

between a specific feature of hippocampal activity—the use of an appropriate hippocampal map—and ability to locate a hidden goal. They also suggest one neural substrate for the impaired performance of aged animals on spatial tasks. A remaining challenge will be to see how the inflexibility of spatial representations seen here in aged rats

might relate to age-related impairments in tasks where self-motion and distal cues are not in conflict with one another.

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Motion perception: read my LIP

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Neural activity in the enigmatic lateral intraparietal area (LIP) of the monkey brain is now reported to reflect the perceived direction of ambiguous motion more faithfully than does activity in other areas apparently specialized for motion analysis.

Consider the dynamic trail of lights moving on a marquee outside a movie theater. A single bulb is lit at any point in time, and when it goes dim, one of its neighbors lights up. As this sequence propagates, there emerges a compelling impression of motion. For scientists studying the brain mechanisms of visual perception, this pattern of lights poses an interesting puzzle: why do we see such vivid movement when each light is, in fact, stationary? Nearly a century ago, Wertheimer's¹ observations of a related sort of 'apparent' motion launched the Gestalt psychology movement. The existence of such visual illusions reminds us that we do not perceive raw sensory data, but instead our perceptions are continually shaped by finely tuned interpretive processes in the brain.

The study by Assad and colleagues in this issue² investigates how neural activity in several areas of the macaque monkey brain might contribute to motion perception. The authors used apparent motion, which is known to activate many neurons in the visual cortex³, along with a trick (described below) to focus on the purely perceptual aspects of this activation. The responses of neurons in LIP were closely linked to the direction that the monkey perceived a stimulus to be moving, an unexpected result given that LIP is usually associated with spatial attention⁴ or the planning of eye movements⁵. Furthermore, the middle temporal (MT)

and medial superior temporal (MST) areas of parietal cortex, which have been linked with the perception of motion and three-dimensional shape derived from motion^{6–8}, showed comparatively little correspondence with perceived direction in the present study.

The primary function of LIP is the topic of a long-standing debate: some claim that it is fundamentally involved in spatial visual attention⁴, and others insist that its main role is in the planning of saccadic eye movements⁵. Still other studies have considered LIP activity to reflect decisional processes⁹, shape analysis¹⁰ or the guidance of hand movements for grasping three-dimensional objects¹¹. In previous work, Assad and colleagues showed that LIP neurons could reliably signal the direction of a visual target, even when it was temporarily invisible¹². This observation does not fit neatly into any of the putative functions of the LIP described above, but it does suggest that neurons in this area might contribute to the internal representation of stimulus motion. And, in a sense, it sets the stage for the current experiments.

Here the authors used apparent motion created by two-dimensional arrays of evenly spaced dots to elicit visual responses from neurons in the three brain areas (Fig. 1a; note that only one spatial dimension is depicted in the figure). With such patterns, the perceived direction depends on the distance that the dots hop sideways with each new frame. In one condition, neurons were tested with two different directions: 'preferred' (the direction eliciting the largest neural responses) and 'anti-preferred' (the opposite direction).

In the most crucial condition, the authors carefully adjusted the distance of the hops to exactly half of the inter-dot spacing. This resulted in a stimulus whose perceived movement direction was equivocal (Fig. 1a, right). Humans viewing such a pattern see vivid motion, but its direction spontaneously reverses after a few seconds. Likewise, when Assad and colleagues² presented such stimuli briefly, the monkeys reported that identical stimuli moved in opposite directions on different trials. In this testing, the monkeys reported, with a hand movement, whether or not two subsequently viewed stimuli—an ambiguous one and an unambiguous one—moved in the same direction. This ensured that there was no systematic correspondence between the percept and hand movement—an important safeguard given that motor movements themselves might influence neural responses in this part of the brain. Thus, armed with an ambiguous motion stimulus and monkeys willing to report their subjective impression of direction, the authors proceeded to investigate how individual cortical neurons responded to perceived movement.

In comparing responses across the different areas, Assad and colleagues² found that activity in LIP seemed to correlate more strongly with the perception of movement than activity in the 'motion areas' MT and MST (Fig. 1b). They reached this conclusion by examining the selectivity of the neurons (roughly speaking, the difference in activity when the preferred versus the anti-preferred stimulus is seen). In the unambiguous stimulus condition, responses in the motion areas were selective for the direction of

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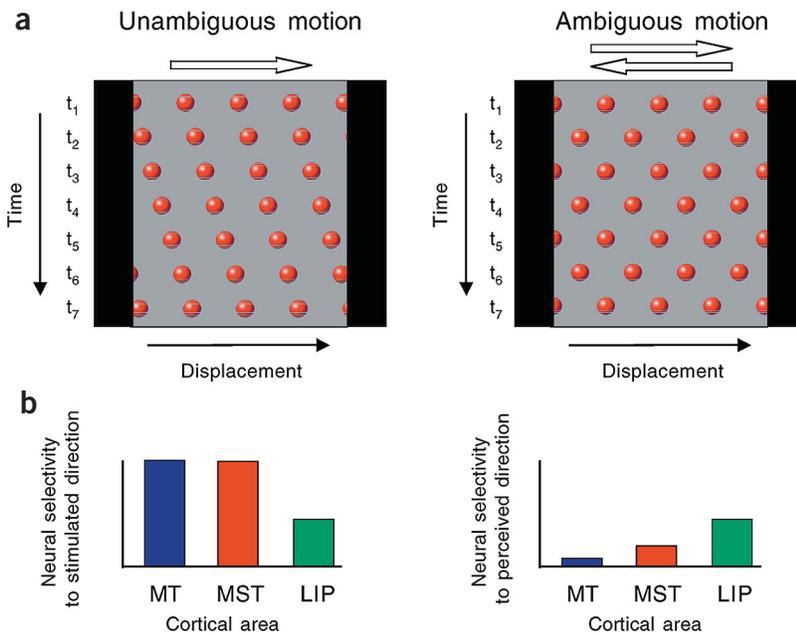


Figure 1 Stimuli and direction-selective neural responses for the two main conditions used by Assad and colleagues². **(a)** One-dimensional depiction of the dot array stimulus used in this study (horizontal direction), jumping as a function of time (vertical direction). In the unambiguous condition, the dots were shifted by less than half the inter-dot distance with each jump ($\Delta t \approx 150$ ms). This results in a stable percept of motion direction (seen here by the prominent upper-left to lower-right diagonal pattern in the space/time diagram). In the ambiguous condition on the right, the dots jump exactly half their spacing with each new presentation, resulting in an equal probability of seeing leftward or rightward motion. The inherent ambiguity in the stimulus can be seen as two equally prominent diagonal orientations. **(b)** Relative neural responses during the unambiguous (left) and ambiguous (right) stimulus conditions in three areas of the parietal cortex: the middle temporal (MT), medial superior temporal (MST) and lateral intraparietal (LIP) areas. In the unambiguous condition, all areas, particularly MT and MST, were highly selective for one direction of motion compared to the opposite direction. In the ambiguous condition, however, activity in these motion areas was much less correlated with the monkey's percept than that in area LIP.

the apparent motion, as expected from previous studies. During ambiguous stimulation, however, when selectivity was defined not by differences in the stimulus but rather by differences in the perceived direction, activity in these same areas showed little (MST) or no (MT) selectivity. In contrast, the direction-selective responses in area LIP were similar in the ambiguous and unambiguous conditions, suggesting that the activity of neurons in that area is more closely related to the subjective perception of motion than to any particular physical stimulus attribute.

How might this new observation fit with the other putative roles of LIP? One additional detail may shed some light on this question. Namely, when Assad and colleagues examined perception-related activity differences on a trial-by-trial basis, they found that such differences were generally present even before the stimulus motion began. In other words, activity in LIP predicted the impending percept. One interpretation might be that ongoing activity fluctuations continually bombard this and other motion-processing areas, and, by affecting basic sensory responses, randomly tip the balance as to which directional signals reach perception. However, given the complex role of the posterior parietal cortex in attention

and motor planning, it might be worthwhile to entertain other explanations as well. For example, it is possible that the early activity is not random, but instead reflects for each trial the imposition of a particular neural context for the interpretation of the sensory data. According to recent psychophysical results, the interpretation of a briefly shown ambiguous pattern is not random on each trial, like the toss of a coin. Instead, it seems that the brain can be strongly biased for one or another based on its perceptual history or expectation¹³. It is therefore possible that the predictive activity measured by Assad and colleagues² may reflect the rumblings of the brain's internal interpretive machinery. The prominence of such activity in LIP may suggest that mechanisms responsible for such interpretive elements of vision are closely linked to the circuitry of attention and motor planning¹⁴.

When Wertheimer made his first observations of apparent motion in 1911, he was already entertaining ideas regarding its possible physiological substrates¹⁵. Now, nearly 100 years later, we are still struggling with similar questions. In that respect, the current study is a humbling reminder that we lack a basic understanding of how the brain derives a percept from its visual input. Nonetheless, the present results² provide a new angle on

this puzzle, and it will be of great interest to see whether future studies will similarly point to attentional and motor planning centers as being critical for shaping visual perception.

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