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Parietal activity and the perceived direction of ambiguous apparent motion

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We recorded from parietal neurons in monkeys (*Macacca mulatta*) trained to report the direction of an apparent motion stimulus consisting of regularly spaced columns of dots surrounded by an aperture. Displacing the dots by half their inter-column spacing produced vivid apparent motion that could be perceived in either the preferred or anti-preferred direction for each neuron. Many neurons in the lateral intraparietal area (LIP) responded more strongly on trials in which the animals reported perceiving the neurons' preferred direction, independent of the hand movement used to report their percept. This selectivity was less common in the medial superior temporal area (MST) and virtually absent in the middle temporal area (MT). Variations in activity of LIP and MST neurons just before motion onset were also predictive of the animals' subsequent perceived direction. These data suggest a hierarchy of representation in parietal cortex, whereby neuronal responses become more aligned with subjective perception in higher parietal areas.

A fundamental goal in neuroscience is to understand how perception arises from the activity of neurons in the brain[1]. This has been explored most extensively for visual motion perception in monkeys. Many neurons in monkey parietal cortex are selective for the direction or speed of moving stimuli and are thus reasonable candidates to mediate motion perception[2,3]. This linkage is strengthened by experiments showing that the motion sensitivity of parietal neurons is similar to the animal's motion sensitivity[4] and that microstimulating parietal cortex can influence motion perception[5]. Trial-by-trial variability of neuronal responses can also be correlated with the animals' perception of motion[6]. For example, responses of neurons in the middle temporal area (MT) are modulated by the perceived direction of perceptually bistable motion stimuli[7] (stimuli in which motion can be perceived in either of two directions while the stimulus itself remains constant). Bistable motion can be produced by presenting opposite directions separately to the two eyes[8] or by structure-from-motion displays that appear to rotate either clockwise or counterclockwise in depth[9,10].

Direction-selective parietal neurons can also respond differently to the same visual stimulus if the animal expects motion in a particular direction. For example, we have previously shown that some neurons continue to fire after the disappearance of a spot of light that, based on its recent history, could be expected to move in a particular direction[11,12]. This activity was common in the lateral intraparietal area (LIP), but less common in the medial superior temporal area (MST), suggesting a transformation within parietal cortex toward neuronal responses more closely aligned with the animal's subjective interpretation of motion. In the present study, we directly tested this idea by probing direction-selective neurons from several parietal areas with a perceptually bistable motion stimulus that could be perceived to move

in one of two opposite directions. We trained the animals to signal their perceived direction after each presentation of the stimulus, and then we examined the neuronal responses as a function of the animal's perceived direction. Using the same stimulus in several parietal areas, we examined the extent to which neuronal responses in different areas are related to the animal's subjective perception.

RESULTS

Behavioral task

Two rhesus monkeys were trained to fixate while viewing a visual stimulus consisting of columns of white dots evenly spaced by 0.8° and surrounded by a 7°-diameter gray aperture (**Fig. 1a**). The dot-columns were centered within the receptive/response field of each direction-selective neuron under study and were oriented perpendicular to the preferred–null axis for each neuron. On successive stimulus updates, the dots were displaced perpendicular to the columns by a fraction of the inter-column spacing, producing apparent motion in either the preferred or null direction. If the displacement was a small fraction of the inter-column spacing, the motion was reliably perceived in the direction of the smaller possible displacement. With larger fractional displacements, however, it became more likely that the motion could be perceived in either direction, until by a displacement of 1/2 it was equally likely that motion could be perceived in either the preferred or null direction. Although 1/2 displacements have no inherent motion direction, human subjects perceive vivid, concerted motion in one of the two possible directions[13]. We used four fractional displacements of the inter-column spacing: 5/16 (0.25°), 3/8 (0.3°), 7/16 (0.35°) and 1/2 (0.4°). The rate of stimulus updates was adjusted for all four conditions to produce close to the same average speed (~3°/s). For the ambiguous (1/2) condition, the stimulus was thus updated every

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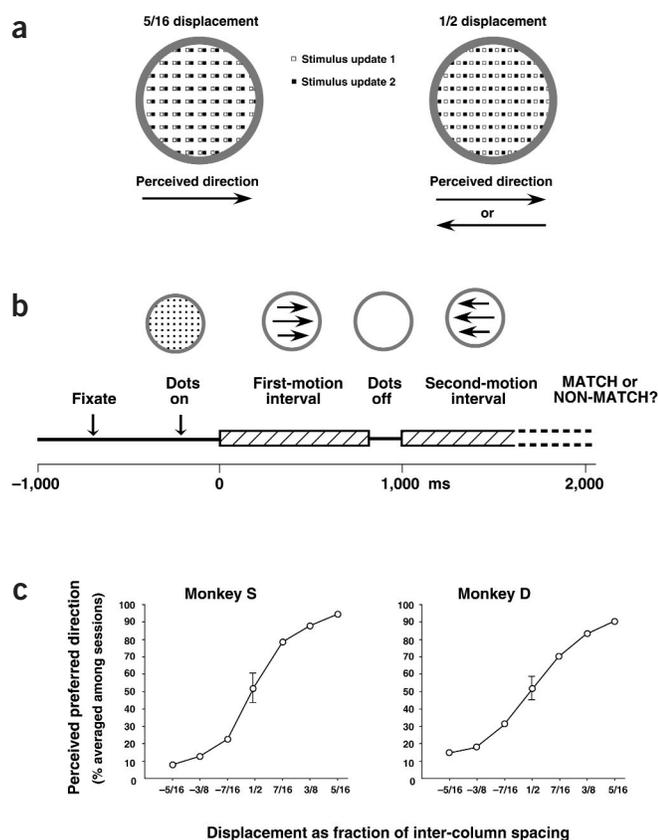
Figure 1 Visual stimulus and behavioral task. (**a**) White and black dots indicate two consecutive updates of the motion stimulus (dots not drawn to scale). If the dots are displaced to the right by 5/16 of the inter-column spacing, motion would be reliably perceived to the right. If the dots are displaced by exactly 1/2 of the inter-column spacing, motion could be perceived to either the left or right. (**b**) Time course of the match-to-sample behavioral task. Hatched rectangles indicate the two motion periods. (**c**) Behavioral performance for the two monkeys averaged among all individual sessions (one session = the period of electrophysiological recording from one neuron). Positive fractional displacements along the horizontal axis indicate smaller displacements in the preferred direction for each neuron; negative fractional displacements indicate the null direction. Vertical lines indicate ±1 standard deviation (s.d.) of the mean performance (among individual sessions) for the 1/2 fractional displacement only.

133 ms. With more rapid updates, the ambiguous stimulus appeared to flicker rather than move.

On a given trial, the dots appeared after the animals fixated, briefly remained stationary, and then moved for ~800 ms (**Fig. 1b**). The dots then disappeared and reappeared moving a second time. For the first motion interval, the direction and size of the fractional displacement were chosen at random. For the second motion interval, the direction was also chosen randomly, but was made perceptually unambiguous by using the smallest possible fractional displacement. The monkeys moved a bi-directional lever to the left or right to report whether the direction in the second motion interval was the same or different from the direction in the first motion interval (two-interval forced choice). Thus the monkey's perceived direction in the first motion interval could be inferred from the known direction of the second motion interval and the animal's report of whether the second direction matched the first direction. Because the directions were randomized in both the first and second motion intervals, trials

in which the monkey perceived motion in one direction would include both matches (leftward hand movements) and non-matches (rightward hand movements). The animals' perception could thus be examined independent of the direction of hand movement used to signal their perception.
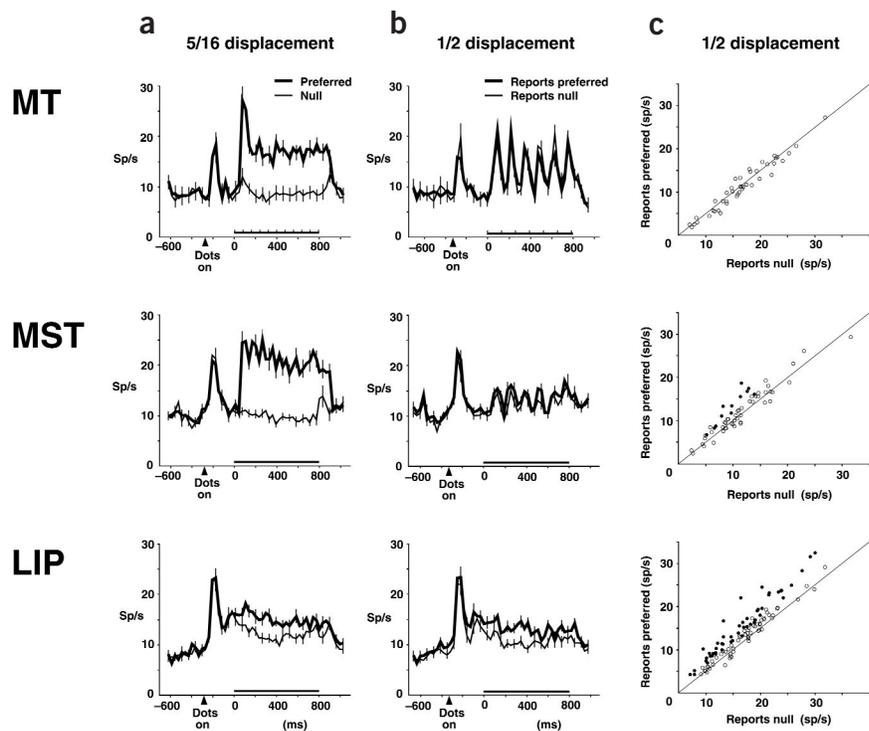
For fractional displacements <1/2, the animals were rewarded if they reported perceiving the direction that corresponded to the smaller possible displacement. As there was no correct or incorrect choice for the 1/2 (ambiguous) condition, the animals were rewarded at random with a probability equal, on average, to that of the 7/16 condition.

Several observations suggested that the animals accurately reported their perceived direction on ambiguous trials. First, we chose the set of fractional displacements to be as close to 1/2 as possible so that the animals could not recognize the 1/2 condition as being unique (Methods). In fact, for both animals, the average probability of perceiving motion in one direction or the other changed as a gradual function of the fractional displacement, making it unlikely that the animals adopted a unique behavioral strategy for the ambiguous condition (**Fig. 1c**). Second, we found that if human observers viewed smooth, unambiguous motion in the first motion interval followed immediately by ambiguous motion in the second motion interval, they were more likely to perceive the ambiguous motion moving opposite to the preceding unambiguous motion ('report non-match'), probably as a result of motion adaptation. This was also true in control experiments with the monkeys. In separate blocks of trials, the ambiguous motion was presented either in the second motion interval following unambiguous motion, or as usual in the first motion interval. When ambiguous motion followed unambiguous motion, the animals reported 73% non-match responses, whereas they reported 51% non-match responses when the ambiguous motion was presented in the first motion interval ($P < 0.001$; χ^2 test). Third, if the animals were guessing on ambiguous trials and they received reward on the previous trial, it is possible that they would guess the same direction or make the same lever movement as on the previous trial. However, we found no such dependence ($P > 0.2$, binomial test; null hypothesis, 50% of trials with the same percept/lever response as on previous trial).

Neuronal responses during motion

Neuronal activity was recorded from a total of 213 neurons: 46 in MT, 60 in MST and 107 in LIP. When a unit was isolated, we first mapped its receptive/response field and then determined its preferred direction before running the main task (Methods). The responses to ambiguous trials in the main task were sorted by whether the monkey perceived the preferred or null direction (as determined from the direction-tuning task). Population-average responses from the first motion interval are shown in **Fig. 2**. In all three parietal areas, most neurons were direction-selective for unambiguous motion (**Fig. 2a**). The responses of many neurons also varied with the perceived direction of ambiguous motion, but this differed widely among parietal areas. For the 46 MT neurons, the population-average responses on ambiguous trials were similar whether the monkey perceived the preferred or null direction, whereas for the 60 MST and 107 LIP neurons, the average responses were larger when the monkey perceived the preferred direction (**Fig. 2b**). For each unit, we calculated the firing rate during the first motion interval of ambiguous trials, and then averaged the rate separately among trials in which the animal reported perceiving the preferred or null direction (**Fig. 2c**). None of 46 MT neurons showed a significant difference in mean firing rate according to whether the animal reported the preferred or null direction, whereas 13/60 (22%) of MST neurons and 48/107 (45%) of LIP neurons showed significant

Figure 2 Neuronal responses. (**a**) Response histograms from the first-motion interval for the 5/16 fractional displacement condition averaged for all 46 MT, 60 MST and 107 LIP neurons. The horizontal black bars indicate the first-motion interval, and the tick marks on that bar in the top panel indicate the times of the stimulus updates. Responses were sorted by the preferred and null direction determined in the direction-tuning task. Error bars are ± s.e.m. Only correct trials were included in the averages. Cells in all three areas had transient responses to the onset of the dots, and then sustained direction-selective responses after the start of the unambiguous motion. (**b**) Response histograms for the 1/2 fractional displacement condition (ambiguous condition) sorted by trials in which the monkeys reported perceiving preferred or null direction. MT responses were strongly temporally modulated by the stimulus updates (133-ms periodicity). Average MT responses were also temporally modulated by the more frequent stimulus updates in 5/16, 3/8 and 7/16 conditions, but the temporal modulation is not evident in **Fig. 2a** because of the 25-ms bin width. (**c**) Average spike rates during the first-motion interval for ambiguous trials only. Each circle indicates the spike rate for one neuron when the animal reported perceiving the null direction versus the spike rate for that neuron when the animal perceived the preferred direction. Filled circles indicate cells with statistically significant difference in spike rates for the two reported directions ($P < 0.05$). Diagonal lines have unity slope.

differences (two-tailed t-test; $P < 0.05$). All neurons with significantly different firing rates had a higher mean firing rate when the animal reported perceiving the preferred direction. One such LIP neuron is shown in **Fig. 3**. Across the populations, MST ($P < 0.05$) and LIP ($P < 0.0001$), but not MT ($P > 0.5$) neurons showed significantly higher firing rates when the animals reported the preferred direction on ambiguous trials (one-tailed paired t-test).

Neuronal activity before motion onset

A notable feature of the average LIP activity on ambiguous trials was that the activity was elevated before the dots began to move if the animals subsequently reported perceiving the preferred direction (**Fig. 2b**). To examine this effect further, we used choice-probability (CP) analysis to determine the trial-by-trial relationship between neuronal firing and the animal's perceptual report on ambiguous trials[6]. CP captures how well the animal's perceived direction can be predicted from the neuronal response on a given trial. For each unit, we calculated CP based on spike counts in two periods: the 800-ms first-movement interval and the 600-ms period before the onset of motion. We used a permutation test to determine whether individual CP values were significantly different from chance. For both the pre-movement and movement intervals, neurons with statistically significant CP values ($P < 0.05$) were common in LIP, less common in MST, and virtually absent in MT (**Fig. 4a,b**). Average CP was significantly above chance during the movement period across the populations of MST and LIP neurons, but not MT neurons; during the pre-movement period, average CP was significantly above chance only for the population of LIP neurons ($P < 0.05$; one-tailed t-test; null hypothesis; mean CP = 0.5). Thus variability in the activity of many LIP and

MST neurons before motion onset was predictive of the animals' subsequent perceived direction on ambiguous trials. The pre-movement activity had the same range of variability on unambiguous trials. Because we sorted unambiguous trials based on the actual direction, any differences in pre-movement activity would have averaged out.

We also analyzed CP as a function of time during the trial. In MST, average CP for ambiguous trials was slightly higher than 0.5 before movement began, and then it increased during the movement. In LIP, CP for ambiguous trials was well higher than 0.5 before movement began, and then it increased slightly during the movement (**Fig. 4c**).

For LIP neurons, we also calculated CP during the 600-ms pre-movement period on trials in which the monkeys reported the wrong direction in the 7/16 condition. As these error trials were relatively infrequent (**Fig. 1c**), the CP measurements would be expected to be less reliable. Nonetheless, 23% of LIP neurons still showed statistically significant CP > 0.5 (versus 9% with statistically significant CP < 0.5).

Controls for stimulus eccentricity

Variations in CP among neurons could have been related to the eccentricity of the stimulus used for each neuron. For example, if the receptive fields of the MT neurons in our sample were systematically more eccentric than the receptive fields of the MST and LIP neurons, it is possible that the monkeys may have reported the direction less accurately for MT neurons, producing low CP values. However, there was considerable overlap in the distribution of stimulus eccentricities between MT (median 6.3°, range 4.7–12.1°), MST (median 10.5°, range 6.0–23.2°) and LIP (median 8.4°, range 5.0–17.3°). Moreover, there was no systematic relationship between the value of CP and
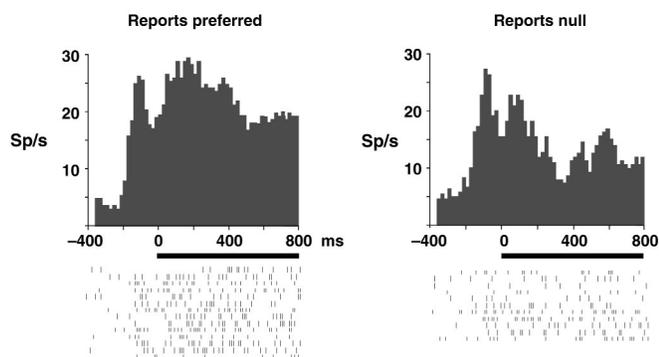
Figure 3 Responses of one LIP cell to the ambiguous (1/2 displacement) condition, separated by whether the animal reported perceiving the preferred direction or the null direction. The horizontal black bars indicate the first-motion interval.

stimulus eccentricity among neurons for any of the three parietal areas (linear regression analysis; $r^2 < 0.001$ and $P > 0.5$ in all cases).

Controls for lever movement to signal match/non-match

The choice-probability analysis suggested that the activity of many neurons during and before the motion was predictive of the monkey's perceived direction. This is not the same as predicting the monkey's behavioral response (the direction of lever movement) because perceiving a particular direction included trials that resulted in both match and non-match responses (leftward and rightward lever movements). This is underscored by segregating ambiguous trials with respect to both perceived stimulus direction and match/non-match (**Fig. 5a**). Responses averaged among the 107 LIP neurons were larger when the animal perceived the preferred stimulus direction and were hardly affected by whether the trials ended in a report of match or non-match. For each unit, we also separately pooled responses for ambiguous trials that resulted in match or non-match choices, regardless of whether those choices corresponded to perceiving preferred or null stimulus direction, and we calculated CP with respect to match versus non-match choices (**Fig. 5b**). No more than 11/107 (10%) of the cells had significant CP with higher activity for either matches or non-matches in either the 600-ms pre-movement period or the 800-ms movement period ($P < 0.05$; permutation test). Thus on ambiguous trials, the differences in neuronal activity were not due to the subsequent lever movement that the animals used to report their perceived direction.

Controls for actual or planned eye movements

We examined whether differences in neuronal responses could have been caused by fixation eye movements that may have varied systematically with perceived direction. One *a priori* argument against such an

Figure 4 Choice probability (CP) analysis for pre-movement and movement intervals. (**a**) Each circle represents the CP value for one unit. Filled circles are cells with CP greater than that expected from chance using a permutation test. Points are spread along the horizontal axis for clarity. Average CP is indicated for each area. (**b**) Percentage of cells from MT, MST and LIP with statistically significant CP. Filled bins show percentage of cells with significant CP > 0.5; open bins show percentage of cells with significant CP < 0.5. (**c**) CP as a function of time for 5/16 and 1/2 fractional displacements, averaged among all MST and LIP neurons. CP was calculated in 100-ms bins centered every 50 ms. Thick lines indicate bins in which CP was significantly larger than expected by chance using a permutation test. The horizontal black bars indicate the first-motion interval and the triangles indicate the appearance of the dots and aperture.

artifact is that there was little modulation in MT neurons, which can be quite sensitive to small changes in eye position[14]. Nonetheless, from the eye-position data saved while recording from the 167 MST and LIP neurons, we analyzed the mean eye position and the distribution of microsaccades when the animals reported perceiving the preferred or null direction on ambiguous trials (Methods). Only 5/167 (3%) of sessions showed a significant difference in the distributions of mean eye position (two-dimensional Kolmogorov-Smirnov test; $P < 0.05$), and only 6/167 (4%) of sessions showed a significant difference in the distribution of microsaccades projected as a component along the preferred–null axis (Mann-Whitney test; $P < 0.05$). Moreover, for a given reported direction, the amplitude of the mean microsaccade was generally far less than the mean amplitude of the microsaccades, indicating that the distributions of microsaccades were not skewed in a particular direction. We also measured the mean eye velocity between microsaccades to determine whether there may have been slow drifting eye movements that varied systematically with perceived direction (Methods). Only 12/167 (7%) of sessions showed a significant difference in the mean inter-microsaccadic eye velocity projected as a component along the preferred-null axis (Mann-Whitney test; $P < 0.05$). In addition, only 6/167 (4%) of neurons showed a statistically significant relationship between the spike counts during the first motion interval on ambiguous trials and the mean inter-microsaccadic eye velocities (linear regression analysis; $P < 0.05$). Thus we found no evidence that eye movements within the fixation window could have accounted for the neuronal selectivity on ambiguous trials.

Many LIP neurons are selective for the locations of planned saccades[15], so we also needed to ensure that the perceptual modulation in LIP was not an artifact of saccade planning. Although the animals fixated throughout all trials, they may have planned a saccade toward the
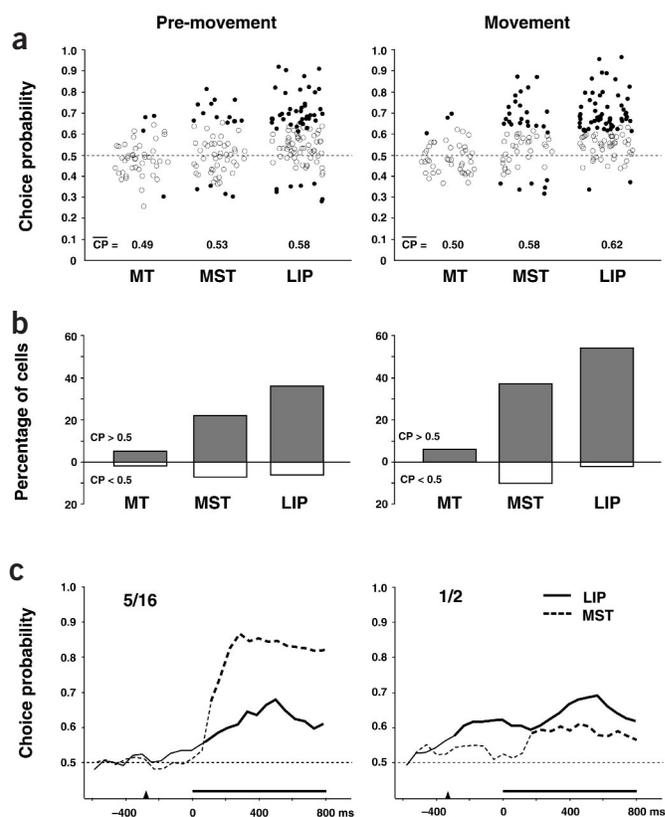
patch of moving dots, and the exact target of that planned saccade may have depended on perceived direction. For example, the animals may have planned saccades toward opposite sides of the stimulus aperture when they perceived the opposite directions of motion, or the animals could have been biased before a trial to saccade to one or the other side of the aperture. We tried to minimize this potential artifact by placing the stimulus in the center of the response field for each LIP neuron. Moreover, on rare trials when animals broke fixation and made saccades to unambiguous moving stimuli, we did not notice any obvious bias in the saccade endpoints depending on the motion direction. Nonetheless, for 13 LIP neurons that showed significant perceptual modulation on ambiguous trials, we also had the animals make delayed saccades to the two opposite sides of the stimulus aperture, along the axis of motion (**Fig. 6a**). We measured the firing rate during the delay period and calculated CP with respect to the two saccade directions. None of the 13 cells showed CP significantly different from chance (permutation test; $P > 0.05$), nor was there a systematic difference in mean firing across all 13 neurons (paired t-test; $P > 0.5$). There was also no relationship between the CP observed in the main task and in the saccade-control trials (**Fig. 6b**). Therefore, activity related to potential saccade planning could not account for the selectivity observed for ambiguous trials in the main task.

Perceptual modulation and MT

According to previous studies, MT responses can be affected by the perceived direction of ambiguous stimuli[6], including directionally bistable stimuli[8–10]. One reason for our different results could be that the motion stimulus we used was not optimized for MT neurons. For example, the apparent speed of our ambiguous motion stimulus was only ~3°/s. This speed was determined by the frequency of stimulus updates, which was <10 Hz so that the dots would appear to move rather than flicker[16]. MT neurons were nonetheless still directional for unambiguous motion at ~3°/s (**Fig. 2a,b**), suggesting that low speed *per se* was not the reason for the lack of directionality on ambiguous trials.

A related explanation could be that the spatiotemporal 'jumps' on ambiguous trials exceeded the range for directional interactions in MT (refs. 17,18 and Shadlen, M.N. *et al.*, *Soc. Neurosci. Abstr.* **19**, 1282, 1993). We examined this by testing ten MT neurons from one animal on trials in which the dots were displaced by the same distance (0.4°) and with the same timing as on ambiguous trials (every 133 ms), but with the dot columns spaced twice as far apart (1.6°) so that the fractional displacement would only be 1/4 of the inter-column spacing. On these trials, the monkey reliably reported the direction as that corresponding to the smaller possible displacement (86% of trials). The direction selectivity of MT neurons was weak under these conditions (average response among the ten neurons: 22.0 ± 4.1 spikes per second (sp/s) for the preferred direction and 16.7 ± 3.6 sp/s for the null direction), but all ten neurons still had significantly larger responses when the smaller possible displacement was in the neurons' preferred direction (t-test; $P < 0.05$). With the dots spaced by the usual 0.8° (ambiguous trials), none of the ten cells had a significantly different response when the animal reported preferred versus null direction (t-test; $P > 0.05$; average responses of 19.4 ± 4.1 sp/s and 19.4 ± 4.4 sp/s). Thus, whereas MT neurons were at least weakly direction selective for apparent motion with the same spatiotemporal jumps used in the ambiguous stimulus, their activity did not predict the monkey's perceived direction on ambiguous trials.

DISCUSSION

Our main finding was that the responses of many direction-selective parietal neurons were predictive of the monkey's perceived direction
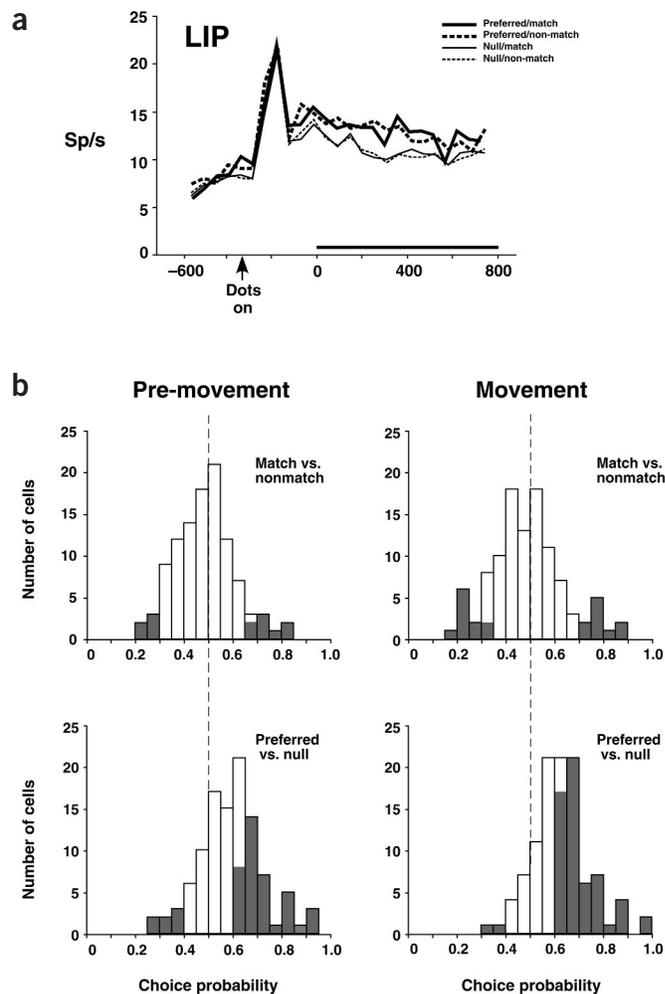
Figure 5 Responses of LIP neurons were modulated by perceived direction and not by report of match (lever movement left) or non-match (lever movement right). (**a**) Average population responses for all 107 LIP neurons divided by whether the animals perceived the preferred direction or the null direction and by whether the animals reported matches or non-matches. The horizontal black bar indicates the first-motion interval. (**b**) Distributions of choice-probability values among all 107 LIP neurons for the pre-movement period (left) and movement period (right). CP was calculated with respect to whether the animals reported match or non-match (top) and with respect to whether animals perceived the preferred or null direction (bottom). Shaded bins indicate the distribution of cells that had CP significantly different from chance. For match versus non-match, CP values >0.5 indicate units with the distribution of responses shifted toward larger responses for matches.

of perceptually bistable apparent motion. The prevalence of these neurons varied markedly among parietal areas: common in LIP, less common in MST, and nearly absent in MT. This variation mirrors the anatomical hierarchy of MT, MST and LIP in the parietal visual stream[19], suggesting that neuronal responses become more aligned with the subjective perception of apparent motion in higher parietal areas. In particular, we found that the directionality of LIP neurons was similar for unambiguous motion and ambiguous motion, as if the direction selectivity in LIP were related largely, if not exclusively, to perceived direction (**Fig. 2a,b**). Such a hierarchical view is consistent with findings in both the parietal and temporal visual streams. For example, average choice probability relating neuronal firing to the perceived direction of noisy random-dot stimuli is higher in MST[20] than
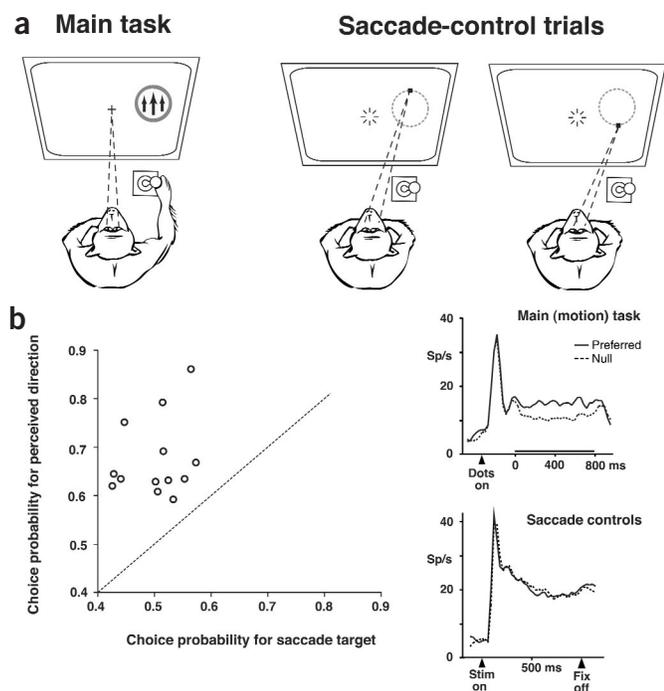
Figure 6 Control for planned saccades. (**a**) Design of the delayed saccade controls. After the animals had finished with the main task for a given neuron, we also had them make saccades to spots placed at the two sides of where the aperture had been, along the diameter parallel to the preferred–null axis for the cell under study. The position of the aperture is shown as a light dashed circle for the saccade controls, but neither the aperture nor the moving dots were shown during those trials. On each trial, after the animal had fixated at the center, one of the two spots was turned on. After a 1-s delay, the fixation point disappeared and the animals were required to saccade to within 2° of the remaining peripheral spot. The spot was left illuminated to ensure a more accurate saccade. Four saccades were made toward each of the two targets during eight-trial blocks, with the order randomized from trial to trial. (**b**) CP for the saccade-control trials versus CP for perceived direction calculated in the main task. CP was calculated from spike counts during the 1-s delay period. For saccade controls, CP > 0.5 indicates units with the distribution of responses shifted toward larger responses for saccades made to the target corresponding to the preferred direction of motion in the main task. Diagonal line has unity slope. Right, average responses among the 13 neurons in the main task (top) and for saccade-control trials (bottom). For the main task, solid and dashed traces indicate trials in which the animals perceived the preferred or null direction, respectively. For the saccade-control trials, solid lines and dashed lines indicate trials in which the saccade target appeared on the sides of the aperture corresponding to the preferred or null direction, respectively.

MT[6]. In addition, perceptual modulation for binocularly rivalrous stimuli is more prevalent in inferotemporal cortex[21] than in V1, V2 or V4 (refs. 7,22).

The relationship of parietal activity to perceived direction that we observed may have an interesting parallel in attentional modulation. There is evidence that attention is required to perceive concerted motion in bistable apparent motion displays[23]. At the neuronal level, however, attentional modulation is generally weaker in MT than in MST, LIP or the ventral intraparietal area[24,25]. Thus for bistable apparent motion stimuli like those presented on our ambiguous trials, MT neurons might only provide a balanced, non-directional representation of the stimulus, leaving higher areas to 'interpret' a direction. This view is consistent with recent results from human patients with parietal lesions that spare MT. These patients are not impaired in perceiving smooth, low-level motion, but are impaired in perceiving higher-level apparent motion stimuli[26]. In this view, our findings should not be assumed to extend beyond the specific apparent motion case that we tested. For smooth, low-level motion, neuronal activity in cortical areas other than LIP might be more closely related to the subjective perception of direction.

A second finding in our study was that for many LIP and MST neurons, the level of activity before the start of movement predicted the direction that the animal subsequently perceived on ambiguous trials. Neuronal 'biases' of this sort have been observed for eye-movement related neurons in the cortex[27,28] and superior colliculus[29] when animals are given a choice of saccade targets. In those studies, variations in firing rate were largely related to where the animal subsequently made a saccade. Thus the neuronal biases presumably reflected the animal's decision of where to move its eyes. The pre-movement activity that we observed in parietal neurons was distinct in that it did not predict the animals' behavioral report (the hand movement indicating match or non-match), but rather it predicted the perceived direction of the upcoming ambiguous motion. This raises the intriguing possibility that parietal pre-movement activity might have a causal relationship to the animal's subsequent perception of the direction of ambiguous motion (or it could reflect activity from other brain areas that influence perception). If so, the level of pre-movement activity probably covaries among many neurons with similar direction preference.

Although variability in pre-movement activity was related to perceived direction, we do not know the origin of the variability. One possibility is that the level of pre-movement activity is related to events occurring on previous trials[30]. For example, the animal might expect motion in a particular direction based on the pattern of directions presented on recent trials. A thorough analysis of the pre-movement activity should take into account all of the possible factors from previous trials, including the animal's report, whether the animal was rewarded and the neuron's firing rate. Regardless, it is interesting to speculate that variations in the ongoing activity could provide a 'guess' about the visual scene under conditions in which visual stimuli are ambiguous or otherwise non-ideal[7]. Consistent with this view, LIP neurons also signal direction under conditions in which the animal can expect motion in a particular direction, even if no motion is visible[11,12]. What emerges is a view that some parietal neurons are actively involved in motion perception, filling in the gaps when visual information is incomplete or ambiguous.

METHODS

Behavioral paradigm. The motion stimulus consisted of columns of white dots (68 candela (cd) per m², 0.1°-wide) drawn against a dark background (0.5 cd/m²). Adjacent columns were separated by 16 pixels (0.8°). The dot columns were surrounded by a dim gray aperture (14 cd/m²) with a 7° inner diameter and a 1°-wide rim. The aperture was required to support a perception of concerted motion rather than back-and-forth flicker. On successive video updates, the dots were displaced perpendicular to the columns by 5, 6, 7 or 8 pixels, corresponding to 5/16, 3/8, 7/16 and 1/2 fractional displacements. For the 5, 6 and 7-pixel displacements, the smaller possible displacement was either in the preferred or null direction; there was only one possible 8-pixel (1/2) displacement. The fractional displacement and direction for the first motion interval were purely randomized from trial to trial so that the animals could not predict the upcoming stimulus. The probability of each of the four fractional displacements was 0.25. For the 1/2 condition, the two possible stimulus configurations were alternated every ten frames (133 ms at 75 Hz video refresh). The number and density of dots and the stimulus-update rate were chosen in

preliminary experiments to give human observers the most robust sense of motion on ambiguous trials over a wide range of eccentricities. In particular, it was critical to keep the stimulus-update rate <10 Hz to make the 1/2 condition appear as movement rather than flicker. The rate of stimulus update for all fractional displacements was adjusted to keep the average apparent speed as close as possible to 3°/s. For example, for the 5/16 fractional displacement (0.25°), the stimulus was updated after every six frames (80 ms). The same set of stimuli was used for all neurons, except that the stimulus aperture was centered in the receptive/response field for each neuron, and the dot columns were rotated to produce motion along the preferred–null axis for each neuron.

On each trial, the animals first fixated within ±0.5° of the fixation point. Fixation had to be maintained for as long as the fixation point was visible, or the trial would abort without reward. After 500 ms, the dots and aperture appeared. The dots remained stationary for at least 279 ms before moving so that the initial on-transient response would be separated in time from the motion response. (This delay was inadvertently slightly different among the four fractional displacements: 279 ms for the 5/16 condition, 306 ms for the 3/8 and 7/16 conditions and 333 ms for the 1/2 condition. This should not affect any of our conclusions.) The first motion interval was limited by the integral number of stimulus updates that could fit within 800 ms. In preliminary experiments with human observers, we found that 800 ms was sufficient to produce a robust sense of motion on ambiguous trials, yet was short enough that perceptual reversals were extremely rare. The dots then disappeared for 200 ms, leaving only the empty aperture. During the second motion interval, the animals were free to move the lever to indicate match/non-match at any time, but had to wait at least 200 ms from the start of stimulus motion to discourage guessing. In practice, the animals rarely waited longer than 500 ms to make their choice. The time from reward to the start of the next trial was 1,000 ms.

Electrophysiology and receptive-field mapping. Two adult male rhesus monkeys weighing 8 and 12 kg were used. A titanium headpost, plastic recording chamber and scleral search coil were surgically implanted, following guidelines of the Harvard Medical School Standing Committee on Animals. The recording chambers were centered at stereotactic coordinates (P3, L10) and allowed a dorsal approach to parietal cortex. Before recording, we obtained a T-1 weighted MRI scan (1-mm sections) to guide electrode penetrations. Single-unit recordings were made with tungsten microelectrodes using a guide-tube and grid system. Once a unit was isolated, we first tried to map its receptive field using a moving spot or bar under the experimenter's control. This generally was effective for determining the receptive field boundaries (if on screen) for MT and MST neurons. For LIP neurons, we used a delayed saccade task to map the response field. The animal first fixated on a point at the center of the screen. After 500 ms, a spot was turned on at one location, in one of eight directions and three eccentricities. After another 1,000 ms, the fixation spot was extinguished and the animal made a saccade to the target spot. The vast majority of LIP neurons were selective among saccade locations in this task. The location that gave the largest response during the delay period was used as the center position for the subsequent tasks. Once we determined the response/receptive field, we tested every neuron with a direction-tuning task that was identical to the main task except that direction was pseudo-randomized among eight directions (spaced at 45° intervals) from trial to trial, and the motion was updated at video-frame rates to make it as smooth as possible. The preferred–null axis was determined online for use in the main task. A clear preferred direction could be determined for nearly all MT and MST neurons. Most LIP neurons were less directional in this task, but usually showed directional bias. The direction that elicited the largest average response was designated the preferred direction, regardless of the response increment. In the main task, 'preferred direction' always refers to that assigned in the direction-tuning task. Every neuron was tested in the main task, including all LIP neurons. For each neuron, we tried to record until the animal had accumulated 15–20 reports in the less frequently perceived direction for the ambiguous condition. Among all 213 behavioral sessions (neurons), the mean number of the less frequent report was 16.5 trials. Neither animal showed much bias in the ambiguous condition: the percentage of the more frequently reported direction exceeded 65% in only 12/213 behavioral sessions.

Identification of parietal areas. The pre-experimental MRI allowed us to target electrode penetrations to the intraparietal sulcus (IPS) and the superior temporal sulcus (STS). With our dorsal approach through the IPS, we were usually able to discern medial and lateral banks based on the presence of a quiet intervening sulcus. We generally targeted the more ventral aspect of the lateral bank. Over the anterior–posterior range of our penetrations within the lateral bank, we found the vast majority of units were active and spatially selective during the stimulus onset, delay and perisaccadic periods of the delayed saccade task. These units (plus all intervening units in the same penetrations) were considered to be in LIP. We also recorded a few units near the fundus of the IPS, probably from VIP. These units were clearly distinct from LIP in that they responded strongly during passive receptive field mapping, and gave only transient on- and off-responses during the delayed saccade task. Within the STS, for more lateral penetrations we could often discern the anterior and posterior banks by the presence of the quiet, intervening sulcus, but this was not a useful landmark for more medial penetrations. Therefore, we distinguished MT from MST based on physiological criteria. MT units had smaller receptive fields that were generally proportional to their eccentricity, did not overlap the fovea, and rarely extended into the ipsilateral hemifield. MST units had much bigger receptive fields that often approached or included the fovea and often extended into the ipsilateral hemifield. For many MST neurons, the borders of the receptive field extended past the edge of the stimulus monitor. Without histological verification (the two animals are still in use), it is possible that a few MT units were assigned to MST, and vice versa, but this should not affect our main conclusions.

Data analysis. For neuronal data, we counted spikes on each trial during the 800-ms first-movement interval and during the 600-ms pre-movement interval. For saccade-control trials, spikes were counted during the 1-s delay period. Choice probability (CP) was calculated for each unit using a method described previously[6]. CP was determined after trials were sorted according to whether the animals reported perceiving the preferred or null direction and trial-spike counts were binned into 20-bin histograms. To determine whether a CP value was different than that expected from chance, we used a permutation test[6]. For each unit, spike counts were randomly reshuffled into two groups and CP was re-calculated for the shuffled data. This procedure was repeated 1,000 times to obtain a distribution of permuted CP measures. If the actual CP value was larger or smaller than 95% of the permuted values, we considered the CP to be beyond that expected from chance. To examine CP as a function of time during trials (**Fig. 4c**), we calculated CP in 100-ms bins centered on every 50 ms and then averaged across all units. Statistical significance was determined for each 100-ms bin using the same permutation test as above, except that for each of the 1,000 iterations, we calculated the permuted CP values for each bin for each unit and then averaged among all units. Average CP for a given bin was considered to be significantly different from chance if it was larger or smaller than 95% of the averaged permuted CP values for that bin.

For eye-movement analyses, eye position was recorded every 5 ms. For each unit, mean horizontal and vertical eye position within the fixation window was calculated for the 800-ms first-motion interval for each ambiguous trial. A two-dimensional Kolmogorov-Smirnov test was used to compare the distribution of eye positions between trials in which the animals perceived the preferred or null direction of motion. To examine eye movements within the fixation window, we used a method adapted from previous work[10]. For each trial, we determined the eye velocity throughout the 800-ms first-movement interval by differentiating the eye position after averaging position over 50-ms intervals. If the eye speed exceeded 10°/s, we considered that to be a microsaccade event. We measured the actual speed and direction of each microsaccade as a component projected onto the preferred–null axis of the cell. For each trial, we also excluded the identified microsaccades, and then calculated the mean inter-microsaccadic (slow) eye velocity as a component projected onto the preferred–null axis of the cell. For each unit, we used a Mann-Whitney test to compare the distributions of microsaccades and mean inter-microsaccadic velocities between trials in which the animals perceived the preferred direction or the null direction. In addition, for each unit we also calculated a 'mean' microsaccade for the two perceived directions by treating each identified microsaccade as a vector with amplitude and direction, and then used vector averaging.

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