

Visual attention is not limited to the oculomotor range

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Edited by Michael I. Posner, University of Oregon, Eugene, OR, and approved March 27, 2019 (received for review August 5, 2018)

Both patients with eye movement disorders and healthy participants whose oculomotor range had been experimentally reduced have been reported to show attentional deficits at locations unreachable by their eyes. Whereas previous studies were mainly based on the evaluation of reaction times, we measured visual sensitivity before saccadic eye movements and during fixation at locations either within or beyond participants' oculomotor range. Participants rotated their heads to prevent them from performing large rightward saccades. In this posture, an attentional cue was presented inside or outside their oculomotor range. Participants either made a saccade to the cue or maintained fixation while they discriminated the orientation of a visual noise patch. In contrast to previous reports, we found that the cue attracted visual attention regardless of whether it was presented within or beyond participants' oculomotor range during both fixation and saccade preparation. Moreover, when participants aimed to look to a cue that they could not reach with their eyes, we observed no benefit at their actual saccade endpoint. This demonstrates that spatial attention is not coupled to the executed oculomotor program but instead can be deployed unrestrictedly also toward locations to which no saccade can be executed. Our results are compatible with the view that covert and overt attentional orienting are guided by feedback projections of visual and visuomotor neurons of the gaze control system, irrespective of oculomotor limitations.

visual attention | saccades | premotor theory of attention

We are surrounded by far more visual information than we can process simultaneously. To ensure goal-directed behavior, we need to attend to the most relevant input, ignoring other aspects of the available information (1, 2). This attentional selection is usually achieved by a succession of rapid eye movements (saccades) toward the most crucial information of the visual scene (3). Interestingly, various studies demonstrated that spatial attention reaches a location of interest not only when the eyes arrive but already before they start to move (4–7), and it has been argued that this presaccadic attention shift is mandatory (4, 5). However, attentional selection can also occur in the absence of eye movements (8, 9), which raised the question of whether overt spatial attention (with eye movements) and covert spatial attention (without eye movements) are based on the same neural processes. Based on the oculomotor readiness hypothesis (10), the premotor theory of attention (11–14) states that both spatial attention and oculomotor processes rely on the same neural substrate, the oculomotor system, and that any shift of spatial attention is elicited by preceding motor activation. Indeed, the same brain structures are active during both overt and covert attention tasks (15, 16). These overlapping neuronal circuits include the parietal cortex, the frontal eye fields (FEFs), and the superior colliculus (SC)—oculomotor structures that form the so-called priority maps (17–19). Feedback signals arising within these structures projecting back to early visual areas (e.g., V1–V4) are assumed to enhance visual processing (19–21). Accordingly, subthreshold microstimulation of FEF and SC—which, if stimulated above threshold, would lead to the execution of a saccade—affects early visual processing (22) and biases spatial attention, as directly demonstrated by behavioral improvements at the movement field location of the stimulated neurons, such as

increased contrast or motion sensitivity (23, 24). However, since microstimulation likewise affects visual and motor cell activity, these studies demonstrate a link but no causal role of motor activity for attentional orienting.

Further evidence of a tight coupling between visual attention and the oculomotor system is based on patients who cannot perform eye movements as a result of cortical or subcortical lesions (25–27), peripheral oculomotor palsy (28), or limited elasticity of their eye muscles (29). These patients also seem to show attentional deficits. This deficit is reflected, for example, in a reduction of reaction time benefits normally observed when healthy participants have to detect a target at a cued compared with an uncued position (9). These results may suggest that any limitation of oculomotor processes, even at the level of the extraocular muscles, affects the proper functioning of cortical and subcortical oculomotor structures, causally biasing spatial attention.

Interestingly, similar effects were observed in healthy participants using the eye abduction paradigm to limit the range of possible saccades. In this paradigm, participants rotated their heads in the opposite direction of an exogenous cue, making saccades to it no longer possible. As a result, the exogenous cue attracted less or no attention, again indicated by extinguished reaction time benefits at the cued target and also by smaller deviations of the saccade trajectories away from the cued location (30–33). These effects are particularly remarkable, as such an absence of exogenous attention indicates that even a temporary inability to execute saccades affects the neural functioning of oculomotor structures driving attentional orienting. In this

Significance

Various studies have claimed that attention can only be deployed to where we can potentially make an eye movement. Here, we measured the ability to shift attention toward a cue presented within or beyond participants' oculomotor range. Participants rotated their head to the left (eye abduction), making a cue presented far to the right unreachable by their eyes but still visible. We found that attention was deployed toward the cue regardless of whether participants were able to look at it. This contradicts the results of earlier studies based on experimental or pathologic eye movement restrictions and supports the view that attention-modulating feedback from gaze control areas, relying on visual and visuomotor cell activity, is not bound by oculomotor limitations.

Author contributions: N.M.H., M.S., and H.D. designed research; N.M.H. performed research; N.M.H. analyzed data; and N.M.H., M.S., and H.D. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

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Data deposition: All files are available from the Open Science Framework database (<https://osf.io/a2vbd>).

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1813465116/-DCSupplemental.

Published online April 19, 2019.

regard, these and the above effects have been considered strong evidence for the claim that attention shifts depend on motor preparation. However, it is important to note that none of these studies experimentally determined and reliably monitored their participants' individual oculomotor range, nor did their paradigms include the preparation of a saccade—a methodological feature that can provide important insights into the interaction between spatial attention and the oculomotor system.

To test whether the deployment of visual attention is dependent on the ability to execute a saccade, we developed a paradigm that allowed us to disentangle these processes. For this purpose, we measured presaccadic orientation sensitivity at different locations within and beyond participants' oculomotor range. According to the rationale of earlier eye abduction studies, if motor programming precedes the deployment of visual attention, high sensitivity should be limited to locations reachable by the eyes. In contrast, we found high presaccadic sensitivity at cued locations, both within and beyond each participant's motor range. When participants aimed to saccade outside their oculomotor range, resulting in considerable saccadic undershoot, sensitivity at their actual saccade endpoint was not enhanced. Crucially, in a second task in which participants maintained fixation, the cue likewise captured visual attention, irrespective of whether it was potentially reachable by the eyes or not. These results clearly demonstrate that both covert visual attention and overt visual attention can reach beyond the oculomotor range.

Results

Participants rotated their heads about 35° to the left, preventing them from performing rightward saccades larger than 8° of visual angle. During each trial, we assessed visuospatial attention at one of four locations on the horizontal meridian ($\pm 6^\circ$ and $\pm 10^\circ$ relative to the central eye fixation) using a discrimination task based on oriented pink noise patches (34). The positions of the patches were chosen such that due to the leftward head rotation, the right proximal patch ($+6^\circ$) lay close to the edge but was still within the oculomotor range, while the right distal patch ($+10^\circ$)

lay beyond it (Fig. 1A). A cue was briefly flashed randomly at one of the four locations (Fig. 1C). The sudden onset of such a salient peripheral stimulus can be assumed to capture exogenous attention (9), leading to increased visual sensitivity at the cued compared with the noncued locations (35). If the deployment of attention relies on the ability to perform a saccade, a cue occurring outside their reach should not increase participants' discrimination performance at its location. Critically, in contrast to previous studies, while trying to discriminate the orientation presented at any of the four locations, participants were either instructed to make a saccade toward the cued location (saccade task) or to maintain fixation at the screen center (fixation task). Whereas the saccade task enabled us to monitor each participant's oculomotor range and to disentangle motor processes from visual attention, the fixation task allowed us to examine whether the results of the saccade task were specific to motor preparation or could be generalized to previous exogenous attention tasks (31–33).

We analyzed the head-tracking data to verify that each participant maintained a consistent level of rotation across trials and tasks. While the average amount of head rotation differed between participants (Fig. 1E; range: 30.2° – 43.0° ; mean: 35.3°), each participant maintained a consistent rotation angle over time (Fig. 1D) and within each block in both the saccade and fixation tasks (with the exception of one participant for whom the rotation angle had to be lowered between the saccade task blocks to ensure that the proximal location could be reached by the eyes).

To determine whether the head rotation manipulation indeed prevented eye movements to the right distal location, we analyzed the saccade landing positions obtained in the saccade task. Fig. 24 shows the distribution of saccade endpoints observed across participants as a function of the cue location. For targets within the oculomotor range (cue at -10° , -6° , and $+6^\circ$), 76.7% [73.2, 80.2] (mean [95% CI]) of the saccades ended within a radius of 1.5° around the target center (average landing errors for -10° : 1.25° [1.11, 1.39], -6° : 0.79° [0.59, 0.99], $+6^\circ$: 1.11° [0.99, 1.23]). This demonstrates that despite the uncomfortable

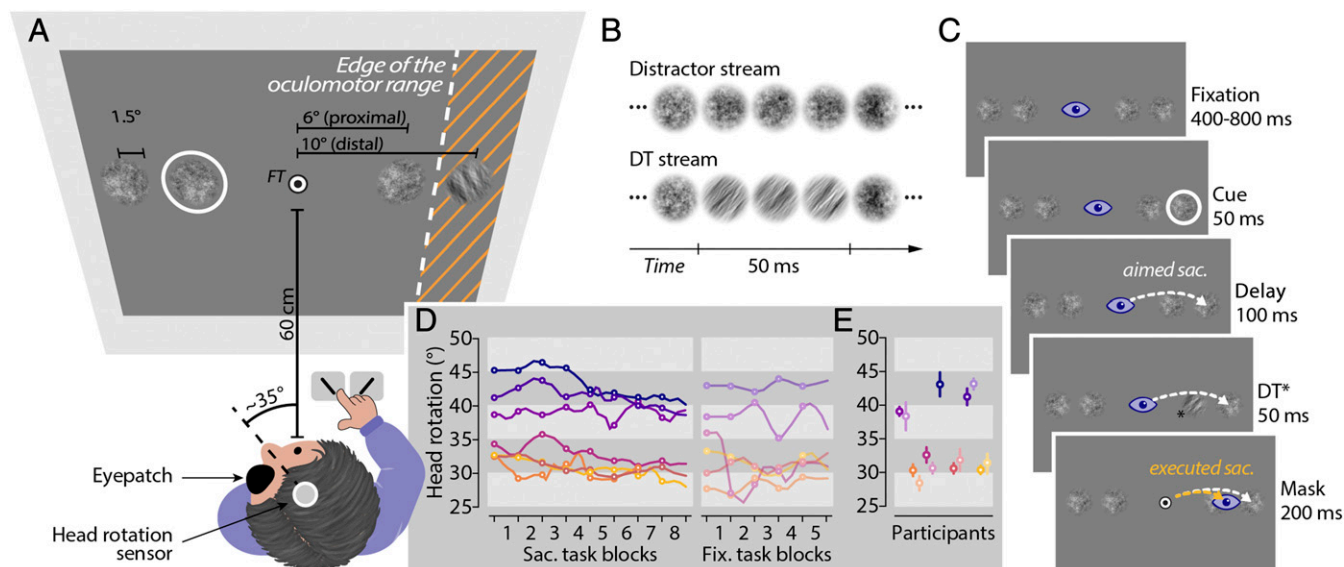


Fig. 1. Apparatus and procedure. (A) Participants viewed the stimuli with their left eye patched and their head rotated to the left. Four pink noise streams were presented on the screen horizontally, at two eccentricities (proximal: $\pm 6^\circ$ and distal: $\pm 10^\circ$) from the central FT. The right distal patch fell outside participants' oculomotor range. (B) Each pink noise stream consisted of a succession of randomly generated pink noise patches, flickering at 60 Hz. The DT stream included a sequence of orientation-filtered noise patches (50 ms), showing a 40° clockwise or counterclockwise tilt relative to the vertical axis. (C) After a fixation period, a circular white cue was flashed around one randomly chosen noise stream. In the saccade task, participants were instructed to make a saccade toward it and to report the orientation of the DT presented before saccade onset; in the fixation task they kept fixation at the FT (Movies S1 and S2). (D) Rotation angles over the time course of the saccade task (Left; eight blocks) and the fixation task (Right; five blocks). Each dot marks the beginning of a new experimental block; different colors show different participants. (E) Mean head rotation angle in the saccade (dark colors) and fixation (light colors) tasks for each participant. Error bars represent 95% confidence intervals.

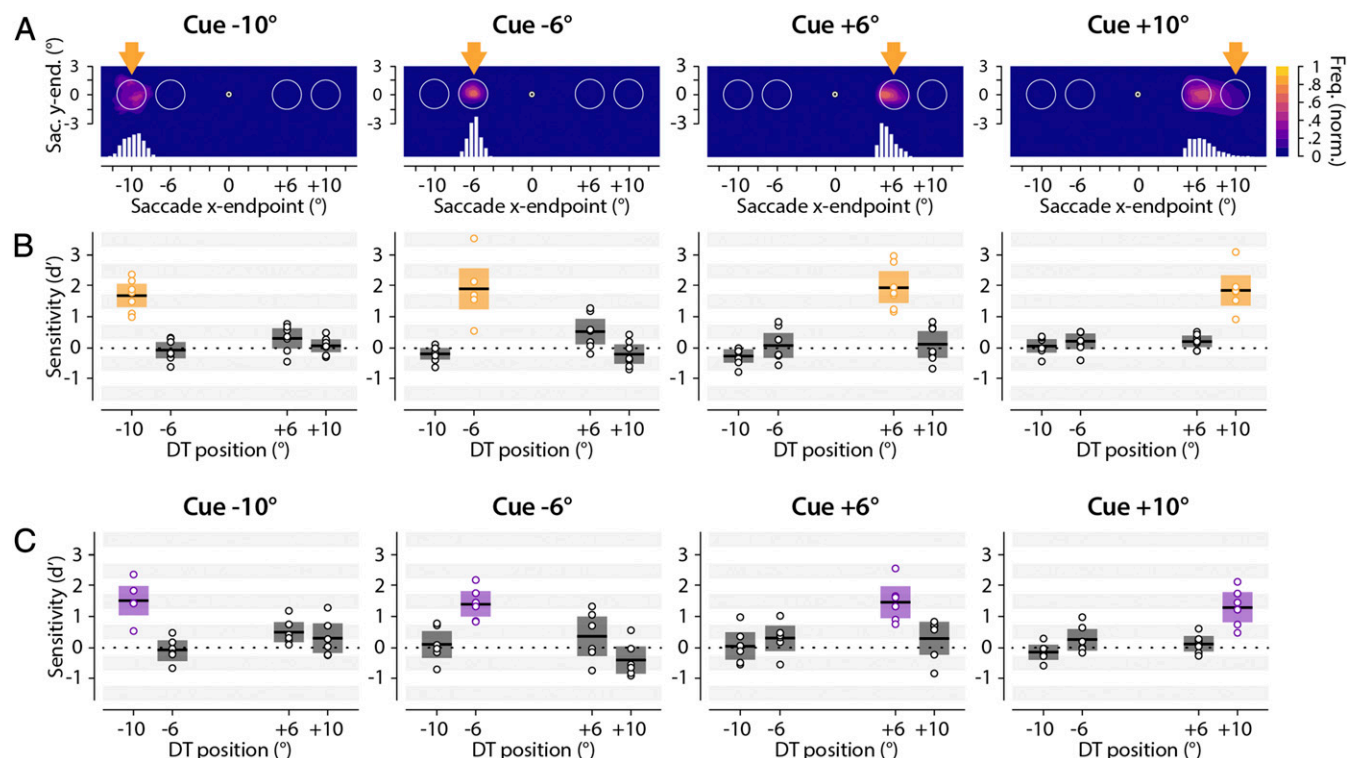


Fig. 2. Results of the saccade and fixation tasks. (A) Normalized saccade landing frequency maps averaged across participants as a function of the cue location (-10° , -6° , $+6^\circ$, and $+10^\circ$) in the saccade task. Histograms illustrate the normalized frequencies of horizontal saccade endpoints per cue location. (B and C) Visual sensitivity in the saccade task (B) and the fixation task (C) at the cued location (orange and purple whisker plots) and at the noncued locations (black whisker plots) as a function of the cue location. Horizontal lines within each whisker plot indicate the averaged visual sensitivity (d') at the respective DT position. Error bars depict 95% confidence intervals, dots represent individual participant data, and dashed lines mark chance level.

head rotation, participants were able to prepare precise saccades to these targets. However, when participants aimed to saccade toward the right distal target, we observed a consistent saccadic undershoot ($+10^\circ$: 3.60 [3.25, 3.95]). In these cases, saccades ended about 3° too short ($+6.95^\circ$ [6.52, 7.38]). Since the distal location could not be reached by the eyes in a large majority of trials (92.5% [88.8, 96.2]), this location can be considered to fall beyond participants' oculomotor range, which is the first requirement to investigate whether visual attention is limited to locations reachable by saccades. Saccade latencies did not differ as a function of the saccade target location (median latency of 225.4–238.9 ms; $0.715 > P > 0.111$).

A second requirement involves the measurement of presaccadic visual sensitivity at different locations within and beyond the participants' oculomotor range. Since we aimed to investigate presaccadic attention, the discrimination target (DT) was always presented during saccade preparation (DT offset was, on average, 54.9 ms [39.0, 70.8] before saccade onset). As shown in Fig. 2B, when the cue was shown within the oculomotor range, sensitivity for DTs presented at the cued location (DT@cue) was significantly increased compared with the average sensitivity observed for DTs presented at the three other noncued (DT@noncue) locations (cue -10° and DT@cue: 1.71 [1.32, 2.10] vs. DT@noncue: 0.10 [−0.06, 0.26], $P < 0.001$; cue -6° and DT@cue: 1.93 [1.26, 2.60] vs. DT@noncue: 0.06 [−0.08, 0.20], $P < 0.001$; cue $+6^\circ$ and DT@cue: 1.97 [1.44, 2.50] vs. DT@noncue: −0.06 [−0.32, 0.20], $P < 0.001$). Importantly, in contrast to a previous report using a similar design (33), we found the same attentional benefit when the cue was presented outside participants' oculomotor range (cue $+10^\circ$ and DT@cue: 1.88 [1.39, 2.37] vs. DT@noncue: 0.18 [0.06, 0.30], $P < 0.001$). Further analysis revealed that the majority of the undershooting saccades aimed toward the distal right target actually

landed at the proximal right location (within a radius of 1.5° from patch center; 62.2% [50.0, 74.4]). Crucially, for these trials, the spatial deployment of attention toward the cue at the distal location was dissociated from the actual saccade vector. If the deployment of attention is coupled to the executed saccade plan, we should observe an attentional benefit at the saccade endpoint. However, we found that when participants aimed to make a saccade to a cue presented outside their oculomotor range and landed too short, visual sensitivity at their actual saccade endpoint was not enhanced compared with the sensitivity at the other noncued locations (DT@ 6° : 0.22 [0.04, 0.40] vs. DT@ -10° : 0.07 [−0.14, 0.28] and DT@ -6° : 0.23 [−0.03, 0.48]; $0.895 > P > 0.254$). Rather, we observed an unaltered deployment of attention toward the intended but not reached saccade goal (DT@ 10° : 1.88 [1.39, 2.37], $P < 0.001$).

So far, however, our results cannot be directly compared with those observed in previous eye abduction studies (31–33), in which attention was assessed exclusively while participants kept fixation. Therefore, we conducted a second experiment wherein participants performed the same task but were instead instructed to continuously fixate on the screen center rather than preparing a saccade to the cue. Importantly, as in the saccade task, the cue was uninformative about the location of the discrimination target, and the most eccentric location on the right side of the screen ($+10^\circ$) lay outside the range reachable by saccadic eye movements. We observed a strikingly similar pattern of results (Fig. 2C). Even without programming a saccade to it, the cue captured visual attention, irrespective of whether it was shown within or beyond the participants' oculomotor range. Visual sensitivity for DTs presented at the cued location (DT@cue) was significantly increased compared with the average sensitivity of DTs presented at the other three uncued (DT@noncue) locations (cue -10° and DT@cue: 1.52 [1.04, 2.00] vs. DT@noncue: 0.26 [0.02, 0.51], $P < 0.001$; cue -6° and

DT@cue: 1.42 [1.00, 1.84] vs. DT@noncue: 0.06 [−0.30, 0.41], $P < 0.001$; cue +6° and DT@cue: 1.48 [0.97, 1.99] vs. DT@noncue: 0.22 [−0.16, 0.60], $P < 0.001$; cue +10° and DT@cue: 1.32 [0.83, 1.80] vs. DT@noncue: 0.12 [−0.02, 0.26], $P < 0.001$). The results of our two experiments demonstrate that neither covert attention nor the presaccadic shift of attention is limited to locations reachable by the eyes. Overall, the attentional modulation by the cue was less pronounced in the fixation task than in the saccade task, as indicated by lower average discrimination sensitivity at the cued locations (saccade task DT@cue: 1.74 [1.41, 2.08] vs. fixation task DT@cue: 1.41 [1.09, 1.73], $P = 0.191$). This nonsignificant trend might indicate that in the saccade task, in addition to the exogenous attention capture by the cue, oculomotor preparation shifted attention toward the cued motor target. A unilateral post hoc test revealed that when the cue was presented at a location unreachable by the eyes, oculomotor preparation toward it further boosted visual sensitivity (saccade task cue +10° and DT@cue: 1.89 [1.31, 2.46] vs. fixation task cue +10° and DT@cue: 1.32 [0.83, 1.80], $P = 0.029$).

Discussion

We found that an exogenous cue increased visual sensitivity regardless of whether it was presented within or beyond the oculomotor range. This effect was observed both when participants kept fixation and when they prepared a saccade toward a cue unreachable by the eyes. In other words, we found no evidence that attention is limited to locations reachable by saccades. This result directly conflicts with previous eye abduction studies reporting impaired visual attention at locations to which no eye movements could be performed (30–33), casting some doubt on the use of oculomotor patient studies (25–29) to validate a causal link between attentional and motor processes (11–13).

The supposed restriction of attention to the oculomotor range has been interpreted as strong evidence that motor activity must precede the deployment of attention. This assumption, however, was based on limited measurements and partially inconsistent evidence. First, previous studies deduced the spatial deployment of attention from the measurement of reaction times, which include the time for detecting the stimulus as well as decision- and response-dependent processes (36). Furthermore, a neurophysiological link between manual response times and oculomotor selection or activity is not established. In contrast, it is well known that spatial attention improves visual perception via oculomotor feedback projections converging onto earlier visual areas (17–24). Our psychophysical approach of measuring orientation sensitivity is therefore a more effective way to directly assess spatial attention. Second, our study measures visual attention at multiple locations within one hemifield. While previous work could not rule out a location-unspecific attentional facilitation broadly spreading across one side of view, our paradigm allows us to precisely map localized attention effects. Third, the previously reported restriction of attention by the oculomotor range has only been observed for reflexive or exogenous attention (25–29, 32, 33) and not for voluntary or endogenous attention (29, 31, 33). Even more puzzling, inhibition of return (an effect that follows reflexive attention shifts; ref. 37) was observed after presenting exogenous cues outside the oculomotor range (34). Previous studies also could not agree on whether visual attention at locations not reachable by eye movements is only reduced (30, 31) or eliminated (32, 33). Last but not least, in none of the previous eye abduction studies was participants' actual oculomotor range recorded and monitored. In our saccade task, we verified each participant's saccade reach across trials, and our results demonstrate that the head rotation angle required to prevent rightward saccades to the distal position differed substantially between participants (Fig. 1 *D* and *E*). In the fixation task, we applied this verified, participant-specific head rotation angle to ensure that the distal position did indeed lie outside each participant's oculomotor range. The cause

of the obvious discrepancy between our results and those from patient and abduction studies relying on reaction time measurements remains unclear. It would be interesting to directly compare manual response times and visual sensitivity in an eye abduction paradigm, as well as to apply our sensitivity-based methodology to patients suffering from eye movement disorders.

In our study, when participants aimed to make a saccade to a cue presented outside their oculomotor range, their saccade necessarily fell short. Critically, in this case, the spatial deployment of attention toward the distal cue was dissociated from the executed saccade vector, as the majority of saccades already terminated at the proximal position. By measuring the spatial distribution of visual attention before saccade onset as a function of the actual endpoint, we directly tested the link between the deployment of attention and oculomotor programming. If attention originates from the activation of a saccade plan (11–13), we should have observed an attentional benefit at the actual saccade endpoint. Our data, however, reveal that visual sensitivity was not enhanced at the endpoint of undershooting saccades. Instead, we found an unaltered deployment of attention toward the intended saccade target, verifiably presented outside each participant's oculomotor range. This double dissociation—the deployment of attention toward a point where the eyes cannot move, paired with a lack of attention where they actually went—demonstrates that attentional orienting is not necessarily coupled to the executed eye movement.

In line with our findings, it has been reported that exogenous attention capture is not necessarily linked to oculomotor activation and vice versa (38). Further consistent evidence comes from a study taking advantage of the fact that saccades naturally undershoot the aimed target. Deubel and Schneider (4) found that it is the intended saccade target, rather than the actual saccadic landing position, that receives the attentional benefit. Likewise, when investigating the spatial distribution of attention before the execution of averaging saccades, that is, saccades unintentionally landing in between two nearby saccade targets, Wollenberg et al. (39) found no boost in visual attention at the saccade endpoint. Instead, visual attention was allocated toward the two potential saccade targets, leading the authors to conclude that saccade averaging arises from unresolved target selection. Consistent with our results, these studies show that before saccades, attention is deployed to the intended location irrespective of the movement ultimately executed.

Attention shifts are assumed to arise through feedback activation from neural structures known to be related to oculomotor control, such as FEF, SC, and the lateral intraparietal area (LIP), to the extrastriate visual cortex (17–21). To explain our findings, we assume that eye abduction merely imposes a muscular and/or mechanical limitation that restricts the execution of saccades to an average amplitude of 7° but does not affect the neuronal functioning of oculomotor structures underlying attentional orienting. First, since oculomotor areas are retinotopically organized (40, 41), cells in these maps should still be able to encode larger saccades and thus trigger the deployment of attention. Second, it has been established that gaze shifts to targets far in the periphery are typically achieved by combined eye-head movements, both of which are controlled by oculomotor structures like FEF and SC (42, 43). As locations beyond the current oculomotor range can still be reached by such combined eye and head movements, the observed deployment of attention to locations falling outside the oculomotor range could well be triggered by cell activity within the respective oculomotor areas.

Previous reports of attention being limited by the oculomotor range were claimed to be strong evidence in support of the premotor theory of attention, which states that spatial attention arises from premotor activity in the oculomotor system (11–13). Our results, in contrast, show that attention is not limited by the oculomotor range. Does this argue against the premotor theory of attention? As argued before, motor target representation in

the oculomotor areas biasing spatial attention may not be affected by the limitation of saccade size due to eye abduction. Thus, motor-related activity in these areas would drive attention to the intended target location, rather than that finally reached by the undershooting saccade. Therefore, our results do not contradict the premotor theory of attention but clearly cast doubt on the findings of previous reports used to support it (30–33).

Indeed, consistent with our results, electrophysiological studies have shown that within FEF and SC—oculomotor structures that modulate visual processing via feedback projections to the visual cortex—motor cells remained silent during a covert attention task (44–46), while visual and visuomotor cells exhibited sustained attention-related activity. Furthermore, a recent study revealed that the feedback projections from FEF to early visual areas are mainly composed of neurons with memory delay period activity. Neurons with motor activity, in contrast, have disproportionately little input to the visual cortex, directly indicating that the modulatory input of oculomotor structures on visual processing does not emanate from motor cell activity (47).

We show that a salient peripheral stimulus attracts attention regardless of whether the eyes can reach it or not. Even when the goal is out of reach, attention shifts to the intended saccade goal or exogenously cued location, independent of the ultimately executed saccade program. Visual attention is therefore not bound to the oculomotor range.

Materials and Methods

Participants. Seven participants (four females and three males, ages 22–30 y, one author) completed the saccade task, and six of them also participated in the fixation task. All participants had normal vision and, except for one author (N.M.H.), were naive to the purpose of the experiment. The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München and conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent.

Apparatus. Head rotation was recorded via a single sensor of a Polhemus Liberty 240/8 electromagnetic motion tracking device (Polhemus Inc.) and a personal toolbox. The sensor was attached on top of participants' heads, using an EEG cap (position CZ, i.e., the vertex top of the head). The exact amount of head rotation was determined individually at the beginning of the saccade task and adjusted during the experiment when necessary to ensure that each participant's oculomotor range ended in between the right proximal ($+6^\circ$) and distal ($+10^\circ$) locations. In the fixation task, we applied each participant's average head rotation angle obtained in the saccade task. Eye position of the dominant right eye was recorded using an EyeLink 1000 Tower Mount eye tracker (SR Research) at a sampling rate of 1 kHz. The eye tracker was calibrated with the head rotated at the beginning of the experiment and whenever the head was moved. Calibration targets were presented within 8° from fixation, such that they fell within participants' oculomotor range. According to SR Research, the eye tracker used allows precise tracking of the eye position within the range required for our paradigm (up to $\sim 12^\circ$ on the horizontal axis). Manual responses were recorded via a standard keyboard. The experimental software controlling display, response collection, and eye and head tracking was implemented in Matlab (MathWorks) using the Psychophysics Toolbox (48, 49) and EyeLink Toolbox (50) running on a Dell Precision T1500 Intel Core i5 computer (Round Rock). Stimuli were presented at a viewing distance of 60 cm on a 21-in Sony GDM-F500R CRT screen (Tokyo) with a spatial resolution of 1,024 by 768 pixels and a vertical refresh rate of 120 Hz.

Experimental Design. Participants sat in a dimly illuminated room, with their left eye patched and their head rotated about 35° to the left, positioned on a chin rest (Fig. 1). Each trial began with participants fixating on a central fixation target (FT) comprising a black (~ 0 cd/m 2) and white (~ 120 cd/m 2) bull's-eye (radius = 0.25°) on a gray background (~ 60 cd/m 2). Once stable fixation was detected within a 2.0° -radius virtual circle centered on the FT for at least 200 ms, four pink (1/f) noise streams (radius = 1.5°) appeared on the horizontal axis at -10° , -6° , $+6^\circ$, and $+10^\circ$ relative to the FT (positive values correspond to the right side of the screen). Each noise stream consisted of randomly generated noise patches (mean luminance = ~ 60 cd/m 2) windowed by a symmetrical raised cosine (radius = 1.5° , sigma = 0.5°), refreshing at 60 Hz (Fig. 1B). After a random fixation period between 400 and

800 ms, a cue (white annulus, radius = 1.5° , ~ 120 cd/m 2) was flashed for 50 ms around one randomly selected noise stream. In the saccade task, participants were instructed to perform an eye movement to the cued noise stream upon cue onset. Note that cues flashed at $+10^\circ$ fell outside the oculomotor range due to the head rotation. In the fixation task, participants continuously kept fixation at the FT. One hundred milliseconds after cue onset the DT was presented. The DT consisted of an orientation-filtered noise stimulus, displaying a rotated pattern, tilted 40° clockwise or counterclockwise relative to the vertical. The DT was equally likely to appear within any of the four noise streams and was masked by the reappearance of nonoriented noise patches 50 ms later. Two hundred milliseconds after DT onset the noise streams disappeared, and participants reported the orientation of the DT via button press. They were informed that the DT would appear randomly at any of the four positions and that their orientation report was nonspeeded (they were instructed to take their time to rest and blink before initiating the next trial by giving their response). They received auditory negative feedback for incorrect responses.

Participants performed eight (saccade task) and five (fixation task) experimental blocks of at least 100 trials each. The saccade task comprised more blocks because the corresponding analysis required the data to be split according to the landing position of the saccade. The trial number per block was kept low, and participants took breaks after each block to ensure maximum comfort despite the unusual head position. In the saccade task, we controlled online for incorrect eye fixation (outside 2.0° from the FT before the cue onset), too short (<130 ms) or too long (>400 ms) saccade latency, and incorrect eye movements (saccade landing beyond 2.0° from a motor target within participants' oculomotor range). In the fixation task we checked for correct eye fixation throughout each trial, and participants received auditory feedback whenever their eye position left a radius of 2.0° around the FT. Incorrect trials were repeated in random order at the end of each block. Participants repeated, on average, 23.8% [16.7, 30.9%] of the saccade task trials, and 5.4% [3.2, 7.7%] of the fixation task trials. Following the instructions, participants performed a negligible number of saccades in the fixation task (on average, in 1.1% [0.3, 2.0%] of the trials), and none of these landed at the cued location.

To maintain a consistent level of discrimination difficulty across participants, a threshold task preceded the saccade task. The threshold task visually matched the main experiments, but participants did not rotate their head and were instructed to keep their gaze on the fixation target. Furthermore, participants were informed that the DT would always be presented at the cued location. We used a procedure of constant stimuli and randomly selected the orientation filter strength (corresponding to the visibility of the orientation tilt) out of five linear steps of filter widths. By fitting cumulative Gaussian functions to the discrimination performance gathered in this threshold task, we determined the filter width corresponding to 80% correct discrimination performance and used this value for both tasks.

Eye and Head Data Preprocessing. For the saccade task, we scanned off-line the recorded eye position data and detected saccades based on their velocity distribution (51) using a moving average over 20 subsequent eye position samples. Saccade onset and offset were detected when the velocity exceeded or fell below the median of the moving average by 3 SDs for at least 20 ms. We included trials if a correct fixation was maintained within a 2.0° radius centered on the FT until cue onset and landed within 2.0° of the cued location (or within 5.5° for the cued location outside the oculomotor range) no later than 400 ms following cue onset and if no blink occurred during the trial. We excluded trials with head movement artifacts (rotation angle not within 3 SDs from average head rotation). Due to this criterion, two experimental blocks of one participant were excluded from data analysis. In total we included 7,670 trials in the analysis of the behavioral results (on average, 669.14 trials per participant in the saccade task and 497.66 trials per participant in the fixation task). To visualize the head rotation data (Fig. 1D), we filtered the rotation angle by using a moving average filter of 180 s.

Behavioral Data Analysis. We determined the sensitivity to discriminate the test orientation (d'): $d' = z(\text{hit rate}) - z(\text{false alarm rate})$ separately for each location, depending on the saccade target location. To do so, we took the percentage of correct signal discrimination as the hit rate; the false alarm rate we computed by dividing the percentage of incorrect signal discrimination by the number of potential incorrect choices. Corrected performances of 99% and 1% were substituted if the observed proportion correct was equal to 100% or 0%, respectively. Performances below the chance level ($d' = 0$ corresponding to 50%) were transformed to negative d' values.

Whisker plots to visualize the data show single-participant sensitivity (represented by dots) that we averaged across participants (represented by

black lines), as well as the 95% confidence interval (indicated by colored bars). For all statistical comparisons we resampled our data and derived *P* values by locating any observed difference on the permutation distribution (difference in means based on 1,000 permutation resamples). All files are available from the Open Science Framework database (52).

ACKNOWLEDGMENTS. We are grateful to the members of the H.D. laboratory for helpful comments and discussions, in particular Franziska Schroter. This research was supported by grants of the Deutsche Forschungsgemeinschaft (DE336/6-1 and GI964/1-1, to H.D.) and by a Marie Skłodowska Curie individual fellowship to M.S. (704537).

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