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# The representation of visual salience in monkey parietal cortex

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**When natural scenes are viewed, a multitude of objects that are stable in their environments are brought in and out of view by eye movements. The posterior parietal cortex is crucial for the analysis of space, visual attention and movement[1]. Neurons in one of its subdivisions, the lateral intraparietal area (LIP), have visual responses to stimuli appearing abruptly at particular retinal locations (their receptive fields)[2]. We have tested the responses of LIP neurons to stimuli that entered their receptive field by saccades. Neurons had little or no response to stimuli brought into their receptive field by saccades, unless the stimuli were behaviourally significant. We established behavioural significance in two ways: either by making a stable stimulus task-relevant, or by taking advantage of the attentional attraction of an abruptly appearing stimulus. Our results show that under ordinary circumstances the entire visual world is only weakly represented in LIP. The visual representation in LIP is sparse, with only the most salient or behaviourally relevant objects being strongly represented.**

Single neurons were isolated extracellularly in the LIP in two macaque monkeys. The visual responses and receptive field of each neuron was first assessed in a passive visual task in which visual stimuli were flashed during stationary fixation (Fig. 1a). Neurons were then tested with a stable-stimulus paradigm (Fig. 1b), in which a circular array of eight stimuli, which differed from each other in shape and colour, appeared at the beginning of an experiment and remained stably on the screen for its duration (usually more than 10 min or 100 trials). The array radius matched the eccentricity of the most active portion of the receptive field under study, so that when the monkey made a saccade to the centre of the array, the neuron's receptive field was brought onto one of the array elements. In each trial a peripheral fixation point appeared (FP1 in Fig. 1b), situated such that no member of the array was in the receptive field when the monkey fixated it. This fixation point then stepped to the centre of the array (FP2 in Fig. 1b), and the monkey followed it with a saccade. The saccade brought the same symbol that had driven the cell so effectively into the receptive field, but the response of the cell was far less. To test whether this quiescence was due to the stability of the array stimulus we used a recent-onset variant of this task. In this variant only seven array symbols remained stably on the screen, and the eighth, the one that will enter the receptive field, was turned on anew in each trial while the monkey fixated the peripheral fixation point. After 500 to 2,000 ms, the monkey made a saccade that brought this recently appeared stimulus into the receptive field. The neuron now responded intensely (Fig. 1b, recent-onset stimulus). Of 31 neurons tested, 23 (74%) had significantly greater responses in the recent-onset condition than in the stable-stimulus condition (two-tailed *t*-test, $P < 0.05$). The median response after the saccade (in the 200-ms epoch beginning at the end of the saccade) across all 31 neurons was 29 Hz (range 1–139 Hz) in the recent-onset condition, and 17 Hz (range 0–76 Hz) in the stable-stimulus condition ($P < 0.001$ between conditions, Wilcoxon signed rank test). As can be seen in Fig. 1, the responses of some neurons were predictive, beginning earlier than would be expected from their visual latency alone, consistent with a previous report[3]. It is also clear from Fig. 1 that these responses did not depend on the execution of a subsequent saccade to the receptive field, as the monkey did not look at the stimulus in the receptive field in any of the trials shown.

These results demonstrate that the visual responses of LIP neurons are not simply due to the entry of a visual stimulus onto an appropriate retinal location. Instead, they are critically dependent on the abrupt onset of that stimulus, which renders it salient[4]. Recently appeared visual stimuli are represented in LIP even when they appear outside the receptive field and are brought onto it by a saccade, whereas stable stimuli evoke only weak or no responses.

Lights rarely flash in the world in which primates evolved. Most objects are stable in the environment and not intrinsically salient, but can become salient according to the needs of the animal. To determine whether stable stimuli are represented in LIP when they become behaviourally relevant we used a stable-target task in which all array stimuli were stable, but the monkey was required to make a saccade to just one of them on each trial. The monkey first fixated a peripheral fixation point, and then a cue appeared (outside the receptive field) that matched one member of the array (Fig. 2a). The monkey made a first saccade to the centre of the array, thereby bringing at least one array stimulus into the receptive field, and a second saccade to the cued array element, chosen pseudorandomly on each trial. When the cue informed the monkey that the second saccade would be to the stimulus entering the receptive field, the neuron discharged, starting around the first saccade and continuing until after the second saccade (Fig. 2Aa). In contrast, when the cue matched a stimulus outside the receptive field, the neuron did not respond, even though the same array stimulus entered the receptive field by means of the first saccade (Fig. 2Ab). Thus the neuron responded to the entry of a stable stimulus into its receptive field provided that the stimulus was behaviourally significant. In another version of the task the cue was presented after the stimulus had entered the receptive field (late-cue condition). Trials began when the monkey achieved central fixation. The cue was flashed during this fixation, and after a brief delay the monkey made a saccade to the cued array element. The neuron did not respond before cue presentation, when the stimulus had just entered its receptive field (Fig. 2B, first saccade). The neuron became active following cue presentation and continued until after the saccade, but only on trials in which the cue matched the stable stimulus in its receptive field

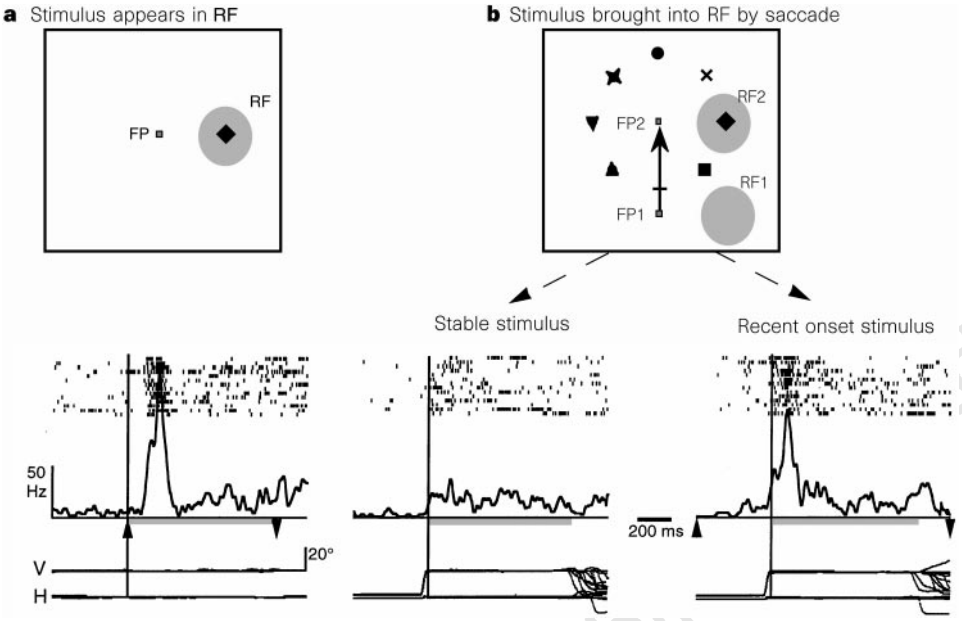



**Figure 1** Effect of a recent onset on responses of one neuron. **a**, Neuron response when a diamond-shaped visual stimulus was flashed for 1 s at 15° right while the monkey maintained central fixation. The approximate location of the neuron's receptive field (RF) is indicated by the shaded area. **b**, Responses during the stable-array task. Top, illustration of the visual display at the time of the saccade from FP1 to FP2 (arrow). Eight symbols arranged in a circular array remained stably on the screen throughout collection of these data. Each subtended 2° and differed from the others in shape (as shown) and in colour (not shown). Fixation points were red squares, 2/3° on a side. The array was centred at the centre of gaze (FP2) and its radius matched each neuron's receptive-field eccentricity (in this case, 15°). During presaccadic fixation (at 20° down, FP1) the neuron's receptive field lay at position RF1, entirely outside the array. The saccade brought the receptive field to position RF2, overlapping a stimulus physically identical with that used in **a**. The neuron had minimal responses in the stable-stimulus condition when all eight symbols remained stably on the screen. It responded strongly in the recent-onset condition when seven stimuli were stable but the diamond was turned on and off on each trial. Its firing rate in a 200-ms interval beginning at the end of the saccade was 20.8 ± 11.5 Hz (mean ± s.d.) in the stable-stimulus condition and 52.9 ± 23.6 Hz in the recent-onset condition. Arrowheads underneath each spike density trace indicate time of appearance and disappearance of the diamond-shaped stimulus. The grey line shows the time the stimulus was present in the neuron's receptive field. Raster lines, spike-density histogram and vertical (V) and horizontal (H) eye position are shown for each condition. Neural responses are aligned on the end of the saccade from FP1 to FP2 in **b** and on stimulus onset in **a**.

(Fig. 2Ba, b). Thus the response begins when the significance of the stimulus is established, whether that stimulus is just entering, or is already inside, the receptive field. The vast majority of neurons tested (78 of 82, 95% in the late-cue condition, and 29 of 29 in the early-cue condition) showed these response patterns.

We hypothesized that the responses in the stable-target tasks were related to the significance of the stimulus present in, or entering, the receptive field. However, LIP neurons are also known to have spatially selective presaccadic motor activity in the absence of recent visual stimulation[5]. To determine whether this presaccadic activity could fully explain the response in the stable-target task, we trained the monkey to make saccades into the receptive fields of the neurons in the absence of current or recent visual stimulation of the receptive field. Neurons were tested with a block of stable-target trials in which the cue always matched the stimulus in the receptive field. In the next trial block the saccade target was removed from the array, but all visual events were identical, and the monkeys were rewarded for making the same saccade as before, but now to an empty region of the array (no-target trials). Blocks of stable-target and no-target trials were interleaved. Neurons responded much more in stable-target than in no-target trials (Fig. 3a). Responses changed during the very first trial within a block and did not decrease systematically in subsequent trials, showing that the difference between the two conditions could not be an artefact of repeated trial presentation. Even though saccades in no-target trials usually had lower peak velocities and larger latencies than those in stable-target trials, there was no trial-by-trial correlation between firing rate and saccade velocity, amplitude or latency, neither within nor between experimental conditions. The decrement in neural response between stable-target and no-target trials, therefore, was not related to differences in these saccade parameters (see Methods). We quantified the difference in neural response between the two conditions using the index NT/(NT + ST), where NT denotes the response in no-target trials, and ST the response in stable-target trials (both measured in the 50-ms epoch ending at the onset of the saccade). We considered NT as a measure of the saccade-related or motor planning activity of the neuron, and any difference between NT and ST was thought to reflect processing of the visual target. The vast majority of indices fell below 0.5 (with ST > NT; median index, 0.39; mean, 0.40; range, 0.11–0.76; significantly different from 0.5, Student's *t*-test, $P < 0.001$; Fig. 3c, left). The median index corresponds to a reduction in response of almost 40% in the absence of the target. Consistent with previous findings, therefore, although some neurons have an independent saccade-related response, much of their presaccadic activity reflects the location of a selected visual stimulus rather than the planning of the saccade itself.

As a final control for our hypothesis that salient stimuli are represented in LIP regardless of the monkey's current motor behaviour, we used a version of the stable-target task in which the cues themselves flashed in the receptive field. In these trial blocks the cue matched, and dictated a saccade to a different array element on each trial, but saccades to the cue were never required. Nevertheless, the appearance of the cue elicited robust visual responses (Fig. 3b), which did not differ between trials in which the cue dictated a saccade to the target inside and outside the receptive field (TI and TO trials, respectively). The mean visual response across 34 neurons was 52 Hz in TI trials (median, 51 Hz; standard deviation, 43 Hz) and 47 Hz in TO trials (median, 47 Hz; standard deviation, 36 Hz;

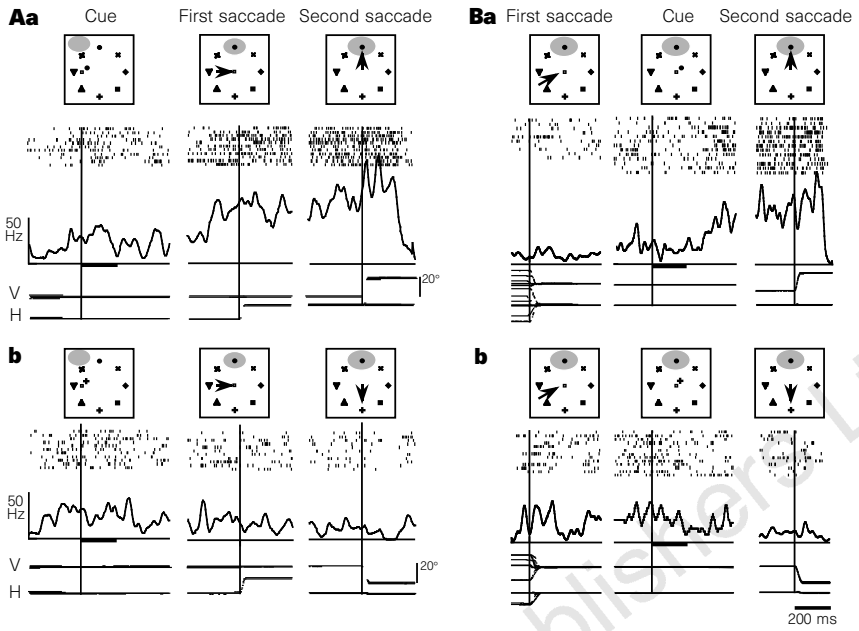
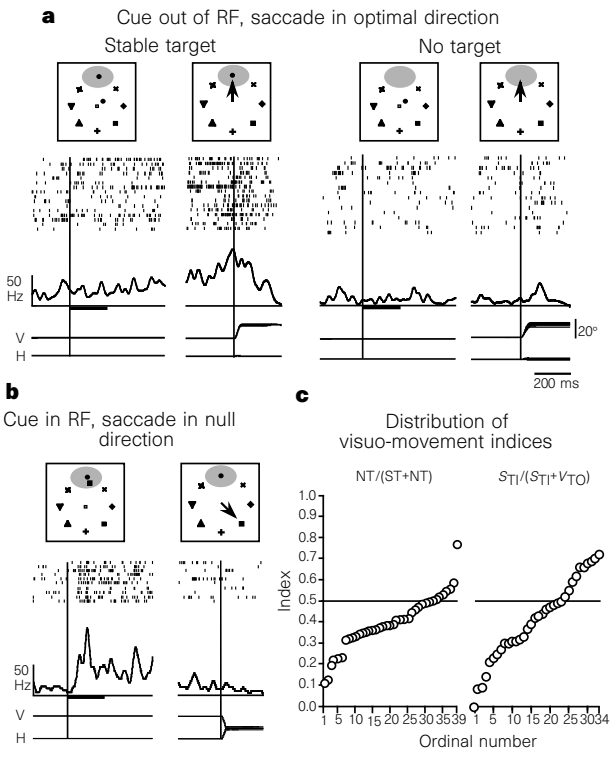



**Figure 2** Responses of one neuron during the stable-target task. **A**, Early cue condition. While the monkey fixated a peripheral fixation point (15° left), where the receptive-field stimulus (the circle) was outside the neuron's receptive field, a cue was flashed for 200 ms 2° upward from this position (cue column, black bar). After a variable delay of 300–500 ms the fixation point jumped to the centre of the screen and the monkey followed it with a rightward saccade (first saccade column). After another 100–200 ms delay the fixation point disappeared and the monkey made a saccade to the array symbol matching the cue (second saccade). The matching symbol was chosen randomly among the eight array elements, though only selected trial types are shown here. The neuron responded when the receptive-field stimulus (**a**), but not the opposite stimulus (**b**), was cued. Array radius, 18°. **B**, Late-cue condition. The monkey began each trial by fixating the centre of the screen, where its receptive field overlapped the receptive-field stimulus. The cue was presented 500–800 ms later for 200 ms at 2° above the fovea. After an additional delay of 300–500 ms, the fixation point disappeared and the monkey made a saccade to the cued array element. The neuron responded when the stimulus in the receptive field became the target for the saccade (**a**) but not otherwise (**b**).



**Figure 3 a**, No-target task. The neuron (same as that shown in Fig. 2) was tested with interleaved blocks of trials in which the saccade target was present (stable-target) or absent (no-target) from the array. The cue matching the stable target (circle) was presented on all trials at 2° up. Removal of the target greatly reduced the response of the neuron. Mean saccade amplitude was 14.5° in both blocks, with standard deviations of 0.5° in the stable-target condition and 1.5° in the no-target condition. Peak saccade velocity was significantly lower in no-target than stable-target trials (506 ± 63 and 599 ± 62 deg $s^{-1}$; $P < 0.0001$, two-tailed $t$-test). **b**, Cue-in-receptive-field (RF) experiment. The neuron had a robust visual response to a cue that was flashed in the receptive field (at 10° up) but dictated a saccade away from the receptive field. Its response returned to baseline during the delay period. The task was identical to the late-cue condition shown in Fig. 2, except that all cues appeared in the receptive field. **c**, Indices NT/(ST + NT) (left) and $S_{TI}/(V_{TO} + S_{TI})$ (right) are plotted in ascending order against ordinal number. See text for further details.



$P = 0.13$, Wilcoxon signed-rank test). Responses were directionally selective in the presaccadic period (50-ms epoch ending at the onset of the saccade). The mean presaccadic response was 37 Hz in TI trials (median, 33 Hz; standard deviation, 28 Hz) and 9 Hz in TO trials (median, 6 Hz; standard deviation, 11 Hz; $P < 0.0001$, Wilcoxon signed rank test).

For most neurons the visual responses to cues that dictated saccades opposite the receptive field ($V_{TO}$) surpassed the presaccadic responses for saccades to stable targets in the receptive field ($S_{TI}$). The distribution of indices $S_{TI}/(V_{TO} + S_{TI})$ for 34 neurons is shown in Fig. 3c. (Here $V_{TO}$ is the average firing rate in the epoch 75–175 ms after cue onset, and $S_{TI}$ is the average rate in the 50-ms epoch ending at saccade onset.) This index was smaller than 0.5 for most neurons, with $V_{TO} > S_{TI}$ (mean index, 0.41; median, 0.42; standard deviation, 0.19; $P = 0.01$ relative to 0.5, two-tailed Student's *t*-test). Because the presaccadic responses for saccades to stable targets were themselves greater than the presaccadic responses in the no-target task, these data suggest that most activity in the bulk of LIP neurons depends on the presence of a salient visual object, and does not simply reflect motor processing for saccades.

Taken together these experiments show that most LIP neurons have strong visual responses which are independent of saccade planning but depend critically on stimulus salience. Stimulus salience can either be intrinsic (produced by a recent abrupt onset) or dictated by the behavioural context. Evidence suggests that visual information that is of no immediate behavioural relevance is filtered out either in or before LIP. Thus neurons in primary visual cortex provide a more complete visual representation, discharging at high rates whenever saccades bring their receptive fields upon adequately orientated stable stimuli regardless of stimulus salience[6]. In contrast, visually responsive neurons in the frontal eye fields resemble LIP neurons in that they respond only to portions of complex, stable scenes that are targeted by the next saccade[7].

Our data confirm and complement previous studies showing that visual responses coexist with saccade-related signals in individual LIP neurons. Recently, Snyder *et al.*[8] studied a subset of LIP neurons that discharged during the delay period of a memory-guided saccade task. They showed that some of these neurons discharged less during the delay period of a memory-guided reach task, especially when the monkey simultaneously performed a saccade to a target in a different direction, and they hypothesized that LIP primarily encoded saccade preparation. The neurons in our sample with responses in the no-target task could participate in saccade preparation, and the projections from LIP to the intermediate layers of the superior colliculus and the frontal eye field[9–11] are appropriate for that function. However, consistent with our findings, Snyder *et al.* also reported that the neurons responded to flashed visual stimuli independently of the monkey's current motor behaviour[8]. Our experiments show that these are not merely 'passive visual' responses but reflect the special salience of the recently appeared stimuli.

We suggest that the representation of visual salience in LIP may subserve a wide range of behaviours including, but not limited to, saccadic eye movements. Similar 'salience maps' have been postulated to guide a variety of behaviours including visual search with or without eye movements[12–14], the perception of unified objects[15], and the phenomenon of positional constancy[16]. LIP could contribute to selective visual processing through its connection with visual areas, including V4, TE and TEO[10,17], which are thought to be important in pattern recognition and which have significant attentional modulation[18]. □

## Methods

**Experimental methods.** Two male rhesus monkeys (*Macaca mulatta*) were prepared for physiological recording during sterile surgery under ketamine and isofluorane anaesthesia. All experimental protocols were approved by the NEI Animal Care and Use Committee as complying with the guidelines established in the Public Health Service Guide for the Care and Use of Laboratory Animals. Behavioural control and data collection were done on personal computer using the REX system[19]. All physiological methods were as described[5]. Visual stimuli were projected upon a tangent screen by an Electrohome video projector driven by personal computer. Array members were 2° in diameter and varied slightly in luminance. Locations of recording sites were identified histologically in one monkey. In the second monkey, LIP neurons were recognized by their consistent visual, delay-period and saccade-related responses in a delayed-saccade task[20,21], and recording sites were localized to the intraparietal sulcus by magnetic resonance imaging. The distribution of neurons with visual, delay-period and presaccadic activity in our sample resembled that reported previously[21].

**Data analysis.** Spike-density histograms were calculated by convolving the spike train, sampled at 1 kHz, with a gaussian of sigma 10 ms (ref. 22). Neural responses were measured as the average of this spike-density trace over the interval of interest, across all correct trials. To analyse the relation between saccade parameters (peak velocity, amplitude and latency) and the neural responses in the stable-target and no-target conditions, we fit the presaccadic responses of each neuron, for each condition (stable-target and no-target), with univariate least-squares linear regressions. Of 78 regressions (two each for 39 neurons), less than 5 were significant for each parameter. To further assess a possible relation between firing rate and saccade velocity at the population level, we computed a saccade velocity index NT/(ST + NT) analogous to the response index described in the text. There was no correlation between the velocity and firing-rate indices across the 39 neurons.

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