

primaries. Many questions remain, ranging from the homology of pterosaur pycnofibers, to whether a hypothetical dinosaurian forerunner with rictal bristles existed, to whether dinosaur babies hatched with unique down feathers. If the past two decades are any guide, future discoveries of feathered fossils will continue to reveal many additional surprises.

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Attention capture outside the oculomotor range

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Neurophysiological studies have demonstrated that attentional orienting is associated with activity in frontoparietal brain areas that play a pivotal role in oculomotor control, such as the lateral intraparietal cortex (LIP), the frontal eye fields (FEF), and the superior colliculus (SC) (e.g., [1]). Accordingly, based on the influential premotor theory of attention, which posits that even covert shifts of spatial attention in the absence of eye movements are elicited by preceding activation in the oculomotor system [2], it has been claimed that attention can only be allocated to where we can potentially make an eye movement [3]. There are two forms of covert spatial attention: *exogenous attention* is automatic, stimulus-driven, and transiently deployed in ~100 ms. Conversely, *endogenous attention* is voluntary, goal-driven, and deployed in a slower (~300 ms) and sustained manner [4]. Notably, it has been postulated that only exogenous attention, but not endogenous attention, would be restricted to locations within the so-called *oculomotor range* that is accessible by saccadic eye movements [5,6]. To test this claim, we used a dissociation approach that allowed us to evaluate exogenous attention shifts to locations within and beyond observers' oculomotor range via their disruptive, attention capturing costs for endogenous attention. We found that salient events equally grab exogenous attention both inside and outside the oculomotor range, demonstrating that exogenous attention can shift to locations not reachable by the eyes.

Across two experiments, 7 observers rotated their heads ~32° leftwards (Figure 1A), which prevented them from performing rightward saccades larger than ~8° (degrees of visual angle). The required head rotation angle was individually

determined prior to the experiment and monitored with an electromagnetic motion tracking device (see Figure S1 in Supplemental Information, published with this article online, for individual head rotation angles). We used a two-alternative forced-choice discrimination task based on oriented pink noise patches [7] (Figure 1B) to assess covert spatial attention across four locations on the horizontal meridian ($\pm 6^\circ$ and $\pm 10^\circ$ relative to central eye fixation). Due to the leftward head rotation, the right distal patch ($+10^\circ$) lied beyond the oculomotor range (i.e., it could not be reached by the eyes but was still visible). Observers were instructed to attend to the left distal location (-10° ; within the oculomotor range), as the brief orientation signal (50 ms; tilted clockwise or counterclockwise) they had to discriminate (Figure 1C) was most likely to occur there. In Experiment 1, this discrimination signal (DS) occurred in 75% of trials at the -10° location (and in 25% of trials at one of the three remaining locations with equal probability); in Experiment 2 the signal occurred at the -10° location in 100% of trials. While observers aimed to maintain endogenous attention at the -10° location, we flashed a salient 50 ms cue at one of the four locations (-10° , -6° , $+6^\circ$, $+10^\circ$; with equal probability). As a highly salient visual event, this cue can be assumed to strongly attract exogenous attention (typically within ~100 ms [4]). By evaluating observers' visual sensitivity — an established proxy for visual attention — at the endogenously attended (-10°) location 100 ms following cue presentation, we inferred the attention-capturing effect of the exogenous cue depending on whether it occurred inside or outside the oculomotor range. While we expected high sensitivity when the exogenous cue matched the endogenously attended location (-10°), sensitivity at the endogenously attended location should be decreased when the cue attracted exogenous attention away from it. Critically, if the cue attracted exogenous attention even at $+10^\circ$ outside the oculomotor range, this would demonstrate that exogenous attention can shift to locations not reachable by the eyes — falsifying previous claims [3,5,6].



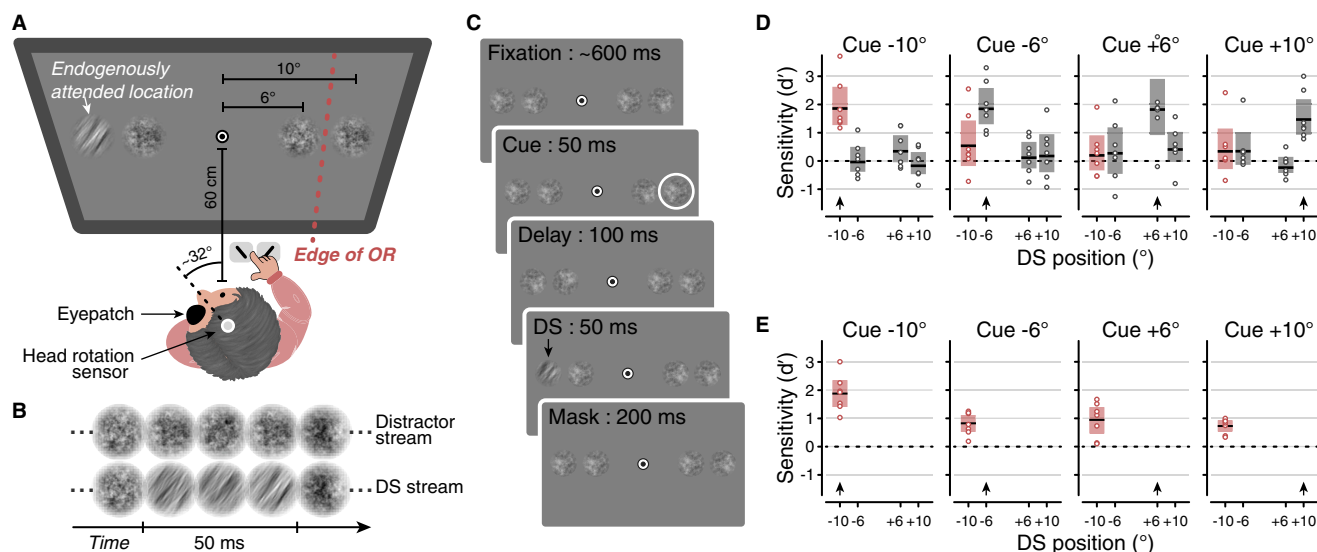


Figure 1. Attention capture task design and results.

(A) Setup. Observers viewed the stimuli with their left eye patched and their head rotated leftwards. Four pink noise streams were presented at four locations, covering two eccentricities ($\pm 6^\circ$ and $\pm 10^\circ$) from a central fixation target. The $+10^\circ$ patch fell outside observers' oculomotor range (OR). (B) Each pink noise stream consisted of a succession of randomly generated pink noise patches that flickered at 60 Hz. The discrimination signal (DS) stream included a sequence of orientation-filtered pink noise patches (50 ms), showing a 40° clockwise or counterclockwise tilt relative to the vertical axis. (C) Experimental task. After a fixation period, an exogenous, circular white cue was flashed around one randomly chosen noise stream. Observers were instructed to ignore this cue, maintain central eye fixation, and report the orientation of the DS presented 100 ms after the cue (Video S1). (D,E) Visual sensitivity in Experiment 1 (D) and Experiment 2 (E) at the endogenously attended -10° location (red whisker plots), and the other locations (-6° , $+6^\circ$, $+10^\circ$; gray whisker plots) as a function of cue location (indicated by the black arrow at the bottom of each plot). Horizontal lines within each whisker plot indicate the mean visual sensitivity (d') at the respective test position. Error bars depict 95% confidence intervals, dots represent individual observer data, dashed lines mark chance level.

For both Experiment 1 (Figure 1D) and Experiment 2 (Figure 1E), we evaluated visual sensitivity (d') at the endogenously attended -10° location depending on whether the exogenous cue matched or did not match this location. We found that visual sensitivity at the endogenously attended -10° location was significantly higher when the cue occurred at the same location (Cue -10° Experiment 1: 2.08 [1.72, 2.45] — mean [95% CI]; Experiment 2: 1.89 [1.65, 2.13]), as compared to when it occurred at a neighboring location within the oculomotor range (Cue -6° Experiment 1: 0.70 [0.27, 1.13], $p < 0.001$; Experiment 2: 0.84 [0.69, 0.99], $p < 0.001$; Cue $+6^\circ$ Experiment 1: 0.34 [0.01, 0.67], $p < 0.001$; Experiment 2: 0.95 [0.71, 1.19], $p < 0.001$). Thus, as expected, the cue decreased visual performance at the endogenously attended location by exogenously attracting attention away from it. Crucially, and in direct contradiction to the predictions of previous work [5,6], this disruptive effect also occurred when the cue was presented at $+10^\circ$,

well outside the oculomotor range — as indicated by an equally reduced sensitivity at the endogenously attended -10° location (Cue $+10^\circ$ Experiment 1: 0.49 [0.11, 0.88], $p < 0.001$; Experiment 2: 0.76 [0.66, 0.86], $p < 0.001$). Moreover, Experiment 1 revealed that the attention costs observed whenever the exogenous cue did not match the voluntarily attended location had corresponding attention benefits: visual sensitivity at the exogenously cued location was superior to all other locations — including the endogenously attended -10° location — and this was independent of whether the cue was presented inside (Cue -6° and DS@cue: 2.08 [1.73, 2.42] vs. DS@ -10° : 0.69 [0.27, 1.13], $p < 0.001$; Cue $+6^\circ$ and DS@cue: 2.04 [1.51, 2.58] vs. DS@ -10° : 0.34 [0.01, 0.67], $p = 0.024$) or outside the oculomotor range (Cue $+10^\circ$ and DS@cue: 1.67 [1.34, 2.01] vs. DS@ -10° : 0.49 [0.11, 0.88], $p < 0.001$). The attention benefit at the cued $+10^\circ$ location shows that exogenous attention was in fact properly allocated outside the oculomotor range.

Our findings demonstrate that exogenous events equally grab our attention both inside and outside the oculomotor range, and are in line with recent evidence from our lab showing concordant attentional benefits beyond the reach of saccadic eye movements [8]. However, as these eccentric locations can be accessed by a combined eye–head movement, we cannot rule out that head movement planning contributed to the observed attention shifts outside the oculomotor range.

The automatic shift of attention to a distracting cue outside the oculomotor range observed here is an exogenous effect that cannot be explained by voluntary, endogenous orienting. As spatial exogenous attention was attracted unrestrictedly toward locations to which no saccade could be executed, the present findings question the coupling of exogenous attention and eye movement control proposed by the premotor theory of attention [2] and its variants [3,5,6]. Our results are in line with a recent study demonstrating

that, unlike previously claimed [9], pathological oculomotor restrictions are not necessarily associated with corresponding attentional deficits [10]. Instead, exogenous attention can be shifted freely over the entire visual range, independent of limitations imposed by the eye movement system. Our results add to the growing body of literature calling for the rejection of the premotor theory of attention as a generally valid theoretical construct for covert attentional orienting.

SUPPLEMENTAL INFORMATION

Supplemental Information contains one figure, one video, and experimental procedures, all of which can be found with this article online at <https://doi.org/10.1016/j.cub.2020.09.054>.

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Lack of evidence for pheromones in lemurs

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As chemicals that elicit unlearned, functionally specialized, and species-specific responses [1] or ‘stereotyped behavior’ [2], pheromones differ from mammalian scent signatures that comprise complex, variable mixtures, convey multiple messages via learned chemical combinations, and elicit generalized responses [1]. Studying ring-tailed lemur (*Lemur catta*) behavior and semiochemistry, a recent study by Shirasu, Ito *et al.* [2] claimed to have identified “the first sex pheromones in primates.” However, reliance on one male in most chemical procedures and on few females in behavioral procedures constrains statistical analyses and challenges the broad applicability of their findings. Also, the non-independent testing of even fewer signaler–recipient dyads downplays the critical role of learning and memory in primate communication [1] — an argument that refuted earlier claims of primate pheromones [3,4]. Here, we challenge each of their four highlighted findings and interpretations.

First, Shirasu, Ito and colleagues [2] noted that female lemurs were “more attracted to male scent gland secretion during the breeding season”. That the scent of breeding (*versus* non-breeding) animals generates more sniffing has been long established [3,4]; however, some of the bias, at least in *L. catta*, is owing to the recipients’ concurrent reproductive state (Figure 1A) [5]. Neglecting relevant behavioral studies [3–6] and constrained by sample limitations, the authors did not test other types of signaler–recipient dyads or scents necessary for contextualization (Figure 1B) [5], nor did they control for signaler variables known to influence recipients, such as familiarity, dominance status, health, or genetic makeup [3–5]. For example, although *not* chemically encoded (note erroneous citation of Scordato *et al.* 2007 in [2]), the signaler’s dominance status is

nonetheless recognized in scent marks, owing to the lemurs’ prior observation of behavioral interactions, retention of that social information and later cross-modal integration with individual scent signatures [3,5]. Most problematic, however, is the authors’ interpretation that sniffing duration, which offers no functional socioecological insight, is the same as pheromonal attraction. Sniffing is generalized investigation required for olfactory processing. Unlike pheromonal attraction, it is not stereotyped, species- or sex-specific, uniquely directed to conspecific scent, or necessarily indicative of reproductive interest. Were that the case, one must conclude that female lemurs are most sexually attracted to female ‘pheromones’ that change seasonally under hormonal control (Figure 1B) [7,8]. Paired odorant presentations test only for discrimination, not for preference [9]. Stereotyped behavior, in this case purported reproductive attraction, is thus not supported.

Second, Shirasu, Ito and colleagues [2] claim that “three C12 and C14 aldehydes are seasonally secreted by the male antibrachial gland” and “are strong candidate compounds for female lemur attraction.” That only one of four males (Bon) consistently met the seasonal criterion (Figure 2C in [2]) undermines this generalization. If such major variability were to exist in pheromone concentrations, it would suggest that only certain males could attract females and mate; however, this scenario is inconsistent with *L. catta* consortship. In this promiscuous, female-dominant species, females control reproduction [10] and sometimes mate with all candidate males during a single estrous cycle. Female choice may determine the order or frequency of partners, but mating is unlikely to be ‘triggered’ by male pheromones. Instead, condition-dependent olfactory signatures [4] likely influence which immigrant males can join the group. Seasonal differences in chemical composition, albeit confounded by other variables known to influence volatile compounds (e.g. diet, microbial communities) [1,4], thus suggest potential individual differences in signaler quality as a more parsimonious explanation. Contrary to claims of unavailable chemical data, primate researchers have identified seasonally varying and hormonally mediated

