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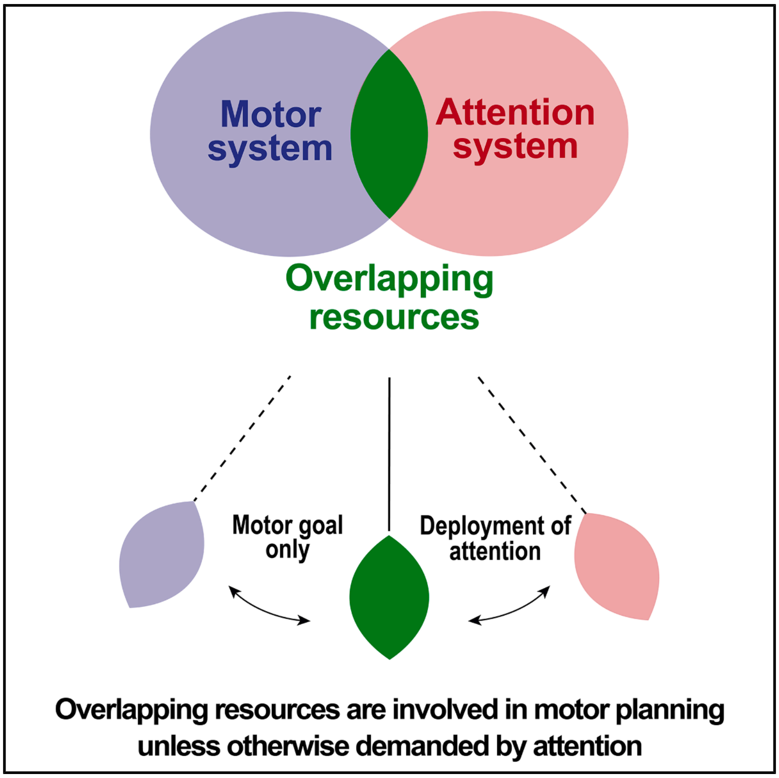
Endogenous and exogenous attentional interplay through mixed prefrontal cortex resources

Graphical abstract



Highlights

- Motor and attention systems in lateral PFC are largely distinct, with some overlap
- The shared resources process motor plans, until recruited for attention processing
- Voluntary deployment and capture of attention both recruit the shared resources

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In brief

Di Bello et al. reveal that some neural resources in lateral PFC are shared between motor and attentional systems, enabling focus to flexibly shift in response to internal goals or external demands.

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Article

Endogenous and exogenous attentional interplay through mixed prefrontal cortex resources

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SUMMARY

Spatial attention can be either involuntarily drawn to salient, unexpected events (exogenous attention) or voluntarily directed (endogenous attention). Evidence suggests a distinction between the two forms of attention, with only endogenous attention believed to operate independently of the motor system. We investigated the role of the lateral prefrontal cortex (lPFC) in this relationship, using a task that spatially dissociated attention from motor goals in two monkeys. Our findings show that some lPFC units exhibit highly dynamic encoding, flexibly representing either the attended location or the motor target, simultaneously or at different time points. We show that these neural resources are crucial in exogenous attention. However, they can also be recruited by endogenous deployment of attention, resulting in two main effects: (1) a reduction in interference between the motor and attention systems; and (2) modulation of exogenous shifts for attentional capture, with stronger shifts occurring when endogenous attention is weak. Overall, our results suggest that exogenous attention helps refine attentional control by rapidly mobilizing neural units shared between the attention and motor systems, even during endogenous attention deployment. We refer to these units as overlapping resources, as they enable a dynamic balance between internal goals and external demands, similar to adaptive buffer systems.

INTRODUCTION

In our daily lives, we often observe a tight coupling between spatial attention and the oculomotor system, with rapid eye movements frequently accompanying shifts of attention. However, attention can also shift covertly, without an accompanying eye movement. Furthermore, attention can be directed either voluntarily based on internal goals (endogenous attention) or involuntarily drawn to salient or unexpected sensory events in the environment (exogenous attention). Endogenous attention is also known as top-down or goal-directed attention, while exogenous attention is also known as bottom-up or stimulus-driven attention.[1]

The interest in the relationship between covert attention and motor system grew in the 80s, following the proposal that spatial attention directly results from motor planning.[2,3] According to this *premotor theory of attention*, a unified system (the motor system) is responsible for both motor planning and attention. This theory predicts that if the motor system is compromised, both endogenous and exogenous attention should be impaired. However, studies with neuropsychological patients with damaged oculomotor control have shown deficits specific to exogenous attention, while endogenous attention remained largely unaltered.[4–7] Using an eye abduction protocol that compromised saccade execution, researchers found behavioral deficits in exogenous attention while endogenous attention remained unaffected,[8] indicating that only reflexive attention relies on oculomotor preparation. These different relationships with the motor system may indicate that endogenous and exogenous attention operates through different mechanisms.[1,9–11] However, others have found a link between them, with endogenous attention influencing exogenous attention.[12–14] For instance, endogenous attention can prevent the attentional capture of an unexpected distractor when attention is oriented elsewhere[15–17] and can enhance the effect of exogenous attention when they co-localize.[18–20] Clarifying the degree of independence between these two attentional mechanisms has important neurofunctional implications, as it indicates whether separate or partially overlapping brain regions are involved.[1,21–23] To date, the interplay between these two types of attention and their relationship with the motor system remain open questions in ongoing research.[24–26]

To address this, we investigated the contributions of the lateral prefrontal cortex (lPFC), a region central to both attentional control and oculomotor processes,[24,27–29] to the interplay between spatial attention and oculomotor dynamics in monkeys performing a task that spatially dissociated these variables. The task included cued and uncued trials. Cued trials involved endogenously attending to one of four possible locations (the attention target) to detect a subtle brightening (the Go-signal) that signaled to make a saccade to a distinct (oculo)motor target location. In uncued trials (20% of trials), only the motor target was specified, making the location of the Go-signal unpredictable and detection of the peripheral brightening a function of exogenous attention.

Consistent with our previous research,[30] we found that in cued trials a high proportion of neural units were dedicated exclusively to either motor or attentional variables, challenging the assumptions of the premotor theory of attention. In this study, to explore the neural interplay between endogenous and exogenous attention, we expanded our investigation into how motor and attentional coding evolves in the lPFC across multiple task epochs and comparing cued and uncued conditions. We identified a small subset of units that flexibly alternated between encoding the attended and motor targets across different task epochs, without necessarily representing both variables simultaneously. We refer to these units as “overlapping resources,” as they can dynamically encode either attentional or motor variables based on task demands. In uncued trials, when endogenous attention was not directed to a specific target, these overlapping resources predominantly encoded the motor goal, enhancing motor target representation but causing interference when attention later shifted to the Go-signal. In contrast, during cued trials, the endogenous deployment of attention coordinated these resources more effectively, reducing interference between motor and attention processing. Interestingly, applying cross-modal decoding from lPFC activity revealed that endogenous attention shared spatial representations with motor planning. For instance, classifiers trained to decode motor variables were also able to detect exogenous attention shifts, the extent of which was modulated by endogenous attention deployment.

Our findings support the notion that the endogenous and exogenous systems are independent yet can interact to enhance attentional control. We found evidence that a partial overlap between the motor and attentional systems within the PFC provides the neural basis for this interaction. This allows for a dynamic balance between internal needs and external demands, much like flexible buffer systems function.[1,31,32]

RESULTS

Behavior

Monkeys R and G performed the behavioral task shown in Figure 1 correctly on 80% and 81% of trials, respectively. Error trials were mostly caused by a lack of behavioral response, suggesting that the Go-signal at the attended location went undetected. Such saccade omissions occurred in 17% of trials for Monkey R and 16% for Monkey G. Saccades to the wrong motor target were much less frequent, occurring in only 3% of trials for Monkey R and 2% for Monkey G. The incorrect saccades were equally distributed among the non-targets for Monkey R, whereas they were disproportionately directed toward the Go-signal location for Monkey G (32% and 52% of incorrect saccades, respectively). Task accuracy on cued trials, where the location of the Go-signal was signaled beforehand, was significantly greater than on uncued trials (Monkey R: 81.5% ± 1.1% versus 75.2% ± 1.6%, 36 sessions, Kruskal-Wallis non-parametric test, $p < 0.001$; Monkey G: 83.8% ± 0.5% versus 73.6% ± 1.0%, 42 sessions, Kruskal-Wallis non-parametric test, $p < 0.001$). Reaction times (RTs) were also faster on cued trials compared with uncued trials (Monkey R: 411 ± 3.4 ms versus 419 ± 3.2 ms, 36 sessions, Kruskal-Wallis non-parametric test, $p < 0.012$; Monkey G: 313 ± 1.6 ms versus 323 ± 2.3 ms, 42 sessions, Kruskal-Wallis non-parametric test, $p < 0.001$). These results suggest that both monkeys used the cue’s center color to covertly attend to the region of space where the Go-signal would be presented.

Prefrontal neurons are modulated by attention and by oculomotor targets

We tested whether the lPFC encoded the attended target and motor target specified by the central cue stimulus. A two-way ANOVA was used to assess neuronal firing rates over a sliding window for 209 individual units, each recorded for three or more trials across the cued and uncued spatial conditions (as illustrated in the 4 × 4 and 4 × 1 matrices in Figure 1B). Units significantly tuned for the motor target emerged ~250 ms after cue onset and increased in number until ~550 ms (Figure 2A, upper panels). Significant tuning for the attended location or for both the motor location and the attended location (hereafter referred to as “Both” units) was less common, with these proportions increasing ~400 ms after cue onset (Figure 2A, upper panels). As expected, on uncued trials (Figure 2A, lower panels), significant attention tuning was largely absent during the delay period because the target of covert attention was not specified. Thus, lPFC activity reflected oculomotor plans as well as whether and where covert attention was directed by the cue.

It has been shown that the lPFC shows a diverse range of responses for various cognitive variables in different task epochs.[33–35] To investigate this in our task, we analyzed how lPFC units were modulated by motor and attention variables in cued trials, using the 238 units (Monkey R = 82; Monkey G = 156) recorded for at least 3 trials in each of the 16 possible spatial conditions (see the 4 × 4 matrix in Figure 1B). Figure 2B illustrates examples of Motor, Attention, and Both units before and after presentation of the GO signal. Of the units exhibiting selectivity before the Go signal (the “pre-Go” epoch), 53% were Motor units, 33% were Attention units, and 14% were Both units (see Figure 2C; Table S1). The breakdown of selectivity shifted in the period after the brightening of the attention target (the “post-Go” epoch), with the proportions of Attention units increasing to 47%, Motor units decreasing to 38%, and the Both units remaining stable at 15%. In the period after the motor response (the “post-Saccade” epoch), there was a jump in the proportion of Motor units (84%) and a drop in Attention and Both units (7% and 9%, respectively). Overall, the number of significantly selective units gradually increased, with 66 units in the pre-Go epoch, 73 in the post-Go epoch, and 106 in the post-Saccade epoch.

Table S1 illustrates the evolution of unit selectivity over time, including units classified as untuned. Some initially untuned units developed Attention (9.3%), Motor (8.6%), or Both (4.6%) selectivity following the Go-signal, while after the saccade, many untuned units developed Motor selectivity (Motor = 27.9%; Attention = 6.4%; Both = 8.1%). Units that were motor selective (i.e., Motor and Both units) in the pre-Go epoch mostly retained their motor selectivity in the post-Go (50%) and post-Saccade (77%) epochs. Most units that were initially attention selective (i.e., Attention and Both Units) retained their attention selectivity into the post-Go epoch (52%) but not the post-Saccade (13%)

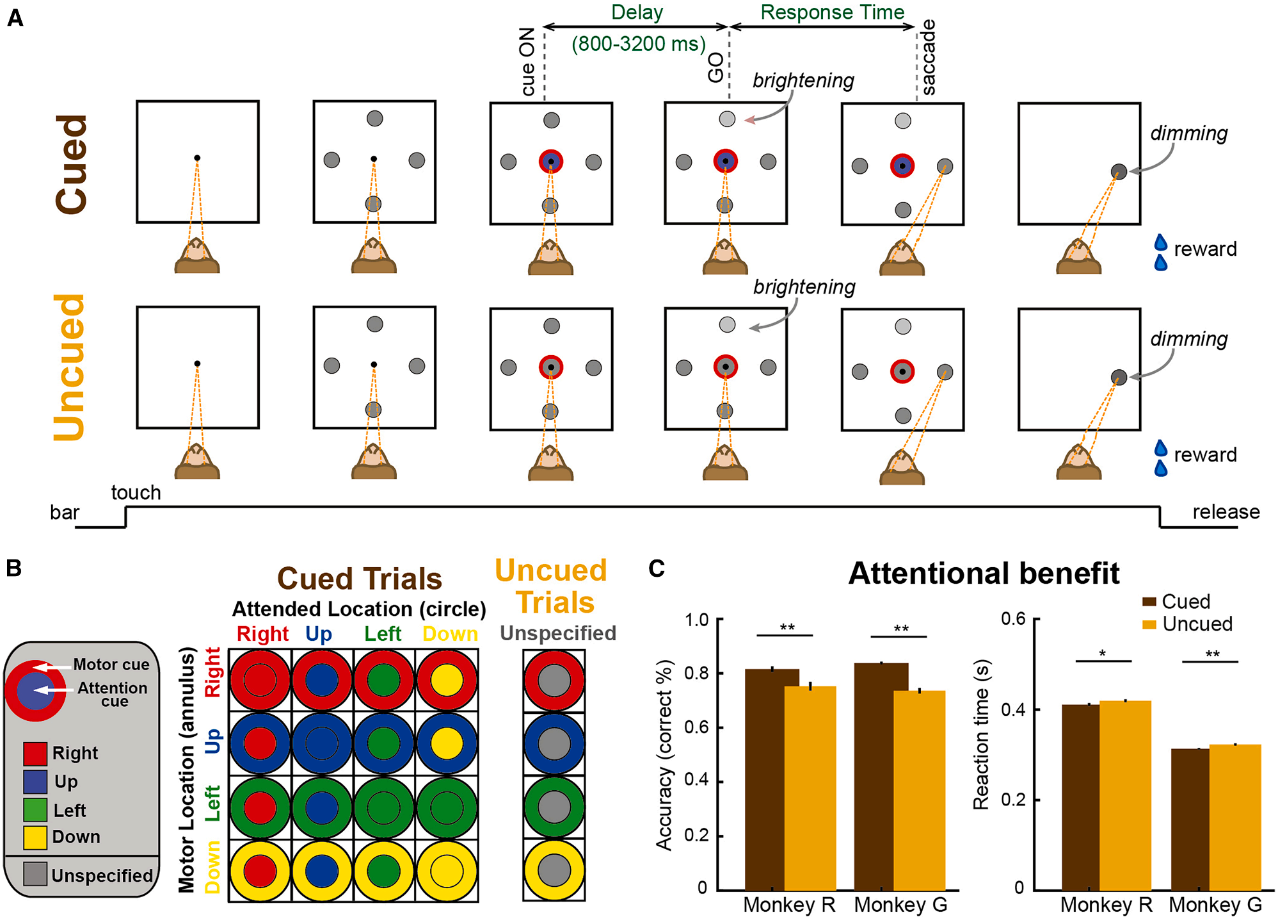

Figure 1. Behavioral task and cueing effect

(A) The monkey pressed a bar to make a central fixation spot appear. After fixation (convergent dashed lines), four peripheral gray landmarks were presented, followed by a two-part colored cue stimulus centered on the fixation point. After a variable cue delay period, a subtle brightening (the Go-signal) of one of the peripheral spots indicated to the monkey to respond by gazing to a particular target spot. On cued trials (example trial at the top), the cue's inner color indicated the Go-signal location: the attention cue. The cue's outer color specified the target of the upcoming saccade: the motor cue. On uncued trials (example trial at the bottom), the inner circle was gray, and the Go-signal location was selected randomly so the monkey did not know where to attend. The motor target was still specified by the color of the annulus. In both example trials, the cue's red outer color specified a saccade to the rightward gray spot (the motor target), which occurred in response to the brightening of the upper gray spot (Go-signal). The occurrence of the Go-Signal at the upper spot was specified on the cued trial by the cue's blue inner color, but on the uncued trial, this same Go-Signal location was unspecified and not predictable.

(B) The stimuli corresponding to each combination of attended and motor locations are shown as a 4 × 4 matrix for cued trials and as a column (4 × 1) for uncued trials.

(C) Behavioral results: percentage of trials in which each monkey succeeded to detect the Go-signal and complete a saccade (left panel) and the average reaction time (right panel), for cued (brown bars) and uncued (light brown bars) correct trials.

Error bars: SEM across sessions. $^*p < 0.05$ and $^{**}p < 0.001$.

epoch. Other units encoded a different single variable between epochs, without ever simultaneously encoding both variables. For example, three Motor units from the pre-Go epoch switched to encoding only the attended location in the post-Go epoch, and nine units initially classified as Attention units became only motor target selective in the post-Saccade epoch.

Decoding of decoupled motor and attentional information

We employed a decoding technique to compare the lPFC's parallel coding of attention and motor variables during both cued and uncued trials (see STAR Methods), focusing on critical epochs (i.e., around cue onset, Go-signal presentation, and reward delivery). To better assess the independent encoding of each variable in cued trials, we focused only on trials for which the attended and motor locations differed (i.e., "different" trials, off-diagonal conditions in Figure 1B).

Motor target information dynamic

Following the cue onset (Figure 3, upper-left panel), we observed above chance decoding of motor information starting at 250 and 200 ms for cued and uncued trials, respectively (cluster-based permutation test, $p < 0.001$, cue onset aligned). This significant motor decoding accuracy persisted throughout the delay period, with uncued trials showing higher motor accuracies than cued trials from 350 ms onward. This enhanced classification

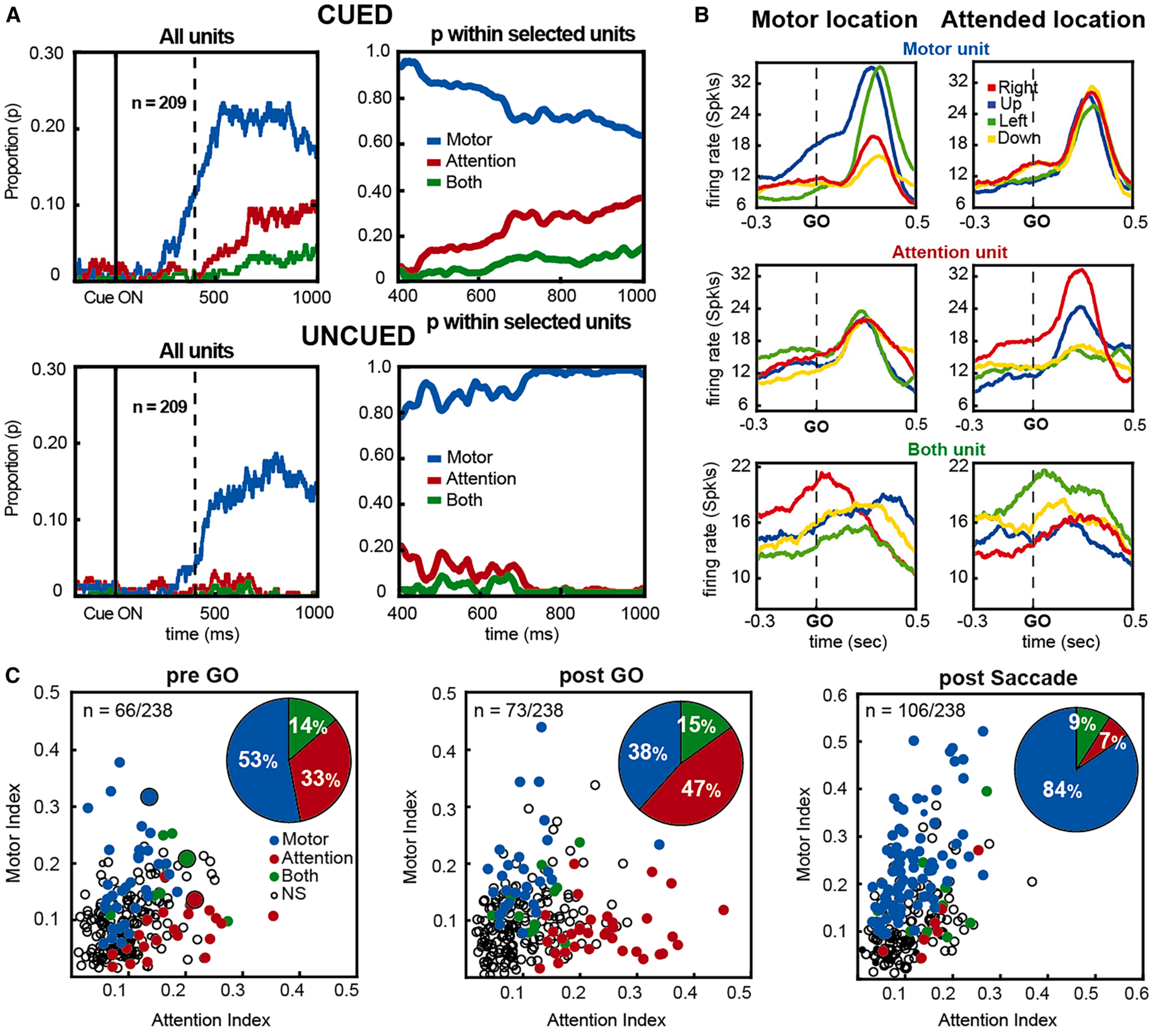

Figure 2. Temporal evolution of attention and motor selectivity in PFC

(A) Motor (blue lines), Attention (red lines), and Both (green lines) tuned units following cue onset (two-way ANOVA over a sliding window, $p < 0.01$) in cued (top panels) and uncued (bottom panels) trials as a proportion of all units (left panels) and of selective units (right panels). The time axes in the right panels begin at 400 ms, corresponding to the dashed lines in the left panels.

(B) Neural tuning following the Go-signal (t = 0) on cued trials for the four motor locations (left column) and the four attended locations (right column) of three example multi-units (rows) modulated by the motor target (Motor unit), the locus of attention (Attention unit), and both locations (Both unit), respectively.

(C) Scatterplots showing the motor versus attention modulation indices for all recorded units on cued trials ($n = 344$), calculated based on firing rates in the pre-Go (−200 to 0 ms before the Go-signal) (see also Table S1), post-Go (100 to 300 ms after the Go-signal), and post-Saccade (600 to 800 ms after the Go-signal) epochs. Units were classified during each epoch based on significant tuning for the attended location (Attention), motor location (Motor), both the attended and motor locations (Both), or neither variable (not significant, NS). Pie charts show the proportions of significant units of each type in each epoch. Larger symbols in the pre-Go scatterplot correspond to the three units shown in (B).

accuracy on uncued trials was still present at the end of the delay period (−200 to −100 ms relative to the Go-signal; Figure 3, upper-middle panel).

Following the presentation of the Go-signal, the accuracy for decoding the motor location on uncued trials dipped to 40.7% ± 9.0% at ~150 ms, which was significantly less than at the time of the Go-signal (51.8% ± 9.2%; Kruskal-Wallis non-parametric test, $p < 0.001$). In contrast, on cued trial, the decoding accuracy did not differ between these same time points (49.8% ± 10.6% at ~150 ms versus 49.6% ± 10.4% at Go-signal time; Kruskal-Wallis non-parametric test, $p = 0.96$). Motor decoding accuracy on uncued trials was significantly worse than on cued trials from 100 to 450 ms after the Go-signal, even as decoding accuracy on both trial types improved to near perfect

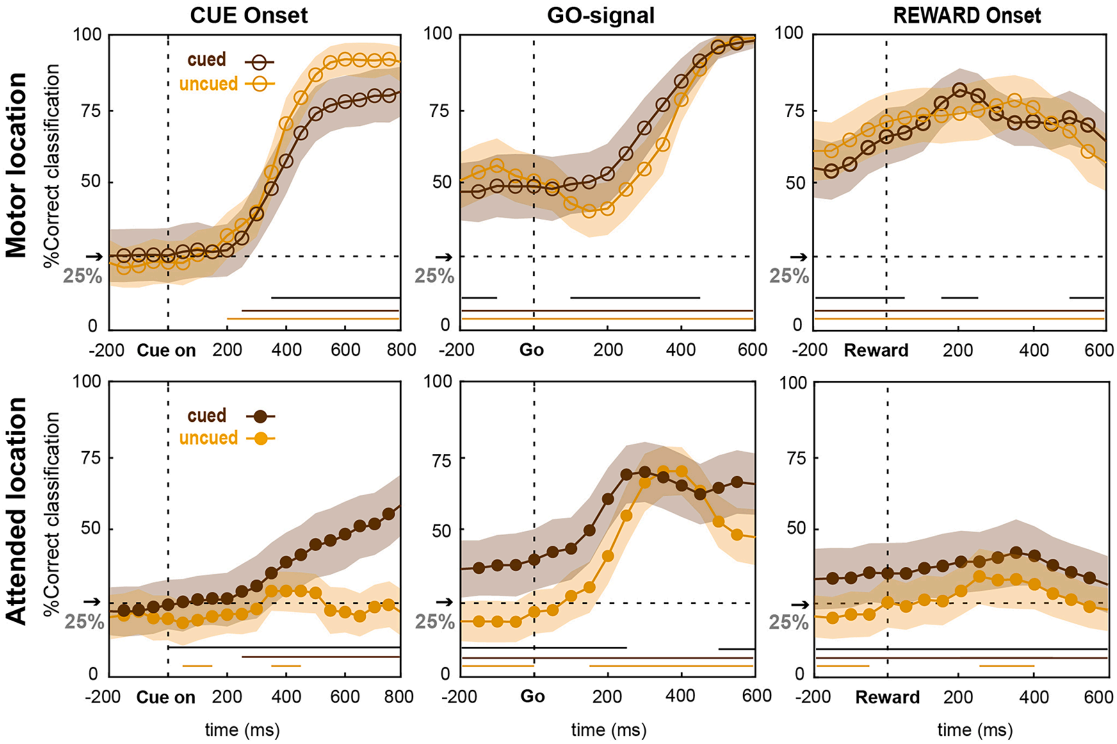

Figure 3. Population decoding of movement and attention during three task periods

Time course of population decoding accuracy for the motor location (top row) and attended location (bottom row) on cued (dark brown) and uncued (light brown) trials, aligned to three critical task events (cue onset, Go-signal, and reward delivery) (see also Figure S1, for saccade onset alignment). Lines and shading show the mean classification accuracy ± SE in each sliding window. Black horizontal lines indicate a significant difference between cued and uncued decoding accuracies (cluster-based permutation test, $p < 0.001$). Colored horizontal lines show significant (cluster-based permutation test, $p < 0.001$) deviation from chance (dashed horizontal line) for cued (dark brown) and uncued (light brown) trials.

classification by 500 ms. Classification of the motor target remained well above chance on cued and uncued trials through reward delivery and beyond (Figure 3, upper-right panel). Classification accuracy was significantly higher on uncued trials than cued trials until 100 ms after reward delivery, after which there were no sustained accuracy differences.

In summary, lPFC represented the motor target from saccade planning until long after saccade completion and reward delivery. Decoding accuracy was significantly different on cued and uncued trials, albeit that the motor target instruction was present on both types of trials. Surprisingly, specifying where to covertly attend on cued trials resulted in a less accurate representation of the motor plan during the delay and less interference from the Go-signal in decoding the motor target, relative to uncued trials.

Attended target information dynamic

In cued trials, we observed significantly above chance decoding of the attention location starting ~250 ms after cue onset, with accuracy climbing throughout the delay period (Figure 3, bottom-left panel). Differently, decoding of the attended location in uncued trials showed brief (~150 ms) periods of both above chance and below chance classification during the delay epoch. These significant classifications in uncued trials were unexpected, given that the location of the upcoming Go-signal was unpredictable. While this pattern might reflect a bias in how the monkeys allocated spatial attention on uncued trials, we interpret it with caution, as it may also reflect limited signal variability in the uncued condition (see STAR Methods).

Following the Go-signal presentation (Figure 3, bottom-middle panel), we observed a sharp increase in decoding accuracy for the attended location in both trial types, peaking at approximately 300 ms in the cued trials and 400 ms in the uncued trials. We interpret these sudden increases in accuracy for the attended location as indicative of successful attentional capture of the attended stimulus (see Discussion). Interestingly, these peaks reached a similar level of accuracy for classifying the attended location (cued = 69.4% ± 10.1% versus uncued = 69.6% ± 8.4%, Kruskal-Wallis non-parametric test, $p = 0.71$), suggesting that the neural population carried a comparable amount of information on both trial types.

Decoding of the attended location remained accurate following the saccade (Figure S1, bottom panel) on cued trials but decreased on uncued trials, with the two conditions significantly diverging starting 200 ms after the saccade. On cued trials, decoding of the attended location remained significantly above chance past the time of reward delivery (Figure 3, bottom-right panel).

Interaction between motor and attentional neural codes

The previous section described parallel motor and attention information coding on cued trials. Here, we explore the stability and the generalization of the coding for motor and attention

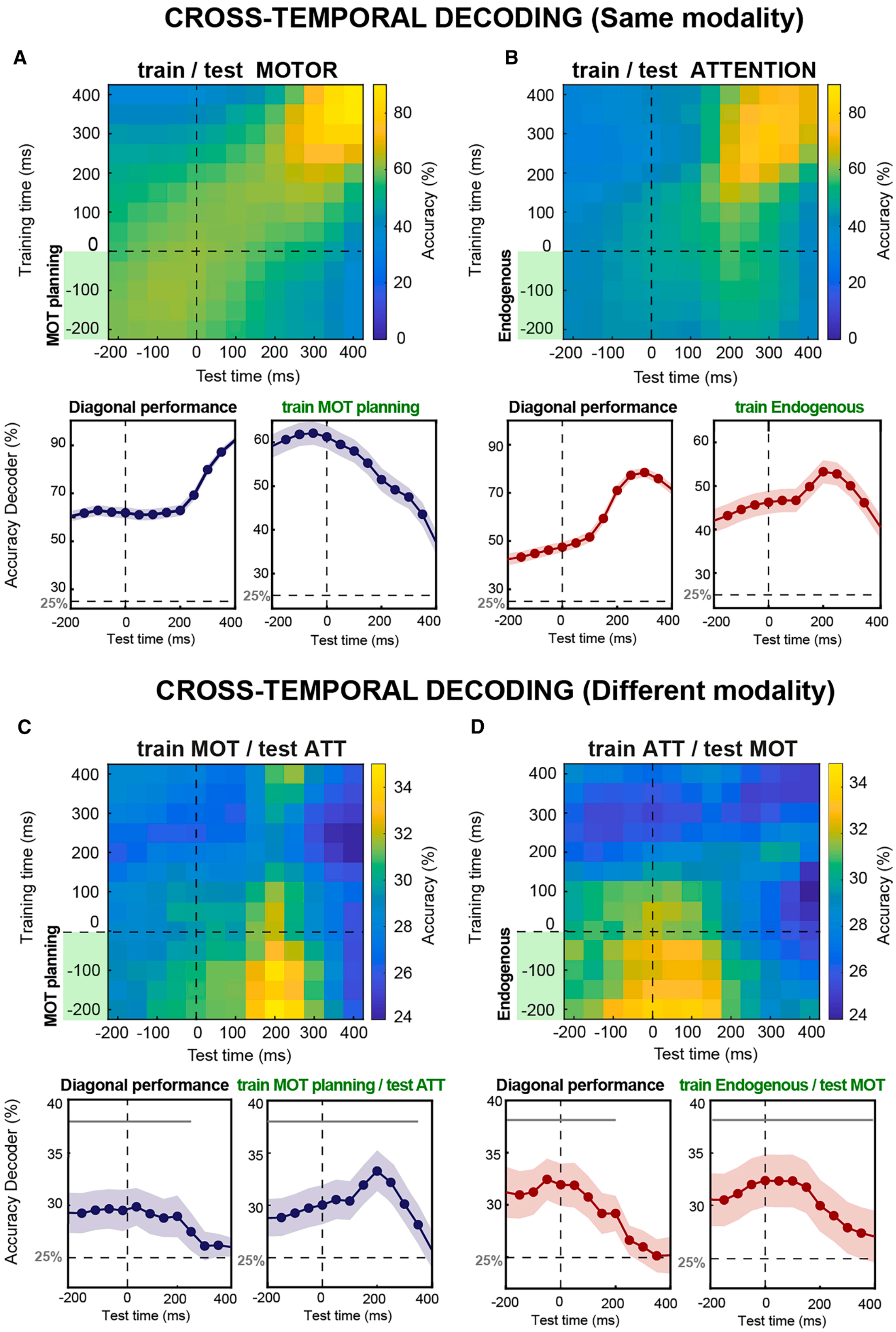

Figure 4. Dynamics and interplay of motor and attention coding around the Go-signal

(A and B) Cross-temporal classification for the motor (A) and attended (B) locations. Heatmap shows mean decoding accuracies over $n = 250$ resamples. The training time of the classifier is shown on the ordinate, and the test time is displayed on the abscissa, both relative to the Go-signal brightening. The green shaded

(legend continued on next page)

across the epochs surrounding the brightening of the attended target (i.e., the Go-signal). For this, we adopted a cross-temporal decoding analysis (see STAR Methods), in which a linear classifier was trained with spatial variables (motor target or attended target variables) using data in one period and tested with data from another period. Both "same" and different trials were taken into account (Figure 1B).

Cross-temporal decoding within modalities—stability

Figure 4 shows the results of cross-temporal decoding when a single variable, either the motor location (A) or the attended location (B), was used for both the training and test phases of classification. The diagonal of the heatmaps (Figures 4A and 4B, top panels) shows classifier performance when trained and tested on the same time bin. Accuracy along the diagonal is plotted in the "Diagonal performance" panel below each heatmap and was significantly above chance for all time bins (cluster-based permutation test, $p < 0.001$). The time course of the accuracy along the diagonal is similar to that of cued trials in the preceding section (Figure 3, middle panels) but with greater accuracy due to the inclusion of same trials. Figure S2 shows that the accuracies shown in Figure 4 were significantly greater with same trials included than without them.

We observed differences in the stability of the motor and attention spatial representations across task epochs. Specifically, we examined how well a classifier trained on delay period activity (green shading on the y axis of Figures 4A and 4B heatmaps) decoded locations from activity following the Go-signal. We found that the motor planning code, which was predictive during the delay, lost its capacity to decode the motor target once the Go-signal was issued (Figure 4A, bottom-right panel). In contrast, the delay period representation of endogenous attention continued to code the attended location after the Go-signal and even exhibited a significant improvement in classification that peaked at ~200 ms (Figure 4B, bottom-right panel; accuracy at Go = 46.4% ± 1.6% versus accuracy at peak = 53.3% ± 1.7%, Kruskal-Wallis non-parametric test, $p < 0.001$).

Cross-temporal decoding across different modalities—generalizability

We next investigated how well each of the spatial task variables was decoded by a classifier trained on the other task variable (Figures 4C and 4D). This allowed us to assess the extent to which the neural representation of the motor target generalized to the encoding of attention and vice versa.[26,36–38] We evaluated both these cross-modal tests along the diagonal (i.e., with matching train and test time windows) and found significant encoding of the tested variables throughout the delay epoch and continuing for ~200 ms after the appearance of the Go-signal (Figures 4C and 4D, bottom panels).

The procedure for the cross-temporal analysis between modalities mirrored that of within modality analysis. A classifier trained to decode the motor target based on delay period activity (i.e., motor planning activity) successfully generalized to the decoding of the attended location during the delay period and the period around the Go-signal (Figure 4C, bottom-right panel). This decoding, while less accurate than within-modality decoding (cluster-based permutation test, $p < 0.001$ for all time bins from -200 to 400, Go-signal aligned), was significantly above chance (cluster-based permutation test, $p < 0.001$ for all time bins from -200 to 350, Go-signal aligned). The accuracy of decoding of the attended location increased abruptly around 200 ms after the Go-signal (accuracy at Go = 30.3% ± 1.5% versus accuracy at peak = 33.7% ± 1.6%, Kruskal-Wallis non-parametric test, $p < 0.001$). This suggests that the representation of space for oculomotor planning generalized to the localization of attention and especially to the capture of exogenous attention by the Go-signal brightening.

For the reverse cross-modal analysis, we trained the classifier on delay period activity associated with the attended target (i.e., endogenous attention activity) and assessed classification of the motor target variable (Figure 4D, bottom-right panel). Significant prediction of the motor target was observed across all time bins from -200 to 400, relative to the Go-signal (cluster-based permutation test, $p < 0.001$). This suggests that the spatial encoding of endogenous attention shows similarities to that for motor planning but differs from that for motor execution.

To explore the role of units simultaneously modulating both types of variables, we tested the generalizability of the delay period activities after excluding the units classified as Both before the Go-signal presentation (see Table S1). The results show that although this subpopulation maintains above-chance generalization ability both before and after the Go-signal onset, delay period activity was less effective in generalizing when Both units were excluded, particularly regarding the role of motor preparation in attentional capture (for further details see Figure S3), thus highlighting the contribution of these units to generalizing between motor and attentional variables.

Neuronal interplay between endogenous and exogenous attention

We have shown that behavioral performance (Figure 1C) and neural classification of the attended location (Figure 3) were better on cued trials than on uncued trials. By extension, we predicted that behavioral performance would be better when endogenous attention was precisely allocated to the attended location. To assess this, we estimated the location of the attentional spotlight (AS) and used its displacement (dAS) from the attended location as a proxy of the distance of covert attention to the cued attention target. Consistent with our expectation, we found (for further details see Figure S4) that the AS was

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bars on the ordinate correspond to the training time interval used for the decoding shown in the bottom-right panels. For both motor and attention classification, average accuracies were calculated along the diagonal (bottom-left panels) (see also Figure S2) and when training was restricted to the delay epoch only (bottom-right panels) (see also Figure S3). Lines and shading show the mean classification accuracy ± SE. All classifications in the bottom panels were significantly (cluster-based permutation test, $p < 0.001$) above chance (dashed horizontal line).

(C and D) Cross-modal classification accuracies when the classifier was trained on the motor location and the attended location was decoded (C) and when trained on the attended location and the motor location was decoded (D). Bottom row, same conventions as in (A and B) but for cross-modal classification. Horizontal gray lines in bottom panels indicate time periods when classification was significantly (cluster-based permutation test, $p < 0.001$) above chance.

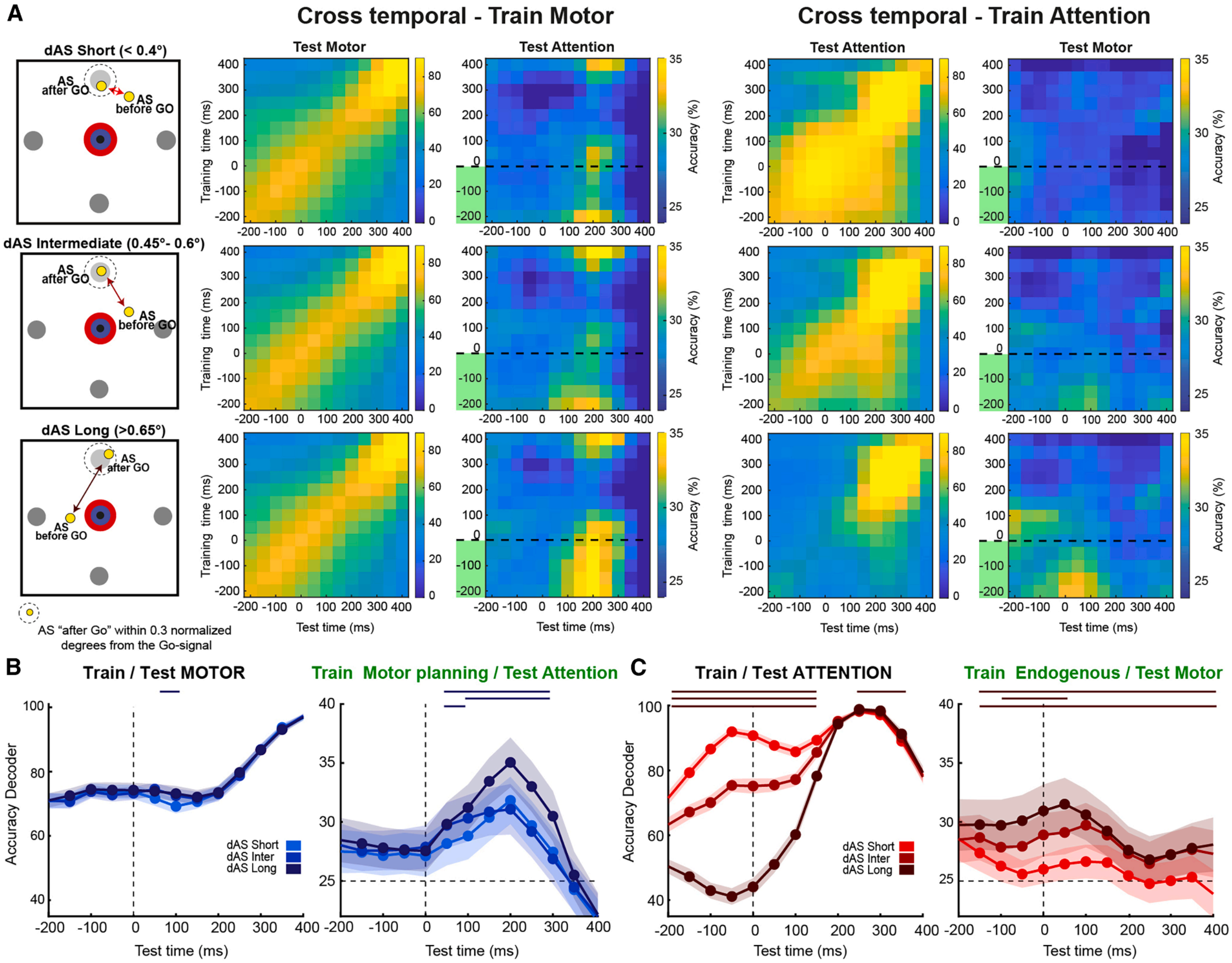

Figure 5. Interplay of neural codes as a function of attention localization

(A) Color maps show decoding accuracy of cross-temporal classifiers trained on the motor code (2nd and 3rd columns) and on the attention code (4th and 5th columns) for within (2nd and 4th columns) and across (3rd and 5th columns) modality decoding. As depicted in the 1st column, rows show analyses for trials with short, intermediate, and long displacements of attention (dAS) from the cued attended location, respectively (see also Figure S4). The dAS is the estimated misalignment of the attentional spotlight (AS) before and after the Go-signal occurs.

(B and C) Left panels show the average within-modality decoding accuracy of cross-temporal classifiers trained and tested along the diagonal using the motor (attention) code derived from short-, intermediate-, and long-dAS trials. Right panels show the average cross-modal decoding accuracy for classifiers trained during the delay period (as indicated by the green shading on the *y* axes of the 3rd and 5th columns in A) using short-, intermediate-, and long-dAS trials. Lines and shading show the mean classification accuracy ± SE. Horizontal lines, from top to bottom, indicate time periods of significantly different decoding accuracy for long- versus short-dAS trials, long- versus intermediate-dAS trials, and intermediate- versus short-dAS trials, respectively (cluster-based permutation test, $p < 0.001$).

significantly closer to the attended location (i.e., smaller dAS) on correct trials than on saccade omission trials, when the Go-signal was not detected. Our finding accords with previous studies that assessed attention through signal detection.[15,33,39]

To get insight into the neural dynamics underlying the interplay between endogenous and exogenous attention, we grouped trials into short (<0.4°), intermediate (between 0.45° and 0.6°), and long (>0.65°) normalized dAS groups, based on the proximity of endogenous attention to the attended location at the time of the Go-signal. Our analysis focuses exclusively on trials exhibiting exogenous attentional capture—that is, an automatic shift of attention toward the Go-signal (for further details see STAR Methods). To this end, we restricted analysis to trials where, at the expected time of Go-signal detection (~250 ms after the Go-signal), decoded attention was near the Go-signal location (dAS < 0.3°, see STAR Methods). On average, 42.2% of correct trials met this criterion. Motor decoding along the diagonal was largely similar across the three dAS groups (Figure 5B, left panel). In contrast, attention decoding along the diagonal had substantial differences across the three dAS groups (Figure 5C, left panel). Accuracy at the Go-signal was highest for short-dAS trials (90.8% ± 1.4%) and progressively lower as endogenous attention deviated further from the attention target (intermediate-dAS = 75.2% ± 2.3%; long-dAS = 44.1% ± 2.6% trials). This inverse relationship between dAS and decoder performance was present throughout the delay period and until 200 ms after the Go-signal.

Unlike within-modality decoding, cross-modal decoding was more accurate when the AS was *further* from the attention target. Decoding of the attended location by classifiers trained on motor planning activity (Figure 5B, right panel) exhibited an increase in accuracy following the Go-signal that peaked at ~200 ms. The accuracy increase was progressively larger the further endogenous attention was from the cued attention target at the time of the Go-signal (long-dAS accuracies > short-dAS accuracies from 50 to 300 ms; long-dAS accuracies > intermediate-dAS accuracies from 150 to 300 ms; intermediate-dAS accuracies > short-dAS accuracies from 50 to 150 ms; Kruskal-Wallis non-parametric test, $p < 0.05$). This improvement in attention decoding suggests that the attention representation was most like that of motor planning when shifts in exogenous attention were required to capture attention.

The other cross-modal classifier, trained on the endogenous attention signal and tested on decoding of the motor target, also performed better on trials where the endogenous AS was estimated to be further from the attended location (Figure 5C, right panel. Long-dAS accuracies > short-dAS accuracies from −150 to 400 ms; long-dAS accuracies > intermediate-dAS accuracies from −100 to 50 ms; intermediate-dAS accuracies > short-dAS accuracies from −150 to 400 ms; Kruskal-Wallis non-parametric test, $p < 0.05$). For short-dAS trials, cross-modal decoding was not significantly different than chance, indicating that when attention was precisely allocated, there was little overlap in the neural representations of attention and motor planning. For long- and intermediate-dAS trials, however, accuracies were better than chance during the delay period and for the first 150 ms following the Go-signal (Kruskal-Wallis non-parametric test, $p < 0.05$) before gradually declining to chance level before the saccadic response. Thus, the less attention focused on the Go-signal location during the delay epoch, the greater the degree of crosstalk between the neural resources involved in saccade planning (but not execution).

Overall, our results indicate a partial overlap between the attentional and motor systems, enabling the use of exogenous attention when endogenous attention has not been accurately allocated to the attended position.

DISCUSSION

Recent evidence indicates that voluntary (endogenous) attention is largely independent of the motor system[30] while involuntary reflexive (exogenous) attention is strongly connected to it.[4,40] While this distinction supports the existence of two separate attentional mechanisms,[1] other studies indicate a connection between the two, with endogenous attention modulating exogenous attention.[12,13] If these are indeed two independent systems that sometimes interact, we would expect them to be implemented in partially overlapping brain regions. However, evidence for such overlap, as well as a detailed neural account of this interaction, remains largely unexplored. In this study, we aimed to determine the lPFC contribution to these two attentional modes during visual selection and their reciprocal relationship with the motor system. To address this, we analyzed neural activity in the lPFC of two monkeys performing a behavioral task that spatially dissociated motor targets from the target of endogenous attention.

Briefly, we found that monkeys could use a centrally fixated cue to endogenously direct attention to a peripheral location that was distinct from their planned saccade target. Endogenous attention accelerated detection of the Go-signal both in terms of behavioral RTs (Figure 1C) and neural decoding of this peripheral brightening event (Figure 3, bottom). Neuronally, most units encoded either the locus of attention or the motor target, with relatively few units encoding both variables (Figure 2). Tuning changed over the course of the trial, with attention tuning being most common from 400 ms following cue presentation until Go-signal detection. Directing voluntary attention away from the saccade target on cued trials impaired decoding of the motor plan but also made it resilient against a drop in decoding that occurred on uncued trials, when both the timing and location of the Go-signal were unpredictable (Figure 3, top). Cross-temporal and cross-modal decoding revealed further interplay between the attention and motor representations. A classifier trained to decode the motor target during the delay period (saccade planning stage) was not effective at decoding this variable around the time of saccade execution. However, it was effective at decoding where the Go-signal occurred, especially on those trials where we estimated that endogenous attention had strayed from its target (Figures 4 and 5). In contrast, a classifier trained to decode the attended location based on delay period activity (i.e., an endogenous attention signal) showed improved decoding before the Go-signal for both attention (within modality) and the motor target (across modalities), again especially on trials where attention was off target.

Overlapping motor and attention information in lPFC

In our original study, we showed that the delay period activity of single units in the lPFC encoded either the oculomotor plan or covert spatial attention, but not both.[30] Notably, in contrast to the other areas analyzed (premotor and pre-arcuate cortex), the lPFC was highly informative about both motor and attention variables. In the present study, we expanded on this finding by investigating the neural interplay between endogenous and exogenous attention during visual selection, investigating multiple task periods using the larger pool of lPFC multi-units recorded on cued and uncued trials. The observation that motor planning and spatial attention signals are encoded by distinct neural populations challenges the notion of obligatory coupling between these processes and contrasts with the assumptions of the premotor theory of attention, which posits that spatial attention is functionally equivalent to planning eye movements.[3,41]

Although most units were exclusively tuned for attended and motor targets, we found significant and rapid shifts in the relative proportion of such units across different phases of the task. Motor units outnumbered attention units early, during the delay period. Attention units became more numerous later, following the brightening of the attended target (the Go-signal). Finally, the predominance of Motor units re-emerged around the time of the saccade. The proportion of Both units remained almost unchanged throughout these events. Interestingly, units sometimes switched between Motor and Attention selectivity across task periods, in some cases without first simultaneously encoding both variables (i.e., without becoming Both units in the interim). Thus, in any given epoch, largely separate neural units encoded the motor and attention variables of the task, but the makeup of these two pools flexibly updated to reflect changing task demands throughout the trial, with some units serving both cognitive operations in different contexts. We refer to these units as overlapping resources for their ability to be tuned for both variables across the trial depending on task demands. Previous studies have demonstrated that the lPFC can encode and recruit different variables interchangeably depending on task demands.[42–45] Here, we found that such flexibility extends to the interplay between motor and attentional systems.

Notably, in our study, we use the term Motor units to refer to saccade planning activity, primarily for convenience. Although we cannot definitively distinguish whether these motor signals represent the metrics of the motor response or a spatial goal, previous research that has contrasted goal and movement coding in the lPFC (e.g., Saito et al.[46]) suggests that the lPFC's tuning for motor location is more likely to reflect a goal signal rather than the specific movement metrics. Thus, our findings are consistent with the broader understanding that the lPFC contributes to goal generation.[47,48]

lPFC dynamically recruits overlapping resources based on task demands

Our results indicate that the lPFC simultaneously represents both attended and motor targets, using motor selective cells and attention selective cells, respectively. The analysis in Figure 3 shows the decoding of these two variables on cued and uncued trials from a population of lPFC units. Both locations were accurately and independently decoded, despite the fact that only trials with a distinct motor and attention target were used in this analysis.

On uncued trials, the location of the Go-signal was unpredictable, and its detection had to rely on exogenous attention. We found that motor decoding was better in these trials than in cued trials, i.e., when endogenous attention was engaged. Thus, when there were concurrent demands on the motor and attention systems, less motor plan information was encoded in the lPFC. We infer from this result that when endogenous attention is not being taxed, the motor system recruits all available resources (both solely motor and the overlapping resources) to encode the motor parameters, not because these extra resources are strictly required for solving the task but simply because they are available.[49,50] This hypothesis gains support from the observation that the Go-signal resulted in a drop in motor decoding accuracy on uncued only. We attribute this drop in motor accuracy to interference produced by the exogenous attentional demands of the Go-signal brightening. Consistent with our hypothesis, this interference suggests that the motor system was utilizing overlapping resources on uncued trials that were suddenly reclaimed by the attention system to process the unpredictable Go-signal. The suggested neural dynamics imply a high capacity for neural flexibility within the lPFC, where units can encode information from both systems, based on encountered needs. As mentioned earlier, some lPFC units had such neural flexibility.

In contrast to uncued trials, in the cued condition, the sudden increase of attentional information in response to the attended target did not interfere with motor coding, supporting the idea that overlapping resources have already been allocated and/or distributed between the systems before the presentation of the attended target.[51,52] Unlike the uncued condition, we observed that units encoding the attended location maintained their high level of coding even after the attended target appearance. This greater stability of spatial representations likely depends on the involvement of mnemonic processes during endogenous attention. For instance, it is known that spatial attention can rely on functional markers for location-specific representations held in working memory, thereby providing an additional contribution to sustained neural representation without necessitating a shift in resource encoding.[53–55] Further in-depth investigations are required to disambiguate this issue.

Interaction between endogenous and exogenous attention mechanisms

As discussed above, our results suggest a significant role for overlapping resources in exogenous attention. This form of reflexive attention revealed itself through a sharp increase in decoding accuracy following the appearance of a salient or unexpected stimulus.[56] This sudden increase in the processing of attentional information results from the rapid allocation of attentional focus toward the stimulus, a phenomenon commonly known as attentional capture.[20,57]

While stimulus-driven attentional capture has been mainly studied in the context of the distracting impact of irrelevant targets on visual search tasks,[58,59] neurophysiological evidence suggests that it can also occur when attention is endogenously deployed.[15,60] Consistent with this, we observed a sudden increase in attentional information in response to target stimuli during cued trials, revealing the co-occurrence of exogenous shifts aimed at attentional capture alongside endogenous attention (Figure 3). The cross-temporal decoding (Figure 4B) also revealed that the endogenous code (i.e., the signal associated to the attended target location during the delay period) contributes to attentional capture, as evidenced by a rapid increase in predictiveness following the Go-signal. This challenges the notion that attentional capture is exclusively associated with exogenous attention. However, one possible explanation is that endogenous attention utilizes overlapping resources during this period, contributing to the encoding of attentional variables rather than being dedicated to motor encoding or remaining disengaged. In this scenario, these neural resources would serve a dual function, i.e., sustaining endogenous attention while remaining dynamically accessible to exogenous shifts when a salient stimulus appears. Based on our classification, overlapping resources are predominantly visuomotor units, which may be particularly well suited for facilitating rapid shifts of attention toward salient stimuli, compared with purely visual units.[18,61] The recruitment of such visuomotor mechanisms can thus provide a neural basis for the efficient integration of endogenous and exogenous attentional processes, optimizing behavioral responses in dynamic environments. This hypothesis is supported by the cross-modal decoding analysis shown in Figure 4C, where we observed a sudden improvement in decoding the attended target location using a classifier trained on the motor planning signal (i.e., the signal associated to the motor target location during the delay period). This result not only reinforces the notion that exogenous attention can co-occur with endogenous attention but also indicates that some neural units involved in encoding motor-related variables during the delay period also contribute to the shifting of attention toward the Go-signal.

If these neural resources indeed play a key role in the attentional shifts for attentional capture, we expect their coding to be influenced by the extent of such shifts. Consistent with this hypothesis, in the cross-modal decoding analysis, we revealed enhanced decoding of the attended location using a classifier trained on the motor planning signal in trials where endogenous attention was poorly oriented toward the Go-signal, i.e., trials in which larger attentional shifts were expected. This finding suggests that the availability of overlapping resources for attentional capture depends on the endogenous allocation of spatial attention: the more distant the attentional focus, the greater the involvement of these resources in attentional shifts. Further supporting this idea, cross-modal decoding in which the training and test variables were inverted (i.e., decoder trained with attended target location and tested with motor target location) revealed a complementary pattern: when attention was more precisely focused on the target location, the endogenous code's ability to predict the motor target was significantly reduced. In other words, the stronger the endogenous deployment of attention, the less these resources were able to predict the motor target location.

Taken together, our findings support the idea that endogenous and exogenous attention, although largely independent mechanisms, can interact to enhance attentional control. As previously proposed, "Two independent systems that sometimes interact are expected to be implemented in partially overlapping brain regions."[1] In the present work, we show that a partial overlap between the motor and attentional systems in the lPFC may serve as the neural substrate enabling the dynamic interplay between endogenous and exogenous attentional modes. To the best of our knowledge, this is the first direct neural evidence that exogenous attentional shifts can emerge alongside endogenous attention, challenging the traditional view that these two modes of attention function in strictly sequential or separate ways and offering new insights into the neural basis of adaptive attentional control.

Overall, our results indicate that exogenous shifts can support endogenous attention in capturing relevant information. In other words, endogenous attention may rely on a certain "range of action" of exogenous support for its scope. However, we also found that when attention is sufficiently focused, such support may no longer be necessary. Reasonably, such an exogenous range of action can also be influenced by various factors. In particular, the relevance of the to-be-captured stimulus could be a critical variable. In this context, the salience network, especially the anterior insula and the dorsal anterior cingulate cortex, may play a key role in modulating resource recruitment based on the behavioral significance of the stimulus.[62,63] Internal factors such as arousal, attentional load, motivation, and habituation may also shape how exogenous shifts interact with endogenous attention, potentially in ways that differ from situations where endogenous attention is not engaged. We believe that further research to clarify these aspects is essential for a better understanding of the interaction between reflexive and voluntary control of spatial attention, with potential implications for the development of optimal cognitive training strategies and rehabilitative interventions in clinical populations.[64,65]

One or multiple attentional spotlights

A major assumption of our approach is that subjects deploy a single AS rather than multiple spotlights during the task. The presence of two targets (one motor and one attentional) could, in principle, lead subjects to divide their spatial attention between these two goals.[66,67] This possibility could make it difficult to interpret neural activity during saccade planning as independent of spatial attention, since attentional activity directed toward the motor target could be difficult to separate with motor preparation signals. Although we cannot entirely rule out this possibility, we find it unlikely, as it would require anticipatory and unnecessary deployment of attention, given that the motor target is consistently selected after the attention target. Furthermore, the better performance observed in cued trials compared with uncued trials suggests (at least) the presence of a dominant AS directed at the Go-signal location when this information is available. We believe our decoding approach accounts for these alternatives. Given the structure of our decoder, we interpret its output as representing the location of a single attentional spotlight.[15] However, it could alternatively reflect the position of a dominant attentional spotlight, and we believe the main conclusions of our study remain unchanged.

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the corresponding author, Aldo Genovesio (aldo.genovesio@uniupo.it).

Materials availability

The current study has not generated any new material.

Data and code availability

- All data are available upon request from the lead contact.
- Code, including analysis software, is available from the lead contact upon request.
- This paper does not report original code.
- Any additional information needed to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, A.M., A.G., and F.D.B.; data collection, A.M.; methodology, A.M., A.G., and F.D.B.; data analysis, F.D.B.; writing – original draft, F.D.B., A.M., and A.G.; writing – review & editing, F.D.B., A.M., A.G., and F.C.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Macaca mulatta (Rhesus monkey)	National Institute of Mental Health	Monkey R (9.0 kg), Monkey G (7.5 kg)
Software and algorithms		
Matlab, R2020a	MathWorks	https://it.mathworks.com

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Animals

Two adult male rhesus monkeys (Macaca mulatta) participated in this study: Monkey R (9.0 kg) and Monkey G (7.5 kg). All experimental procedures conformed to the Guide for the Care and Use of Laboratory Animals and were approved by the Animal Care and Use Committee of the National Institute of Mental Health (NIMH). Animals were housed in facilities with controlled environmental conditions, and their health was monitored daily by veterinary staff. Both animals were pair-housed when possible and provided with environmental enrichment.

Surgical techniques

Surgical procedures were performed under aseptic conditions with general anesthesia and postoperative analgesia. A metal head post was surgically implanted before training began. After each monkey had learned the task, we surgically implanted a 27 × 36 mm recording chamber over the left frontal cortex, with its long side oriented in an anterior-posterior (AP) plane and its short side in a medial-lateral (ML) plane. A craniotomy was centered at AP +29.5, ML +12 in monkey R and AP +22, ML +15 in monkey G.

METHOD DETAILS

Behavioral task

Each monkey sat in a primate chair facing a video screen 57 cm away with its head fixed by a surgically implanted head post. The experimental design dissociated the locus of covert spatial attention from the target of a future saccadic eye movement. To accomplish this objective, we used a dual conditional visuospatial task. One four-way conditional association provided the spatial goal for a saccade; another four-way conditional association guided the allocation of covert attention. The monkey began each trial by touching a metal bar, which led to the appearance of a small white circle (0.15° radius), the fixation point, at the center of the video screen (Figure 1A). If the monkey continued to fixate this spot [within a square window of 3.3° for a variable period (200 to 1000 ms)], four circular gray spots appeared (0.35° radius): left, right, up, and down from the fixation point at an eccentricity of 4.0°. A bicolored cue stimulus appeared at the fixation point after an additional fixation period of 200 to 1000 ms. The color of the cue's outer component, a 0.25° wide annulus, informed the monkey about which of the four gray spots to fixate after a forthcoming Go-signal. For convenience, we call this spot the Motor Location and its instructing stimulus the motor cue. The color of the cue's inner component, a 0.6° radius circle, indicated which of the four gray spots would subsequently brighten as the Go-signal. We call this spot the Attended Location, and its central instructing stimulus is the attention cue. By design, the monkey should direct covert attention to the Attended Location to facilitate detection of the brightening event (the Go-signal), which triggered a saccade to the Motor Location. The degree of brightening was selected randomly among four calibrated levels such that each monkey failed to respond to the smallest degree of brightening on ∼30% of trials and responded reliably to the largest degree of brightening. We refer to the variable and randomly selected interval (800, 1600, 2400, or 3200 ms) between the appearance of the cue stimulus and the Go-signal as the cue delay period. During this interval, the monkey was expected to covertly attend to the Attended Location while preparing a saccade to the (typically distinct) Motor Location. The Go-signal thus served as the primary attentional target, as its detection triggered the requirement to execute a saccade to the Motor Location within 800 ms (for monkey R) or 600 ms (for monkey G). During this interval, the monkey should direct covert attention to the spot at the Attended Location while simultaneously planning a saccade to the spot at the (usually distinct) Motor Location. Following the Go-signal, the monkey had to complete a saccade to the Motor Location within 800 ms (for monkey R) or 600 ms (for monkey G). If it did so, then all other stimuli disappeared from the screen, and the monkey had to fixate the Motor Location (within a square window of 4.0°) for an additional 800 to 1600 ms until it dimmed. The monkey could then release the bar to receive a juice reward. If the monkey broke fixation before the Go-signal, failed to make a saccade within the requisite time after the Go-signal, shifted fixation anywhere other than to the Motor Location, failed to fixate the spot at the Motor Location for the required interval, or released the bar before this spot dimmed, the trial ended without reward delivery, and the normal interval between trials (600 to 1800 ms) was extended by 1600 ms. The same conditional mapping between the four cue stimulus colors and the four peripheral spots was used for the motor and attention cues. As illustrated in Figure 1B, red was associated with the gray spot to the right of the fixation point, blue with up, green with left, and yellow with down. This arbitrary mapping was overlearned by trial and error before the neuronal recordings. In 20% of the trials, the colored attention cue was omitted and replaced with a gray cue of the same dimensions. On these uncued trials—i.e., uncued with respect to covert attention—the location of the Go-signal was selected pseudorandomly from amongst the four peripheral spots. In our paradigm, exogenous attention is investigated in response to the Go-signal preceded by a cue uninformative of its location. This differs from typical exogenous attention paradigms that examine processing of a target following a non-predictive peripheral cue.[68–70]

Data collection

Recordings were made in broad frontal regions (for a map of the recording sites see Messinger et al. [30]). In the present work, we only included parts of the dorsolateral and ventrolateral PF on either side of the principal sulcus (areas 46d/v, 8, and 45). We did not distinguish between these two subregions, following,[30] who found that the distribution of functionally selective cells was similar across them, supporting the decision to analyze the data jointly. Recordings in this area were made using a multielectrode microdrive, with independently moveable single-contact electrodes arranged in a circle. The initial penetrations in both monkeys were made with a 7-electrode System Eckhorn drive (Thomas Recording GmbH, Giessen, Germany). Later penetrations were made with Alpha Omega's 8-electrode MultiDrive (Alpharetta, GA). Neighboring electrodes were 1.0 mm apart, and the largest electrode separation. MUA signal was extracted using an auto threshold method. The threshold was set at negative 3.5 times the standard deviation. In total, our sample consisted of 238 units, 82 from Monkey R and 156 from Monkey G.

QUANTIFICATION AND STATISTICAL ANALYSIS

Decoding motor and attention signals

To explore motor and attention encoding dynamics in both cued and uncued trials, we applied a decoding analysis on trials where the motor and attention target locations were dissociated (i.e., 'different' trials). To evaluate the classification accuracy with distinct randomly chosen trials, we executed 250 resample runs. In each run, we included all units recorded in at least 8 trials for each of the four possible motor or attention target locations. This created a matrix of 214 units by 32 trials (8 trials per motor or attention target location) for both cued and uncued conditions. For decoding, we employed a leave-one-trial-out methodology. In this approach, one trial is designated the test set, and (nearly) all other trials form the training set. To avoid imbalance in the training set, three trials were removed in addition to the test trial such that all locations were equally represented in the training set.

During the training phase, for each time step, a regularized optimal linear estimator (RegOLE)[15,33,71] associated the neural responses, consisting of a vector containing the neural signals collected at each recording contact, from a structure containing the signal of 28 correct trials (i.e., 7 trials for each target location) to the (x,y) coordinates of the associated target position for each trial. To avoid over-fitting, we used a Tikhonov regularization, which gives us the following minimization equation: norm $(W^*(R+b)-C)+\lambda^*\text{norm}(W)$. The scaling factor λ was chosen to allow for a good compromise between learning and generalization.[39] Specifically, the decoder was constructed using two independent regularized linear regressions, one classifying the x-axis (two possible classes: -1 or $+1$) and one classifying the y-axis (two possible classes: -1 or $+1$). During testing, the classifier's output was estimated from a vector of the average neuronal activity for each of the 214 recorded channels for the time interval of interest on a testing trial, new to the classifier. If the classifier's output fell within the same quadrant as the Go-signal, the classification was considered correct. Classification accuracy was the average proportion of correctly classified trials within each resample run.

To generate a null distribution of accuracy values representing chance performance, we also performed decoding after randomly reassigning the behavioral classification of each trial in each run and recalculating the decoding accuracy. Statistical significance was assessed using a nonparametric permutation test. Specifically, we combined the two distributions (resampled and null) and randomly reassigned the 500 accuracy values into two groups of 250. For each permutation, we calculated the difference in means between the two groups. This procedure was repeated 10,000 times to generate a null distribution of mean differences under the hypothesis that the two distributions were equivalent. The true decoding accuracy of the non-permuted data was considered statistically significant if it fell within the top or bottom 0.01% of the corresponding null distribution of mean accuracies. Although our decoding procedure controls for the number of trials per trial type (i.e., both cued and uncued) in each resample ($n = 8$), the cued condition draws from a pool of trials that is about four times larger (see Figure 1). As a result, each resample in the cued condition uses a more varied set of trials than in the uncued condition. This limited variability in the resampled uncued trials can lead to noisier accuracy estimates compared to cued trials.[72,73]

Similarly, differences in decoding accuracy between conditions (e.g., as shown in Figures 3 and 5) were assessed by randomly reassigning trial labels to generate a null distribution of mean differences under the assumption that the two conditions were equivalent. Statistical significance was then evaluated by comparing the mean decoding accuracy of the real (non-permuted) data to this null distribution, as described above.

When performing computations over time, the large number of consecutive statistical comparisons required controlling for the family-wise error rate (FWER).[74] To address this, we only considered clusters of significant effects that lasted at least 100 ms.[75,76]

Cross-temporal decoding

To explore the stability of attentional and motor codes around the time of the Go-signal on cued trials, we employed a cross-temporal decoding analysis. In this method, a classifier was trained with one spatial variable (the motor target or attended target variable) using data from one period and then tested with data from another period. We performed 250 resample runs to evaluate the classification accuracy with distinct sets of randomly chosen trials. To ensure unbiased comparisons between cross-temporal decoding classifications between same and different modalities (see below), we constructed a symmetric data sample based on trial conditions, which was used for both classifications in each run. For each channel, we randomly selected 10 correct trials for each of the 16 types of cued trials formed by the 4 x 4 combinations of motor and attended targets (Figure 1B). This yielded a matrix of 216 units by 160 trials. The classifier was then trained on 80% of the trials and tested on the remaining 20%, constituting a previously unseen set of trials. Due to the symmetry of the matrix and the simultaneous task instruction, we used the same data to train both the motor and attention classifier on each run. By utilizing the same classifier described earlier (the RegOLE), we associated the neural responses from a dataset comprising signals from 128 correct trials (8 trials for each combination of target locations) with the (x,y) coordinates of the corresponding target positions for each trial for each time-bin. We then tested this association using a dataset for the time interval of interest consisting of 32 testing trials (i.e., 2 trials for each combination of target locations), which was new to the classifier. Classification accuracy was the average proportion of correctly classified trials within each resample run. Thus, by training and testing the classifier using all possible combinations of 50ms, we obtained a classification accuracy matrix where the values along the diagonal were calculated by training and testing on equivalent time bins. In contrast, different time bins were used to calculate the off-diagonal values.

A cross-modal decoding approach was also applied to investigate the generalizability of the motor and attentional codes. We used the same methodology described for cross-temporal decoding. However, in this analysis, the type of variable associated with training and the one being tested belonged to different modalities (i.e., motor and attention target locations were alternately used for training and testing).

Attentional spotlight distance

The (x,y) readout of the attention decoder was not categorically assigned to one of the four possible Attended Locations as is commonly done with classifiers, but was taken as a continuous measure of the position of the attentional spotlight (AS).[15,33,71] Here (Figure S4) we show that this estimated readout of the AS position accounts for variations in behavioral responses. For each trial and each attention location, we measured the normalized Cartesian distance (dAS) between the decoded AS at Go-signal onset and at the estimated time of the perceptual seizure (i.e., at 250 ms – as inferred by Figures 3 and 4) to determine if deviations in the locus of attention were reflected in neuronal MUA responses. We performed 250 resample runs to evaluate dAS distances with distinct randomly chosen trials to collect a large dataset of dAS-associated trials. For each run, we generated a matrix of 216 units by 160 trials by randomly selecting 10 correct trials for each of the 16 spatial cue types. We categorized the fidelity of attention localization on extracted trials as high, intermediate or low based on whether the deviation of the attentional spotlight was short ($dAS < 0.4^\circ$), Intermediate ($0.45^\circ < dAS < 0.6^\circ$), or Long ($dAS > 0.65^\circ$). We used these trial categories in cross-temporal decoding analyses, as previously described, except that the input matrix consisted of neuronal activity on trials belonging to the same dAS category.

Trials selection based on attentional capture

Studies using cueing tasks often assume that the attentional spotlight remains static at the cued location. However, recent evidence challenges this view.[15,32,33,71] Although in these studies the decoder is trained under the assumption that attention stays aligned with cue instructions, its output consistently reveals that attention is dynamic and rhythmic. In other words, while decoded attention is, on average, directed toward the cued location, it is not necessarily fixed precisely on the target position. In line with this, in our task we expect a rapid shift of decoded attention toward the Go-signal location, reflecting attentional capture — a fast and automatic redirection of attention toward a salient or sudden stimulus — especially in correct trials where attention is initially far from the Go-signal at its onset. To focus our analysis on these instances, we selected trials in which, shortly after the Go-signal (within ~250 ms), the decoded attention was near the Go-signal location ($dAS < 0.3^\circ$). Although we recognize that, given the low visual processing demands of our task (i.e., simple target detection), such attentional capture may not be strictly necessary for successful performance,[77] we confirmed that it occurred in a substantial proportion of trials (~42.2%). The analyses presented in this study are based on this subset.