nature neuroscience

Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention

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The analysis of a peripheral visual location can be improved in two ways: either by orienting one's gaze (usually by making a foveating saccade) or by 'covertly' shifting one's attention to the peripheral location without making an eye movement. The premotor theory of attention holds that saccades and spatial shifts of attention share a common functional module with a distinct neuronal basis. Using single-unit recording from the brains of trained rhesus monkeys, we investigated whether the superior colliculus, the major subcortical center for the control of saccades, is part of this shared network for attention and saccades. Here we show that a distinct type of neuron in the intermediate layer of the superior colliculus, the visuomotor neuron, which is known to be centrally involved in the preparation of saccades, is also active during covert shifts of attention.

To improve the visual analysis of behaviorally relevant objects, we and other primates make spatially accurate saccades to move the images of such objects onto the fovea. However, well before such saccades are executed, the visual system has already given priority to the visual information originating from the object and its spatial location by a filtering mechanism referred to as attention. Such covert shifts of attention to new spatial locations can be made without overtly shifting attention by saccades[1,2]. Saccades, however, seem to be contingent on preceding covert shifts of attention that define the target of the upcoming saccade[3–6]. In view of this tight link between covert and overt shifts of attention, the premotor theory of attention[7,8] holds that both might be based on a common shift plan. When searching for the neuronal basis of covert shifts of attention, one of the candidate structures to consider is the superior colliculus. The superior colliculus is the major subcortical center for the control of saccades and related forms of motor behavior (such as head, trunk or hand movements) that allow subjects to orient overtly toward objects of interest[9]. The superior colliculus comprises different layers with specific functional roles. Whereas the superficial layer of the superior colliculus consists of neurons that respond to visual stimuli located in distinct parts of the visual field, the intermediate layer below contains various types of neurons involved in saccade target selection[10–15] and saccade generation[16].

Electrical microstimulation at sites in the intermediate layer evokes saccades to well-defined locations in the visual field[17]. It has been suggested that the intermediate layer might contribute to covert shifts of attention and, moreover, might house the common shift plan[18]. This idea is based on the fact that the direction of microstimulation-evoked saccades is shifted in the direction of a cued target for a saccade or, alternatively, a hand movement, provided the spatial cue precedes the electric stimulus. This observation seems to indicate that a shift of attention associated with the preparation of a saccade can change the saccade vector unleashed by microstimulation. However, an alternative interpretation is that the interaction between two different motor intentions—one evoked by stimulation, the other based on spatial cueing—causes the directional shift in the saccade or hand movement.

In an attempt to resolve this ambiguity, we designed an experiment in which we could induce shifts of attention and intentions for eye movements in orthogonal directions while recording from neurons in the superior colliculus. Here we present evidence that a distinct type of neuron in the monkey superior colliculus, the visuomotor neuron, known to be centrally involved in saccade preparation, is also an important constituent of the network supporting covert shifts of attention. Superior colliculus visuomotor neurons, unlike superior colliculus visual or motor neurons, are active at the time monkeys covertly shift attention to the future location of an item to be foveated, provided the location is indicated by spatially precise cues rather than by symbolic information.

RESULTS

We induced shifts of attention in two rhesus monkeys by cueing the location of a Landolt-C optotype ("C"). The subsequent task was to distinguish the orientation of the C and to respond by making a saccadic eye movement (**Fig. 1a**). The Cs were randomly presented in one of two possible locations at equal distances from the fovea. Varying their size according to a staircase procedure allowed us to determine the minimal resolvable size of the C gap, a measure of visual acuity (**Fig. 1b**). Cueing the future position of the C by a spatially precise spot of light, presented 400–600 ms before the C appeared, led to a significant improvement of acuity on the order of 15% in both monkeys, independent of visual field eccentricity ($P < 0.05$, two-way ANOVA, main effect of cueing; all other comparisons, n.s.; **Fig. 1c,d**). This improvement of acuity indicated that the cue had indeed caused a shift of attention to the cued location[19].

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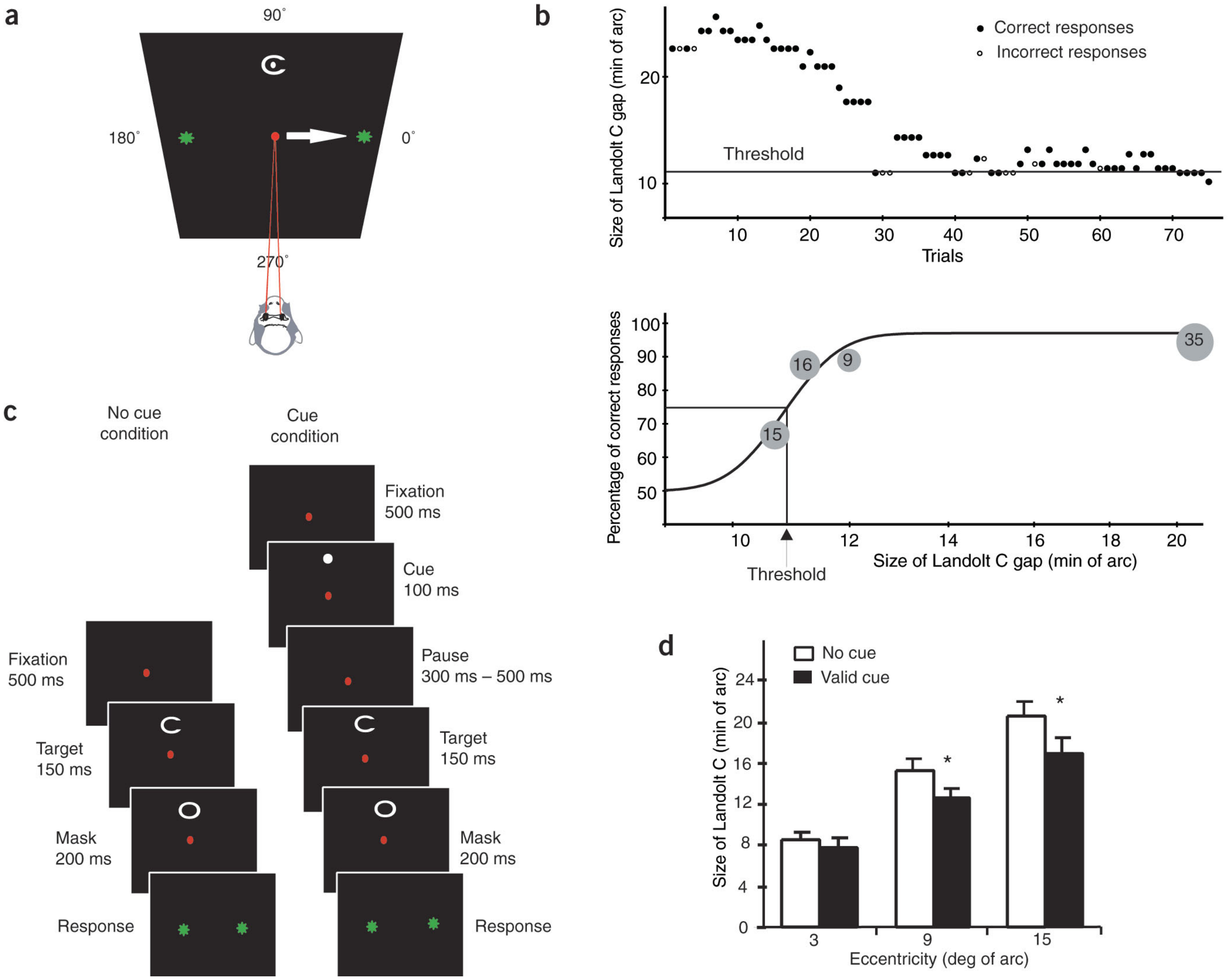

Figure 1 Spatially precise cueing improves visual acuity. (**a**) Monkeys fixated on the central fixation point (red) to initiate each trial. Then a small cue dot (white) appeared in the spatial location where the Landolt-C target would subsequently appear in two alternative orientations. Orientations of the C were orthogonal to the axis connecting the two possible locations of presentation. Monkeys were trained to discriminate the C's orientation and to indicate their decision by making a saccade toward one of two green spots—in the direction representing the perceived orientation of the C. The cue dots and Cs were presented either inside the receptive field of a given neuron or opposite to it at the same eccentricity (50% each, randomized). (**b**) Upper plot, the size of the C was varied according to a PEST staircase procedure[33], which converged on the smallest resolvable C (threshold). Lower plot, percentage of correct responses plotted as a function of C size and plotted by a Probit function. Numbers within the shaded circles specify the number of trials underlying that data point. (**c**) Presentation sequence for cue and no-cue trials, which were randomly interleaved. (**d**) Acuity for three retinal eccentricities with and without valid cueing. The improvement of acuity increased with eccentricity in absolute terms, although the percent increase in acuity was independent of eccentricity.

While two monkeys performed this 'shift of attention task,' we recorded from different types of neurons in the superior colliculus. We used a 'memory saccade task' to elicit shifts of attention into the receptive field of a given neuron: remembered targets were presented in various parts of the visual field and the neuronal responses also allowed us to categorize the superior colliculus neurons encountered. To this end, we compared the relative weights of the different response components—namely the visual response evoked by the peripheral target, the discharge in the 'memory' period between target offset and saccade onset, and the saccade-related response—using a *k*-means cluster analysis[20]. This analysis distinguished five groups of superior colliculus neurons: those with predominantly visual responses (visual neurons, $n = 38$), those with predominantly motor responses (motor neurons, $n = 19$) and three groups of neurons with varying combinations of visual, memory and motor activity, which we pooled into the category of visuomotor neurons ($n = 44$) for the analysis of the responses obtained in the attention task.

In the memory saccade protocol (**Fig. 2**, column I) with the saccade target falling into the preferred spatial region of a given neuron, the visual neuron (**Fig. 2a**) showed a strong visual burst, evoked by the saccade target. The motor neuron (**Fig. 2c**) showed a pure saccade-related burst, and the visuomotor neuron (**Fig. 2b**) exhibited a broad visual response, merging into a comparatively extended motor response. The same neurons responded type-specifically in the attention task, when one of two circumstances occurred: the C and the subsequent mask were presented in the preferred spatial region either

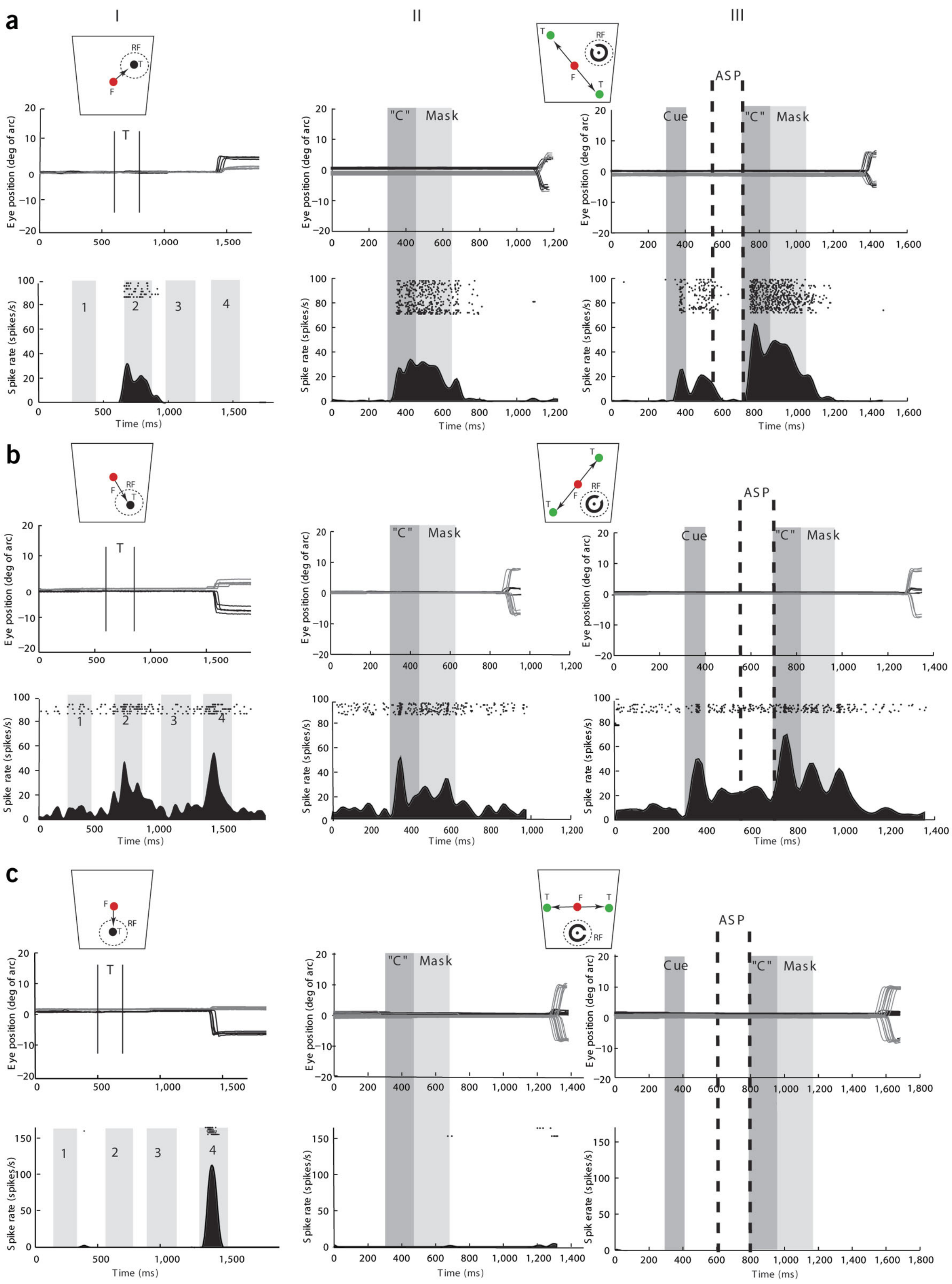

Figure 2 Representative examples of the three groups of superior colliculus neurons distinguished: (**a**) visual neuron, (**b**) visuomotor neuron (**c**) motor neuron. The left panels (column I) depict the responses observed when the monkeys carried out memory-guided saccades to the receptive/movement field of a given neuron. The middle panels (column II) show the discharge in the attention task without cueing, and the right panels (column III) illustrate the responses in the attention task when the position of the C was cued by a spatially precise cue. The neuronal responses shown are based on those 50% of trials in which the cue and the C appeared inside the neuron's receptive field. The upper part of each panel shows records of the horizontal (gray) and vertical (black) components of the eye movements for several trials, and the lower part represents the neuronal activity for the same trials in the form of a raster plot and peristimulus time histogram. The "T" in column I indicates the interval during which the peripheral target was on. The gray vertical bars marked 1, 2, 3 and 4 define the periods of time underlying the quantification of response components (see Methods). The vertical dashed lines before the presentation of the C in column III demarcate the 'attention shift period' (ASP). Cartoons show the relative positions in space of the fixation dot (F), cue (small black dot), C, response targets (T) and the cell's receptive field (dashed circle).

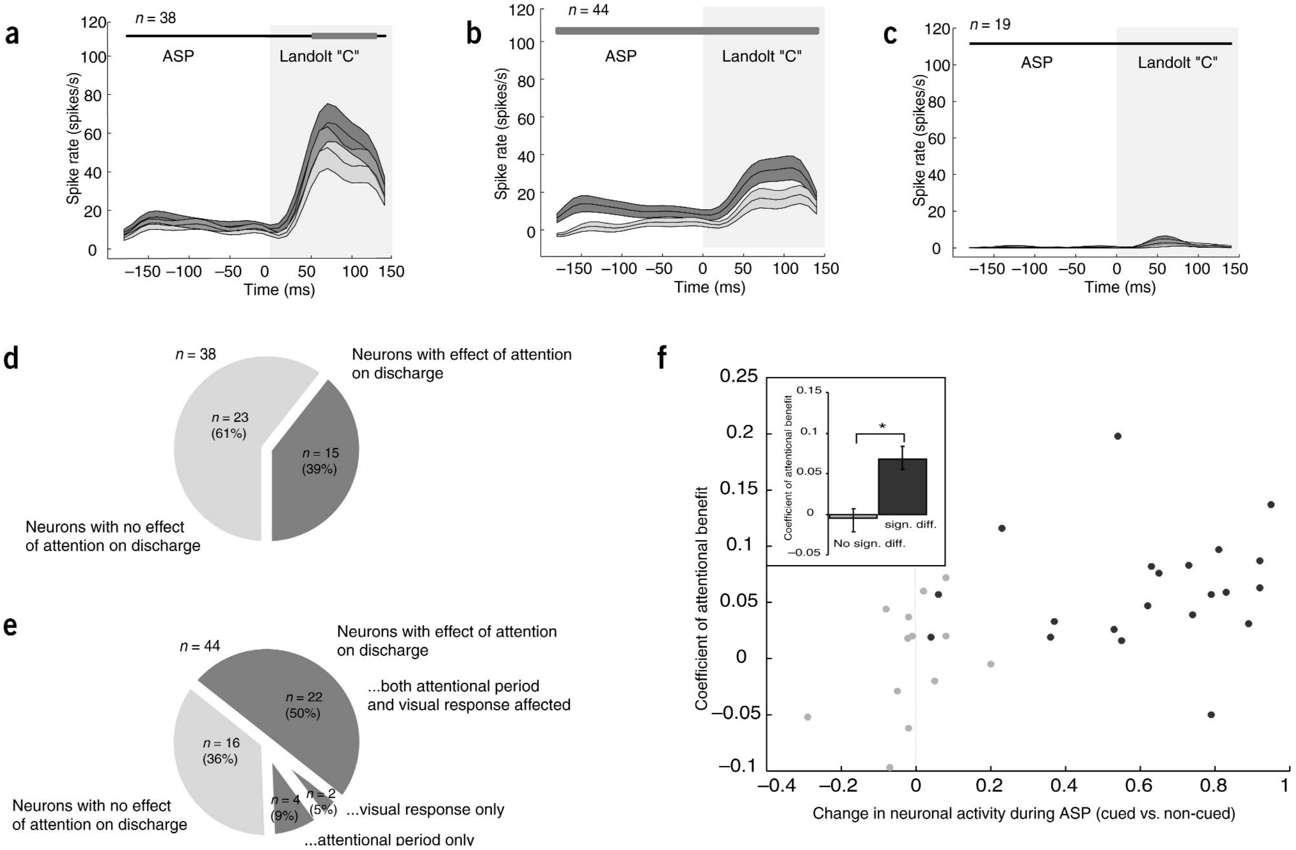

Figure 3 Population responses of superior colliculus neurons (from both monkeys) for shifts of attention induced by spatially precise cueing: (**a**) visual, (**b**) visuomotor and (**c**) motor neurons. Time 0 marks the onset of the C. The black curves within light gray boundaries (± s.e.m.) represent the population mean for non-cued trials; the curves within dark gray boundaries (± s.e.m.) represent the mean for cued trials. The trace above the curves is thick gray for periods of time in which there was a significant difference between cued and non-cued trials; the trace is thin black otherwise. (**d**,**e**) Pie charts showing proportion of visual (**d**) and visuomotor (**e**) neurons for which spatial cueing significantly affected spike rate. (**f**) The scatter plot represents the relationship between changes of neuronal activity in the ASP and changes in the influence of attention as captured by the coefficient of attention benefit (CAB) for visuomotor neurons. The change of neuronal activity in the ASP is calculated according to the formula mean activity$_{\text{cued}}$ – mean activity$_{\text{non-cued}}$ / mean activity$_{\text{cued}}$ + mean activity$_{\text{non-cued}}$. Light gray symbols represent neurons in which cueing did not cause statistically significant changes in ASP-related activity, and dark gray symbols represent neurons in which the cue prompted increased responses during the ASP. The coefficient of correlation calculated for the neurons with versus without significant changes during ASP was $r = 0.49$ ($P = 0.003$). Inset shows the mean (± s.d.) CAB for the group of visuomotor neurons without (left) and with (right) significant effects of cueing on their ASP-related response, their visual response or both (*$P = 0.002$, ANOVA).

without a preceding cue (**Fig. 2**, column II) or preceded by a valid spatial cue (**Fig. 2**, column III). The cue was visible for 100 ms, and there was a pause of 300–500 ms from the offset of the cue to the onset of the C, depending on the experiment (see Methods). The visual neuron showed short-latency visual responses to both the cue and the C. Moreover, the visual response to the C was significantly enhanced by cueing. The motor neuron maintained its baseline level of discharge throughout the whole trial. The absence of a response to the indicative saccades made by the monkey close to the end of the trials was expected, given that these saccades were always made along an axis orthogonal to the preferred direction of the neuron. Note, however, the absence of a significant discharge in the 'attention shift period' (ASP): the 200-ms period before the onset of the C. During the ASP, the monkey shifted his attention to the cued spatial location, congruent with the movement field of the neuron. Visuomotor neurons (**Fig. 2b**) showed visual responses to both the cue and the C, and similar to visual neurons, visuomotor neurons also showed an enhancement of the latter by cueing. However, unlike visual and motor neurons, visuomotor neurons also showed a clear activation (increase in mean discharge rate) during the ASP. To determine whether cueing had specific differential effects on the three groups of neurons, we calculated population averages for a period from 200 ms before onset of the C until the onset of the mask, separately for trials with and without cueing. We then compared the averages bin by bin using a running paired *t*-test. Visual neurons showed a significant enhancement by cueing which reached a maximum of 32.9% at 90 ms after the onset of the C. The mean enhancement (± s.d.) in a period from 60–120 ms after C onset, the period for which the group averages differed significantly, was 21.4 ± 9.5% (**Fig. 3a**). This observation is in accordance with several previous studies of the superior colliculus[1,21–23] showing that attention facilitates responses of visual neurons. Visuomotor neurons showed an even stronger enhancement of the C response by cueing (maximum of 44.7% after 80 ms, mean difference during the 60–120 ms period after C onset, 40.7 ± 6.6%; **Fig. 3b**). However, unlike visual neurons, they also showed a significant activation by cueing during the ASP. Finally, motor neurons

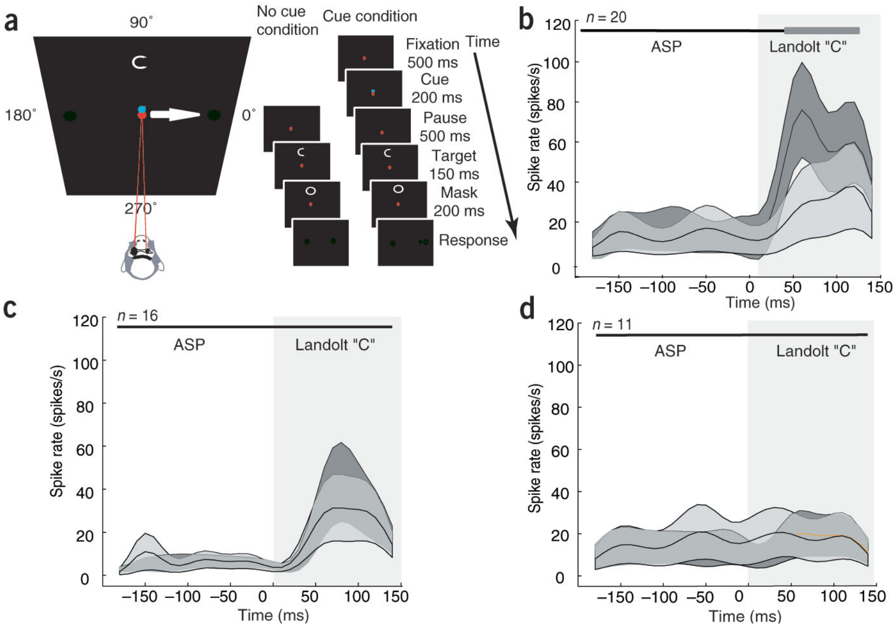

Figure 4 Population responses of superior colliculus neurons for shifts of attention induced by quasi-symbolic cueing of relevant spatial location. (**a**) A small dot presented next to the fixation point determined the direction in which the C would appear 500 ms later at an eccentricity the monkey was able to learn because the eccentricity was kept constant over many trials. The C was presented randomly either inside the receptive field of a given neuron or opposite to it at the same eccentricity (50% each). Trials with and without cue were presented randomly. (**b**–**d**) Population responses of visual (**b**), visuomotor (**c**) and motor (**d**) superior colliculus neurons. Time 0 marks the onset of the C. The black curves within light gray boundaries (± s.e.m.) represent the population mean for non-cued trials; the curves within dark gray boundaries (± s.e.m.) represent the mean for cued trials. The trace above the curves is thick gray for periods of time in which there was a significant difference between cued and non-cued trials; the trace is thin black otherwise.

showed very little activity throughout the whole trial, with no significant difference between trials with and without cueing (**Fig. 3c**). The population responses (**Fig. 3a–c**) were based on neurons obtained from both monkeys. To determine whether neurons from both monkeys contributed similarly to the effects of cueing on visuomotor neurons, we calculated for each neuron the percentage of cueing-induced increase in discharge during the ASP and the subsequent visual response. These two discharge variables were then subjected to a 2-way ANOVA with the main factor 'monkey' and the two discharge variables as a repeated measure factor. ANOVA yielded a signi-ficant effect of cueing on the two discharge variables ($P < 0.05$), but did not reveal any significant difference between the two monkeys ($P > 0.05$), indicating that cueing affected visuomotor neurons similarly, on average, in the two monkeys.

When considering individual neurons, the effects of cueing on the visual responses of visual and visuomotor neurons and the ASP-related discharge of visuomotor neurons varied from neuron to neuron and reached significance in only a portion of the neurons in each group. Only 39% of the visual neurons showed a significant enhancement, with cueing, of the C-evoked visual responses (**Fig. 3d**). Altogether, 64% of visuomotor neurons exhibited a significant response enhancement by cueing in either the ASP in the visual response period only or in both (**Fig. 3e**). To test whether the individual differences in the strength of the ASP-related discharge of visuomotor neurons reflected differences in the reallocation of attention, we compared the single-neuron responses with changes in performance modified by attention. To this end, we calculated neuron-specific acuity thresholds, separately for cued and for non-cued trials, by restricting the psychometric analysis to trials collected during recording from an individual neuron. Based on the acuity thresholds for cued and for non-cued trials, we calculated a coefficient of attentional benefit (CAB) from cueing: CAB = ($\text{acuity}_{\text{non-cued}} \times \text{acuity}_{\text{cued}} / \text{acuity}_{\text{non-cued}} + \text{acuity}_{\text{cued}}$). This coefficient captures the amount of attentional modulation for the period of time during which we recorded from an individual neuron. The mean CAB was positive, indicating an improvement of acuity by attention, for the group of visuomotor neurons showing a significant difference in discharge during the ASP, during the visual response period, or during both. In contrast, the mean CAB did not deviate from zero for the other group of visuomotor neurons whose discharge was not affected by cueing (**Fig. 3f**). The fact that the animals' improved performance depended on changes in ASP-related activity of visuomotor neurons indicates that the ASP-related activity is not simply a prolonged visual response to the cue, independent of shifting attention. Rather, the association suggests a causal relationship between the ASP-related response and perception or, alternatively, a common dependence of both ASP-related activity and perception on an unknown third process.

In the first experiment, spatial shifts of attention were induced by spatial cues. However, cues do not necessarily have to be spatial in order to induce precise shifts of spatial attention, provided they can be associated reliably with distinct spatial coordinates. In a second experiment, we tested whether the ASP-related response of visuomotor neurons is contingent on spatially precise cueing. To this end, we used a dot cue presented adjacent to the fixation point in a location which pointed in the direction of the future location of the C, without providing any information about its eccentricity (**Fig. 4a**). The only way to generate spatially accurate shifts of attention based on such a 'quasi-symbolic' cue is to learn the correct amplitude over the first trials of a block (which usually contains ~200 trials) by retrieving the eccentricity of the C, which was kept constant for a given neuron, corresponding to the location of its receptive field (**Fig. 4a**). That monkeys indeed learned to use such quasi-symbolic cues to shift attention in a spatially precise manner was indicated by the spatially circumscribed changes in acuity we observed. The improvement of visual acuity in cued trials as compared to non-cued trials amounted to 12% on average. It was confined to a narrow spatial zone around the location of the C, as revealed by displacing the C relative to the cued location in 20% of the cued trials (**Fig. 5a**). The difference in acuity for valid cues and for displaced cues was plotted as a function of the displacement angle α (**Fig. 5b**). The Gaussian curve fitted to the data points for quasi-symbolic cueing, shown in black, intersects the level of acuity given if no cue is provided at an α of $\pm 11°$. For $|\alpha| < 11°$, the cued acuity is better than the acuity without cue, whereas for $|\alpha| > 11°$, the cued acuity is actually worse. The profile for spatial cueing (**Fig. 5b**) is qualitatively very similar: cueing leads to an improvement of acuity within a central zone, which, as indicated by an $|\alpha|$ of 3°, is considerably smaller than

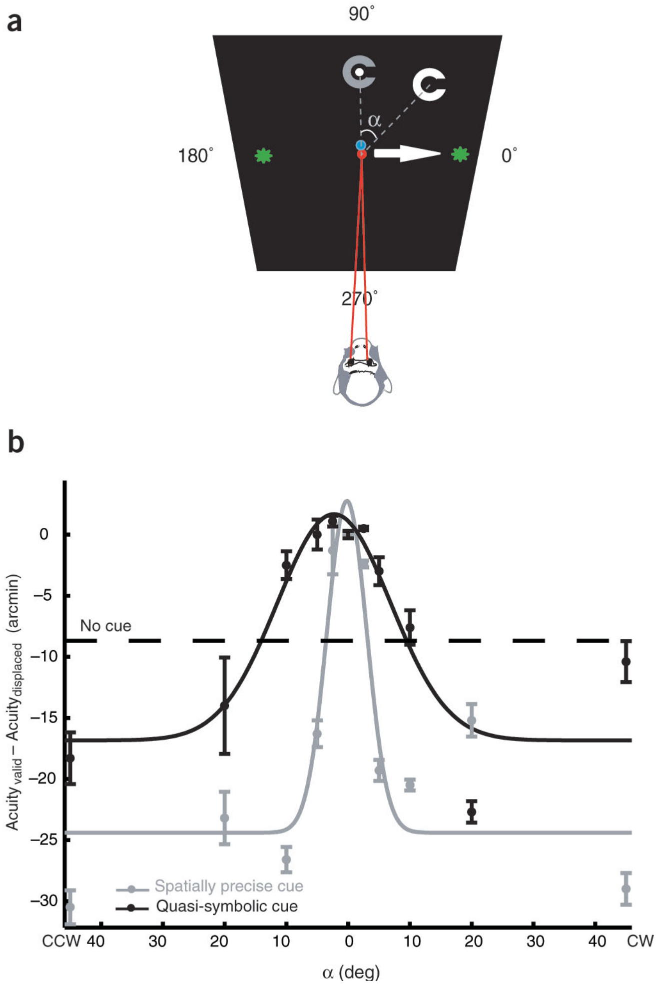

Figure 5 The size of the 'spotlight of attention' is spatially restricted. (**a**) In 20% of trials, the location of the Landolt-C (shown in white) was displaced relative to the expected location (C shown in gray). The expected location was either indicated by a spatially precise cue (white dot) or, in the case of quasi-symbolic cueing suggested by associating the quasi-symbolic cue (blue dot) with the dominating location of the Landolt-C. The C appeared at a fixed eccentricity of 9°, but in different directions relative to the fixation point as given by the displacement angle α ($\alpha = \pm 2.5°$, 5°, 10°, 20° and 45°). (**b**) Plot of a measure of attentional modulation of perception as function of α. The measure on the ordinate is the difference in acuity obtained for fully valid (*e.g.*, no spatial offset) cues and the acuity for a cue displaced by α. The dashed line labeled "no cue" gives the average acuity in the absence of any cue. Black symbols and curves, quasi-symbolic cueing; light gray symbols and curves, spatially precise cueing. The curves fitted to the individual data points are Gaussian functions [$f(x) = a \times \exp(-((x-b)/c)^2) + d$] with $a = 18.52$, $b = -2.293$, $c = 13$, $d = -16.84$, $r^2 = 0.8572$ in the case of quasi-symbolic cueing, and $a = 27.16$, $b = -0.2035$, $c = 4.556$, $d = -24.4$, $r^2 = 0.8449$ for spatially precise cueing. Vertical bars indicate s.e.m.

the corresponding zone for quasi-symbolic cueing. Also for spatial cueing, this central 'spotlight of attention' region is flanked by a surround, in which acuity is actually deteriorated by shifting attention into the wrong location. In summary, although the spotlight of attention was clearly wider when based on quasi-symbolic cueing, it was still surprisingly circumscribed.

In the second 'quasi-symbolic cueing' experiment, we tested 20 visual, 16 visuomotor and 11 motor superior colliculus neurons whose responses in the peripheral cueing experiment had been assessed. Visual (**Fig. 4b**) and motor (**Fig. 4d**) neurons showed population discharge patterns that were similar to those seen during cueing with spatially precise information. Whereas motor neurons did not show task-related changes, visual neurons showed an enhancement of the C-evoked responses by cueing. In contrast, visuomotor neurons lacked both the enhanced visual responses as well as the significant enhancement of the ASP-related activity characterizing their responses during spatially precise cueing (**Fig. 4c**). In other words, visuomotor neurons are involved in shifting spatial attention only when prompted by precise spatial cues.

DISCUSSION

Using methods that allowed us to shift spatial attention reliably to circumscribed locations in the visual field, we could identify very specific involvements of different types of neurons in the monkey superior colliculus. These types of neurons were differentiated by a cluster analysis of their responses in a memory saccade task that allowed us to separate visual and motor response components and to measure discharge during the time between the disappearance of the peripheral target and the execution of the saccade. Out of the three types of superior colliculus neurons distinguished in this way—visual, motor and visuomotor neurons—only motor neurons lacked any discharge in the two tasks that involved shifts of spatial attention. These neurons were active when saccades were made into their well-defined motor fields, but they maintained their background discharge rate when attention was shifted covertly, or without an eye movement, toward their motor fields. Visual neurons, with purely visual discharge, as well as visuomotor neurons, with both visual and nonvisual responses, showed an enhancement of their visual responses following a shift of attention into their receptive fields. An attention-based enhancement of the responses of visual neurons is in accordance with previous work[1,18]. Here we show that this enhancement extends to the visual response components of visuomotor neurons, provided a spatially precise cue underlies the shift of attention. If, however, the shift of attention was prompted by quasi-symbolic information representing learned spatial coordinates, we did not see a significant enhancement of the visual response by attention. Visual neurons, on the other hand, did not distinguish between the two forms of cueing. In the memory saccade task, visuomotor neurons discharged in the period between the presentation of the visual target and the execution of the saccade, in many cases showing a gradual increase in activity before the saccade[24,25]. This is why these neurons have traditionally been discussed as intermediary substrates of the visuomotor transformations for saccades[16]. It has recently been found that some of these neurons seem to be involved in the process of selecting the target for the upcoming saccade[10–15]. An even more general role is suggested by our finding that visuomotor neurons are also active when a covert shift of attention, rather than a saccade, toward the receptive field of the neuron occurs, as indicated by discharge during the period when the covert shift of attention is executed (the ASP-related activity). However, before accepting an involvement of these neurons in the generation of covert shifts of attention, we have to ask if the ASP-related activity could not be a reflection of motor preparation or target selection rather than a reflection of shifting attention, an interpretation which would be more in line with previous work on visuomotor neurons. The Landolt-C optotype whose discrimination was enhanced by attention was never the target of a saccade. The only saccade targets involved, the targets for the indicative saccade, were presented perpendicular to the axis connecting the fixation point with the cued location. Since the latter corresponded to the null-preferred axis of the superior colliculus neuron being recorded, the targets for the indicative saccades and the subsequent saccades prompted by them did not evoke significant visual or saccade-related responses. Moreover, the choice of the target for the indicative saccade and the preparation of the saccade were fully determined by the orientation of the Landolt-C, independent of the Landolt-C location being cued or not. Hence, there is no reason to assume that any aspect of the processing for the planning or preparation of the indicative saccades might be responsible for the ASP. However, a preparatory saccade–related discharge, wrongly interpreted as attention shift–related, might be expected if our monkeys planned a saccade toward the cued location that was not executed. If this were the case, we should expect that the monkeys would at least have occasionally broken fixation and made a saccade to the cued location. However, such saccades did not occur in our highly over-trained monkeys. Moreover, if the ASP reflected the preparation of a suppressed or abandoned saccade, one would have expected to find the ASP-related activity not only in experiments with spatial cueing but also in those with quasi-symbolic cueing. This is suggested by the fact that our psychophysical measurements also demonstrate a spatially well-confined 'spotlight' of attention also for quasi-symbolic cueing, albeit wider than that seen for spatially precise cueing. This means that the monkeys knew quite precisely where the Landolt-C optotype would appear. Hence, if they tended to plan saccades to the C, they presumably would have done so in the experiments with quasi-symbolic cueing as well. However, the ASP-related activity was confined to the experiments with spatially precise cueing, a result that strongly speaks against the ASP-related activity being a reflection of saccade planning. A final argument against this view is the fact that we found a clear correlation between the size of the ASP-related activity and the size of the attentional benefit (**Fig. 3f**). Such a dependence would not be expected if the ASP-related activity reflected motor preparation or target selection. Therefore, we conclude that the ASP-related activity is the neuronal signature of a spatial shift of attention.

The conclusion that the ASP-related activity is actually instrumental in mediating the shift is suggested by two observations. First, the ASP-related activity was only observed when there was also an improvement in visual acuity, the hallmark of shifts of attention to the visual target to be discriminated. Conversely, in the absence of such an improvement of visual acuity, the ASP-related activity was missing. Second, the occurrence of the ASP-related activity was contingent upon the type of cueing. Similar to the enhancement of the visual responses of visuomotor neurons by attention, it was found only for spatial cueing but was absent in the case of quasi-symbolic cueing. Thus, visuomotor neurons seem to be involved in generating spatially precise shifts of attention, independent of whether these shifts are covert or followed by a saccade.

Whereas motor neurons are committed to the overt form of shifting attention, namely making foveating saccades, visuomotor neurons seem to represent a common shift plan, as posited by the premotor theory of attention[7,8], not yet committed to the one or the other form of shifting spatial attention. Actually, the notion of a dual role of superior colliculus visuomotor neurons is in accordance with the results of a previous study[18], which analyzed the metrics of saccades evoked by microstimulation of the intermediary layer of the superior colliculus—the zone were visuomotor neurons are found. This previous study showed that stimulation-evoked saccades were consistently shifted in the direction of a cued target for a saccade or, alternatively, a hand movement, provided the spatial cue preceded the electric stimulus. This observation was taken to indicate that a shift of attention associated with the preparation of a saccade or a hand movement to the cued location had shifted the movement vector. However, an alternative explanation could involve the interaction of two different motor intentions, one based on stimulation, the other based on cueing the location of a target for a saccade or a hand movement and thereby selectively activating either eye-movement[26,27] or hand-movement related neurons[9,28] in the intermediate layer of the superior colliculus. Actually, the fact that superior colliculus visuomotor neurons respond to covert shifts of attention in the complete absence of a motor response supports the original interpretation. It moreover suggests that superior colliculus visuomotor neurons are the likely substrate of the interaction between visual cueing and microstimulation. As shown in the present study, monkeys can also use quasi-symbolic information to enhance visual processing in distinct spatial locations if an opportunity is given to associate the symbol with the coordinates of that location. However, this association seems to be independent of the superior colliculus. Although not compelling, this conclusion is suggested by the absence of a specific involvement of visuomotor neurons when shifts of attention were prompted by quasi-symbolic information. At first glance, this finding seems to be at odds with a previous report[18] showing activation of 'buildup' neurons after the presentation of a central quasi-symbolic cue. However, in the previous study, unlike ours, the vectors describing the spatial shift of attention and the upcoming saccade coincided. Hence, the discharge observed may have reflected preparation of a saccade rather than a shift of attention toward the cued location. In our task, the only type of task-related superior colliculus cell was the visual neuron, which exhibited enhanced visual responses. The association of symbolic information with spatial coordinates may be an achievement of cortical machinery, involving areas such as the frontal eye fields or the lateral intraparietal area, known to be involved in mediating spatial shifts of attention[29–32]. By way of the well-established projections from these cortical areas to the superior colliculus, a reallocation of spatial attention based on symbolic cues or, alternatively, endogenous 'top-down' information, may influence the superior colliculus and cause an enhanced responses of visual neurons. The superior colliculus, on the other hand, seems to be confined to mediating exogenously driven shifts of attention.

METHODS

Psychophysical procedures. Two monkeys (*Macaca mulatta*) were trained to indicate the orientation of a Landolt-C optotype whose size was varied according to a PEST staircase procedure[33] (**Fig. 1**). The orientation decisions (correct/incorrect) were plotted as functions of C size and fitted by Probit functions[34]. Acuity thresholds were defined as the size of the C-gap, for which the Probit function predicted 75% correct orientation decisions. Two types of trials, differing with respect to whether a cue indicated the future position of the C or not, were presented randomly. The cue—a small spot in the center of the display—appeared 500 ms after the onset of maintained fixation, and stayed on for 100 ms (spatial cue) or 200 ms (quasi-symbolic cue). After a gap of 300–500 ms in the case of a spatial cue and 500 ms in the case of a quasi-symbolic cue, the C was presented for 150 ms and then replaced by a mask, which was on for another 200 ms. The mask corresponded to the C with the gap closed, thereby erasing information on the orientation of the C. The C and the mask were presented randomly interleaved in two locations (50% each). In the recording sessions, one was the neuron's receptive/movement field and the other was a location obtained by mirroring the former with respect to the central fixation point. During collection of psychophysics data, the Cs were presented along the horizontal and vertical axis, respectively, at fixed eccentricities of 3°, 9° or 15°. The spatially precise cue used in the first version of the attention task was a small white dot of diameter 20′. The quasi-symbolic cue used to indicate the future location of the C in the second version of the attention task red fixation point in a location, pointing to the position of the C (**Fig. 4a**). For example, the blue dot was presented above the fixation point when the C was presented upwards with respect to the fixation spot, at an eccentricity corresponding to the center of the neuron's receptive/movement field. The monkeys indicated their perceptual decision by making a saccade to one of two response targets representing the two orientations of the C. These two response targets turned on at the same time the fixation dot turned off, immediately after the disappearance of the mask. The response targets were presented on opposite locations with respect to the fixation point at a distance of 9° on an axis orthogonal to the axis on which cue and C were presented. During presentation of the cue and the C, the eyes stayed within a squared eye position window with a diameter of 3° centered on the fixation point. Trials in which the boundaries of this window were violated were discarded.

We measured the extent of the spatial zone in which acuity was improved by attention— that is, the diameter of the 'spotlight of attention'—by displacing the Landolt-C from the location predicted by the spatial cue or, in the case of quasi-symbolic cueing, from the standard cueing location, in 20% of cued trials. The displaced C was presented at a fixed eccentricity of 9° at positions that deviated from the expected position by rotations of the vector connecting the fixation point with the C location, amounting to 2.5°, 5°, 10°, 20° or 45° in either direction (**Fig. 5a**). We calculated the difference in acuity obtained in validly cued trials and in the trials where the C was displaced.

The acuity thresholds (Thr) obtained during recordings from individual neurons depended on their eccentricity. For the range of eccentricities (Ecc) considered during recordings (3–18°), this dependence was well characterized by a linear equation ($\mathrm{Th}r = 9.3 + 4.6 \times \mathrm{Ecc}$; $P < 0.05$). To render acuity thresholds and their cue-induced changes independent of eccentricity, we used this linear relationship to normalize the acuity thresholds relative to the acuity at 10° eccentricity.

Recording and classification of superior colliculus neurons. Two monkeys were prepared for chronic single-unit and eye position recordings using search coils as described previously[35–36]. All animal procedures followed National Institutes of Health guidelines and German national law and were approved by the State Committee supervising the handling of experimental animals. We used post-surgical anatomical MRI to localize the superior colliculus. Identification of the superior colliculus and its major layers during electrophysiological recordings relied on the well-established visual and oculomotor properties of superior colliculus neurons and the characteristic topographical organization of the superior colliculus[36–38]. All recordings were conducted with the monkey in complete darkness. After isolating a superior colliculus neuron, we first used a standard 'memory saccade' task to disentangle visual and motor response components as well as discharge in the memory period and to determine the location of the receptive and/or motor field. The latter was achieved by comparing responses to memory-guided saccades in eight directions (0°, 45° and so on) in the frontoparallel plane, starting from straight ahead, and, furthermore, varying the amplitude within a range of 4–32°. The saccade target was presented after a period of 500–600 ms of stable fixation of a centrally located spot and was on for 100–200 ms. The disappearance of the central fixation spot, 400–500 ms after the disappearance of the peripheral target, served as the go signal for the saccade. Instead of using the traditional subjective criteria to categorize neurons[24,37], we used a cluster analysis for categorization. To this end, we normalized each neuron's discharge with respect to the individual peak discharge rate set to 1. Next we measured the mean discharge rate in four intervals (**Fig. 2a–c**, column I): 1, baseline activity (200–400 ms after the onset of the trial); 2, visual response (interval from 70 ms after target onset to 70 ms after target offset); 3, memory interval activity (200–400 ms after target offset); and 4, motor response (interval starting with the 'go signal' for the saccade and lasting 200 ms). The individual means were fed into a k-means cluster analysis that distinguished five different groups of superior colliculus neurons: visual, motor, visuomemory, visuomotor and buildup neurons. Given the small number of neurons in the latter three groups, we pooled them for the analysis of responses in the attentional tasks, and collectively referred to them as visuomotor neurons. After having determined their oculomotor features, the neurons were tested in the attention paradigm (**Fig. 1a**).

Analysis of neuronal responses. Raster plots and peristimulus time histograms (PSTHs; bin width 5 ms, smoothed by third-order Butterworth lowpass filter with cutoff frequency of 10 Hz) represent single-unit responses recorded in the memory saccade task. Responses that were obtained in the attention tasks are represented by raster plots and PSTHs (bin width 15 ms, smoothed by third-order Butterworth lowpass filter, cutoff frequency 13.3 Hz). Population averages were computed independently for trials with and without cueing for a period of time, starting 200 ms before C onset and ending with C offset, by calculating the mean discharge rate and its standard deviation for bins of 10 ms. Averages were smoothed, applying a third-order Butterworth lowpass filter with a cutoff frequency of 15 Hz. The comparison between the two conditions (cued vs. non-cued) was based on unfiltered data using a bin-wise comparison of the discharge of individual neurons and the population averages respectively, using a paired t-test. To compare the discharge in the ASP, the t-tests were applied to a period of 200 ms before C onset (ASP). For the comparison of the visual responses, the t-tests were applied to a period of 60–120 ms (for population averages) and 50–220 ms (for individual neurons) after C onset. The ASP discharge was considered to differ significantly between the cued and the non-cued condition if at least ten consecutive bins differed significantly ($P < 0.05$). The visual response was considered different if five consecutive bins showed significant differences.

ACKNOWLEDGMENTS
This work was made possible by grants from the Schilling Foundation (TS 013/001.184/98), the DFG Schwerpunktprogramm "Sensomotorische Integration" (Ha 2847/2-1) and the DFG Sonderforschungsbereich (550-A2 and 550-A7).

COMPETING INTERESTS STATEMENT

The authors declare that they have no competing financial interests.

Received 6 August; accepted 25 November 2003

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