compared across conditions and ensures that increases in coherence cannot be the result of an increase in the amplitude of the underlying signal.

\[
S_{XY} \approx FFT(D_X) \cdot FFT(D_Y)'
\]

\[
C_{XY} = \frac{S_{XY}}{\sqrt{S_{XX} \cdot S_{YY}}}
\]

\[
Coh = |C_{XY}|
\]

In the above equations, \(D_X\) is the recorded signal from source X, and \(S_{XY}\) is the co-spectrum between two signals from sources X and Y. Spectral estimates were made using a multi-tapered method and were averaged across trials. A smoothing level of 7.5 Hz was used to generate the discrete prolate spheroidal sequences used as tapers. A detailed description of this method of calculating coherence can be found in Jarvis and Mitra(10). Since only a 200 ms period was used to estimate the spectrum, frequencies below 10 Hz were difficult to estimate, and therefore were excluded from the current analysis.

Coherence was observed for both the visual search and visual pop-out task, and the difference between the two tasks was tested for significance at each frequency independently. Significance was determined through a randomization test similar to the
one used for mutual information: the trial assignments for each observed signal were randomly shuffled and the coherence level was recalculated in order to generate a null distribution. Significant differences in the coherence between signals were determined by calculating the difference in the randomly generated coherence values in order to generate a null distribution of the difference in coherence. This trial-shuffling procedure corrects for any trial-invariant differences between visual search and visual pop-out. Based on the randomly generated null distribution, a z-score was determined for the observed coherence by determining how far our observed coherence was relative to the null mean in units of the null distribution’s standard deviation. To correct for multiple comparisons across frequencies we increased the significance requirement (22 different frequencies were used, therefore significance was measured at $p = 0.05/22$, or $\sim 2 \times 10^{-3}$). The z-score threshold in Fig 4B reflects this adjusted significance level. Non-parametric permutation tests were also used and found the same condition-dependent differences in the same frequency bands(11).

In order to capture the process of attending to the target, coherence was estimated over a 200 ms peri-saccadic window starting 150 ms before the saccade and continuing until 50 ms after the saccade. The baseline period was taken from the inter-trial interval (a 200 ms window starting 500 ms before fixation spot display). The inter-trial interval was chosen to be the baseline specifically because it is a completely uncontrolled period of time, minimizing the amount of structure in the signal. Coherence during the fixation period was very similar to that of the ITI and could also have been used as a baseline. In order to determine the evolution of coherence over the trial, we also estimated the
coherence between LIP and frontal cortex during the sample period (taken to be a 400 ms window beginning 200 ms after sample onset) and the memory delay (a 450 ms window beginning 50 ms after sample offset).

A local differentiation analysis was used to ensure that coherence results were not due to task dependent fluctuations in the ground potential to which all electrodes were referenced (and thus not true changes in coherence between LFPs). We re-referenced all of the electrodes within an area to the average potential for that area (minus the electrode under consideration). This subtracts the common signal across all electrodes, including the common-referenced ground potential. Figure S5 shows the results. The pattern of coherence between LIP and frontal cortex between the search and pop-out tasks was virtually the same pattern as the original results. Coherence was greater for the middle frequency band during search over pop-out \( (p = 3.5 \times 10^{-8}, \text{by paired t-test}) \) and greater for pop-out over search in the upper frequency band \( (p = 3.5 \times 10^{-8}, \text{by paired t-test}) \). Furthermore, as Figure S6 shows, the raw power of the local field potentials within the LIP and within the frontal cortex did not significantly vary between the search and pop-out task conditions, indicating that increases in power per se did not underlie the changes in inter-area coherence. This indicates that the observed differences in coherence are not due to fluctuations in the raw power of the field potentials but true changes in coherence between areas.

The monkeys showed differing reaction times (RTs) during search versus pop-out and, because we averaged data over a fixed time interval this, in principle, might cause
the differences in coherence that we observed. To confirm this was not the case, we recalculated coherence between LIP and frontal areas over a variable window starting 75 ms after visual array onset and ending 50 ms after saccade (the window thus varied with the animal’s reaction time). This time period was chosen to avoid any initial visual response and to capture as much of the process of attending and selecting the target as possible. As shown in Figure S7, we obtained the same results as with a fixed time interval. In the middle frequency band search was significantly greater than pop-out ($p = 5.9 \times 10^{-3}$, by paired t-test), while in the upper frequency band pop-out was significantly greater than search ($p = 9.0 \times 10^{-6}$, by paired t-test).

As a further test to ensure that RT differences between task conditions did not induce our coherence differences, we used a stratification procedure to match the RTs trials between task conditions (12). Trials from each task condition were paired together if they had reaction times within 7 ms of one another. The result was RT distributions for task conditions that were 93% overlapping (compared to 60% overlapping for the original data) and were no longer significantly different ($p > 0.05$ for corrected compared to $p = 5 \times 10^{-4}$ uncorrected; by mutual information). This procedure, of course, reduced the total number of trials, but the pattern of coherence results was the same (Figure S8). As for the original data, coherence between LIP and frontal cortex was significantly greater in the middle frequency band during search ($p = 4.5 \times 10^{-5}$, by paired t-test) and significantly greater in the upper frequency band during pop-out ($p = 7.1 \times 10^{-4}$, by paired t-test). These results confirm the differences in coherence between search and popout while controlling for differences in reaction time.
Supporting References
Supporting Figures

Figure S1. Schematic of Control of Attention. During bottom-up, external direction of attention, selectivity flowed forward from parietal cortex into frontal cortex. In contrast, when attention was directed in a top-down, internal, manner selectivity flowed from the frontal cortex. These results support models of attention with both top-down and bottom-up influences, and suggests that top-down direction of behavior originates in the frontal cortex.
Figure S2. The firing rate of example LIP and LPFC neurons during the visual pop-out task (panel A and C, respectively). Trials were aligned on saccade in order to capture the shift of attention before the saccade. Selectivity for target location, regardless of the identity of the target, can be clearly seen in the firing rate histograms and was captured in the mutual information statistic. Panels B and D show the amount of information about the target location carried in the firing rate for the example LIP and LPFC neurons, respectively. The amount of information over time is shown for both the visual search and pop-out tasks. The asterisk indicates the time-point at which the observed amount of information was significant for two consecutive bins at p < 0.05. This marks the time to first significance. The population effects shown in the main text are reflected in these example neurons: during pop-out, selectivity in LIP precedes LPFC, while during search, LPFC precedes LIP.
Figure S3. Raw cumulative sum of time to first significance histogram for LIP, LPFC, and FEF in both the search and pop-out conditions are shown in colors. The black solid (dashed) lines show the mean (standard deviation) of the number of significant cells expected by chance.
Figure S4. Cumulative histogram of times to first showing significant selectivity when trials are aligned on visual array onset for (A) pop-out and (B) search. Vertical black line indicates visual array onset, grey shaded regions indicate mean and +/- one standard deviation of distribution of saccade.
Figure S5. Coherence between LIP and both Frontal regions is different based on task condition for re-referenced field potentials. (A) Shows the same normalized difference in LIP-Frontal coherence during search and pop-out as Fig 4B, but with the field potentials from each area re-referenced to the area’s average potential. This was done in order to remove any possible role of a common ground in driving the coherence effects. (B) Raw difference in LIP-Frontal coherence between search and pop-out. The coherence between each pair of LIP and Frontal electrodes was determined for both search and pop-out and the difference within each pair of electrodes is shown. Error bars indicate 95% confidence interval around the mean difference. During search LIP-Frontal coherence was significantly greater than during pop-out (p = 3.5*10^-8 by paired t-test), while the coherence in the upper frequency band was significantly greater during pop-out than search (p = 3.5*10^-8, by paired t-test).
Figure S6. Spectral power over frequency during search and pop-out for (A) LIP, (B) FEF, and (C) PFC. The power spectrum was multiplied by frequency in order to make the data easier to visualize. Shaded regions indicate 95% confidence interval about the mean power for each area. As all three regions show overlapping power spectrum between the two task conditions, there is no significant difference in power between the two conditions.
Figure S7. Coherence between LIP and both Frontal regions is different based on task condition in variable time window. (A) Shows the same normalized difference in LIP-Frontal coherence during search and pop-out as Fig 4B, but over a variable time window beginning 75 ms after visual array onset and ending 50 ms after saccade. (B) Raw difference in LIP-Frontal coherence between search and pop-out for same variable window. The coherence between each pair of LIP and Frontal electrodes was determined for both search and pop-out and the difference within each pair of electrodes is shown. Error bars indicate 95% confidence interval around the mean difference. During search LIP-Frontal coherence was significantly greater than during pop-out (p = 5.9*10^-3 by paired t-test), while the coherence in the upper frequency band was significantly greater during pop-out than search (p = 9.0*10^-6, by paired t-test).
Figure S8. Coherence between LIP and both Frontal regions is different based on task condition after task stratification. (A) Shows the same normalized difference in LIP-Frontal coherence during search and pop-out as Fig 4B, but with trials stratified by reaction time. The stratification process corrects for reaction time differences by creating overlapping distributions for search and pop-out. (B) Raw difference in LIP-Frontal coherence between search and pop-out. The coherence between each pair of LIP and Frontal electrodes was determined for both search and pop-out and the difference within each pair of electrodes is shown. Error bars indicate 95% confidence interval around the mean difference. During search LIP-Frontal coherence was significantly greater than during pop-out ($p = 4.5 \times 10^{-5}$ by paired t-test), while the coherence in the upper frequency band was significantly greater during pop-out than search ($p = 7.1 \times 10^{-4}$, by paired t-test).
Table S1. Table of Bayesian Information Criterion (BIC) values of model fit to distribution of time to first significance for each area and task (Fig. 2A and B). The BIC describes the goodness of fit for varying models while correcting for model complexity. The best fitting model is the one with the lowest BIC value, which we found to be a mix of two Gaussians for all three regions on both tasks.

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Table S2. Table of $r^2$ values for fit of mixture of two Gaussians on distributions of time to first significance for each area and task (Fig. 2A and B). The $r^2$ provides a measure of how much of the variance in the data is captured by the model fit.

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