

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

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Attention can be focused volitionally by “top-down” signals derived from task demands and automatically by “bottom-up” signals from salient stimuli. The frontal and parietal cortices are involved, but their neural activity has not been directly compared. Therefore, we recorded from them simultaneously in monkeys. Prefrontal neurons reflected the target location first during top-down attention, whereas parietal neurons signaled it earlier during bottom-up attention. Synchrony between frontal and parietal areas was stronger in lower frequencies during top-down attention and in higher frequencies during bottom-up attention. This result indicates that top-down and bottom-up signals arise from the frontal and sensory cortex, respectively, and different modes of attention may emphasize synchrony at different frequencies.

Volitional shifts of attention are thought to depend on “top-down” signals derived from knowledge about the current task (e.g., finding your lost keys), whereas the automatic “bottom-up” capture of attention is driven by properties inherent in stimuli—that is, by salience (e.g., a flashing fire alarm) (1–3). Imaging and neurophysiological studies have found neural correlates of both types in the frontal and posterior parietal cortices (1, 2, 4–6), but their respective contributions are not clear; they have largely been studied in separate experiments, rendering comparisons difficult and obscuring timing differences that could give clues to information flow (7).

We therefore recorded from multiple electrodes simultaneously implanted in the frontal and parietal cortices as monkeys (*Macaca mulatta*) found a visual target under two conditions (Fig. 1A). The target was randomly located in an array of four stimuli, with conditions differing in how the distractors related to the target. In “pop-out,” the distractors were identical and differed from the target along two dimensions (color and orientation), so the target’s salience automatically drew attention to it (1–3). During “search,” each distractor independently differed from the target. Because the target matched some of the distractors in each dimension, it was not salient and had to be sought using only its remembered appearance (1–3). The monkeys showed the behavioral hallmarks of bottom-up versus top-down attention. Psychophysical testing showed a shallower increase in reaction time with more distractors during pop-out than during search (6 ms per item for pop-out, 22 ms per item for search; $P < 0.001$, t test of least-squares linear regression). During recording, when three distractors were always presented, the monkeys’

reaction time was significantly longer and more variable for search than for pop-out (Fig. 1B).

We focused on the lateral intraparietal area (LIP) in the parietal cortex and the lateral prefrontal cortex (LPFC) and frontal eye fields (FEF) in the frontal cortex (1, 2, 4–6, 8–11). For each recording session, we implanted up to 50 electrodes (25 in frontal and 25 in parietal cortex). We recorded the activity of 802 neurons over 24 sessions (12).

We determined when each neuron first “found” (reflected) the target location by computing when the amount of information in its firing rate about target location first reached significance (13). The data for each trial were grouped by condition (pop-out or search) and by target location, thus factoring out information about target features. The top row of Fig. 2 shows the distribution of these times relative to the start of the saccade. During pop-out, there was a bimodal distribution (Fig. 2A). For each area, there was a population of neurons that first found the target well before the saccade (i.e., shortly after visual array onset) and a separate population that found the target after the saccade. The early population consisted of 35% of all target location-selective LIP neurons (24/68), 51% of selective LPFC neurons (40/78), and 31% of selective FEF neurons (17/54). There were clear differences in timing: LIP neurons found the target first, followed by LPFC neurons and then FEF neurons. Fits of bimodal Gaussians (Fig. 2A) indicated that the early population of LIP neurons was centered at 162 ms before the saccade [95% confidence interval (CI), 200 to 124 ms], followed by the early populations in LPFC and FEF, 77 ms (95% CI, 84 to 70 ms) and 40 ms (95% CI, 56 to 23 ms) before the saccade, respectively (LIP < PFC, $P < 10^{-25}$; LIP < FEF, $P = 6 \times 10^{-8}$; PFC < FEF,

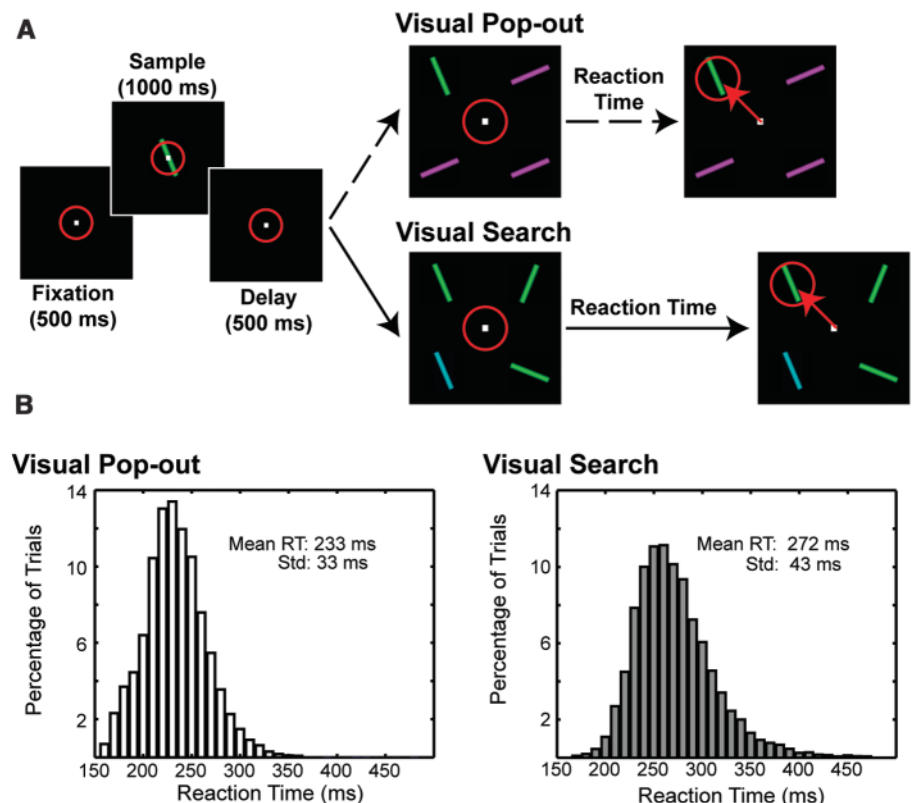


Fig. 1. (A) Behavioral task comparing visual search and pop-out. Red circle indicates eye position. (B) Histogram of reaction times (RTs) during search and pop-out tasks across all recording sessions for one target and three distractors. Average RTs for search (272 ms) and pop-out (233 ms) differed significantly ($P < 10^{-5}$, t test). The variance in RT also differed significantly (SDs of 43 ms for search and 33 ms for pop-out, $P < 10^{-5}$, χ^2 test).

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$P = 6 \times 10^{-5}$; t test) (12). The distribution of the neurons that found the target after the saccade was overlapping in all three areas and centered about 100 ms after saccade (Fig. 2A).

The same ordering was seen in the cumulative distributions of these data (Fig. 2C) (14). LIP, LPFC, and FEF neurons began finding the target 170 ms, 120 ms, and 35 ms before saccade, respectively (LIP < PFC, $P = 0.05$; LIP < FEF, $P = 0.009$; PFC < FEF, $P = 0.002$; randomization test) (12). One-quarter of the selective LIP neurons (17/68) began encoding the target location before the LPFC population first carried significant information. This is more than expected by chance ($P = 2 \times 10^{-5}$, tested against binomial distribution). When aligning trials on visual array onset instead of saccade, we found similar results (12).

In the search task, neurons began finding the target later than in pop-out, just before the saccade, and in the reverse order: The frontal areas (LPFC and FEF) showed selectivity first, followed by LIP (Fig. 2, B and D). About one-third of all selective neurons in FEF and LPFC

began to reflect the target location before the saccade (19/60 and 21/70, respectively), whereas only 14% (8/58) of selective LIP cells did so. This is greater than expected by chance for FEF and LPFC, but not for LIP ($P = 8 \times 10^{-5}$, $P = 4 \times 10^{-5}$, and $P = 0.41$, respectively, tested against binomial distribution). The cumulative distributions in Fig. 2D show that target location information reached significance in the FEF and LPFC at 50 and 40 ms before the saccade, respectively, followed by LIP (LPFC and FEF were earlier than LIP, $P = 0.027$ and $P = 0.006$, respectively; randomization test) (12). Whereas during pop-out, the LIP neurons found the target first (and well before the saccade); during search, target location information in LIP did not reach significance until 32 ms after the saccade. As with pop-out, similar results were observed when trials were aligned on visual array onset (12).

Synchrony of neural activity may increase the effectiveness of connections between brain areas and enhance the representation of attended stimuli (15–19). To investigate this,

we quantified the degree of synchrony between local field potentials (LFPs) in the parietal and frontal cortices. Synchrony was measured between all pairs of simultaneously recorded electrodes that had at least one neuron selective for target location (282 pairs). The degree of synchrony was captured in the coherence statistic, a measure of the co-spectrum between two signals, normalized for the power (20). Significance was determined by randomization tests (12). Because similar results were found between LIP and LPFC and between LIP and FEF, we combined data from the LPFC and FEF.

During both search and pop-out, there was an increase in coherence between LIP and frontal cortex in a middle (22 to 34 Hz) and upper (35 to 55 Hz) frequency band (Fig. 3) that peaked during the perisaccadic period (i.e., around the time of the attention shift) (Fig. 4A). The increase in coherence for each frequency band differed between bottom-up and top-down (Fig. 4A). This was highlighted by subtracting coherence during pop-out from coherence during search. Figure 4B shows a greater increase in middle-frequency (22 to 34 Hz) coherence between LIP and frontal cortex during top-down search than during bottom-up pop-out. By contrast, the increase in upper-

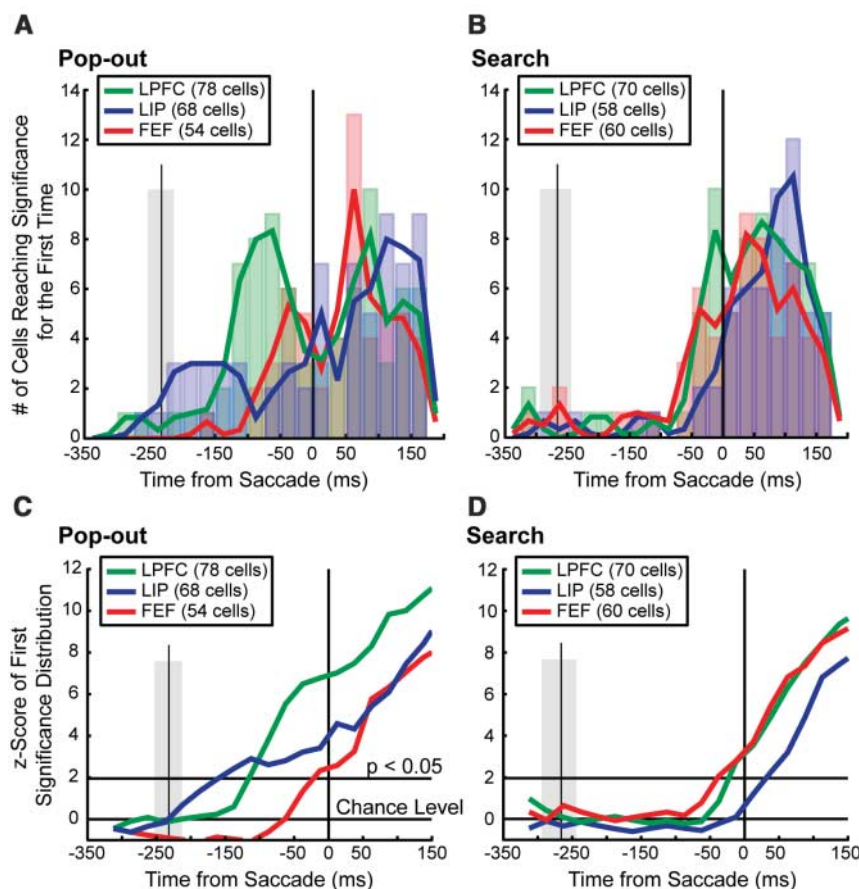


Fig. 2. Timing of target location selectivity during pop-out (left column) and search (right column). Significance was determined through randomization tests (12). (A and B) Distribution of times at which neurons first began to carry significant information about the target location, relative to the saccade. Vertical black line indicates saccade; gray shaded regions indicate mean (± 1 SD) of distribution of visual array onset. (C and D) Normalized cumulative sums of the histograms shown in (A) and (B), respectively. A z-score for the observed distribution was calculated through randomization tests and was corrected for multiple comparisons (12).

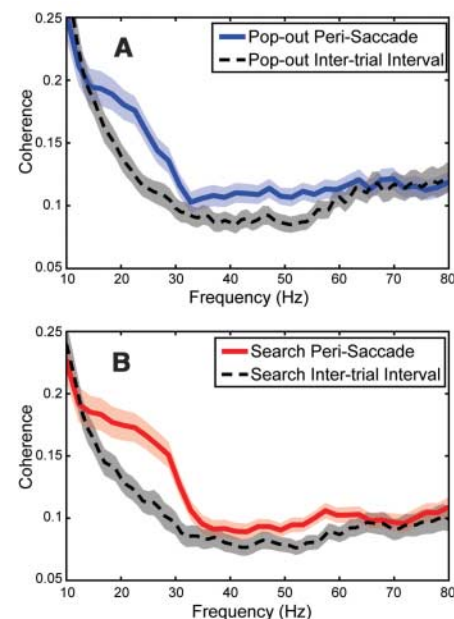


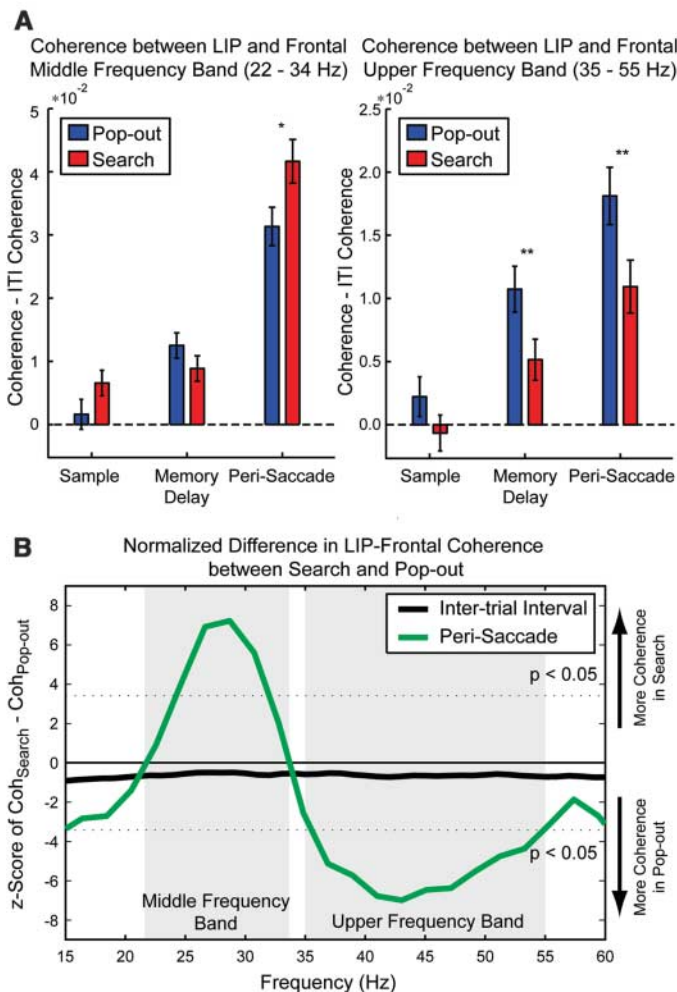
Fig. 3. LFP coherence between LIP and frontal cortex (LPFC and FEF) across frequencies for (A) pop-out and (B) search tasks. Coherence was calculated around the time of the attention shift (in a perisaccadic period, beginning 150 ms before saccade to 50 ms afterward) and compared to a baseline, an intertrial interval (ITI) epoch (a 200-ms window starting 500 ms before trial onset). Shaded regions are 95% confidence intervals around average coherence. Frequencies below 10 Hz are not meaningful (and are not shown) because of the relatively short time epochs used.

frequency (35 to 55 Hz) coherence was greater during pop-out than during search. Thus, bottom-up and top-down attention may rely on different frequency bands of coherence between the frontal and parietal cortex.

The source of top-down signals has largely been inferred from indirect evidence such as patterns of anatomical connections (7). In the case of visual attention, previous research has shown its neural correlates throughout the cortex, with control attributed to parietofrontal networks (1, 2, 5). Our results suggest that within this network, fast, bottom-up target selection occurs first in LIP, whereas longer-latency top-down selection occurs first in the frontal cortex. This supports the hypothesis that parietal neurons form “saliency maps” for bottom-up selection (21–23) as well as studies showing that stimulation of the frontal cortex causes attention-like effects in the extrastriate cortex (24). It also fits with attenuation of top-down effects in the posterior cortex after PFC damage (25–27). Although both the frontal and parietal cortex are involved in attention, our results illustrate that bottom-up signals appear first in LIP and top-down signals appear first in the frontal cortex.

Localized synchrony of activity within a brain area may help resolve competition for attentional selection (18, 19), and interareal synchrony may aid in long-range communication between areas (15–17). Our results suggest that the flow of top-down and bottom-up information is aided by coherence emphasizing different frequency bands. Lower-frequency bands are more robust to spike timing delays and thus may be better suited for longer-range coupling between multiple, distant areas (28–30). The increase in low-frequency synchrony during search could reflect a “broadcast” of top-down signals on a larger anatomical scale. Synchrony at higher-frequency bands might support the local interactions needed to enhance stimulus representations (28–30). The emphasis of higher-frequency synchrony during pop-out could reflect local enhancement of stimulus representations that are passed forward from parietal to frontal cortex. This suggests that the brain may emphasize coherence at different frequency bands for the dynamic modulation of interareal connections, which in turn engages the network best suited for the current task.

Fig. 4. (A) Level of coherence for pop-out and search during the middle (left, 22 to 34 Hz) and upper (right, 35 to 55 Hz) frequency bands in different trial epochs. * $P < 0.05$, ** $P < 0.01$ (t test). (B) Differences in LFP coherence between LIP and frontal cortex during pop-out and search for the perisaccadic period (green) and ITI (black). Pop-out coherence was subtracted from search coherence (Fig. 3). Dashed lines indicate significance levels ($P < 0.05$, corrected for multiple comparisons). Differences above the upper dashed line indicate significantly more coherence during search than during pop-out; differences below the lower dashed line denote significantly more coherence during pop-out than during search.



References and Notes

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13. A sliding window of 25 ms was stepped every 25 ms. Significance was determined by constructing a null distribution through randomization tests (12). A neuron was said to first indicate the target location when significant at $P = 0.05$ for two bins in a row.
14. The cumulative distribution is the cumulative sum of the histogram of when each cell first carried significant information about the target location (Fig. 2, top row). The cumulative sum was then normalized for the number of significant cells expected at each point in time by chance. This procedure corrected for multiple comparisons and determined when an area carried information about the target location, allowing us to infer the order of selectivity. See (12) for details.
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Supporting Online Material

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Materials and Methods
Figs. S1 to S5
Table S1

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