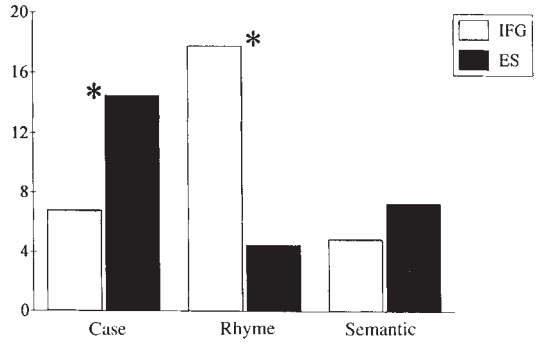

FIG. 3 Task by region of interest. Ordinate represents mean activations for case, rhyme and semantic subtractions in the inferior frontal gyrus (IFG; grey bars) and extrastriate (ES; black bars) regions, respectively. A significant interaction between task and region was observed, $F(2, 72) = 9.94$, $P < 0.001$. The means for the case, rhyme and semantic subtractions in the IFG region were 6.8, 17.8 and 4.9; corresponding means in the extrastriate region were 14.5, 4.5 and 7.3, respectively. Separate contrasts revealed that in the IFG region rhyme significantly differed from both case, $F(1, 36) = 10.0$, $P < 0.001$, and semantic, $F(1, 36) = 13.88$, $P < 0.001$, whereas case and semantic did not differ ($F < 1.0$). In the extrastriate region, case significantly differed from both rhyme $F(1, 36) = 8.37$, $P < 0.001$, and semantic, $F(1, 36) = 4.27$, $P < 0.05$. The rhyme and semantic conditions did not differ ($F < 1.0$). To test the hypothesis further that extrastriate areas subserve orthographic processing while the IFG region subserves phonological processing, we contrasted activation produced in a rhyme–case versus a rhyme–line subtraction. By the logic of the design, the former subtraction differs only in phonology whereas the latter subtraction differs in both orthography and phonology. A significant difference between these two subtraction conditions should therefore be observed in the extrastriate as only the rhyme–line should isolate orthography and there should be no difference in the IFG region as both conditions should isolate phonology. As expected, the effect was significant in the extrastriate area, $F(1, 36) = 17.89$, $P < 0.001$. The means were 4.5 and 19.0 for the rhyme–case and rhyme–line conditions, respectively. In the IFG region, the contrast was not significant ($P > 0.10$) with means of 17.6 and 23.1 for the rhyme–case and rhyme–line conditions, respectively. Asterisks indicate tasks that significantly differ between regions ($P < 0.001$).

bilaterally. Error rates on each task were extremely low (on average one error per 20 trials) and did not vary systematically with task or by sex, suggesting that the tasks did not differ significantly in their difficulty. The three-way interaction between region of interest, hemisphere and sex was significant ($F(1, 36) = 7.77$, $P < 0.01$) and is shown in Fig. 2. Activation in the IFG region was left-lateralized for males but bilateral for females, whereas extrastriate activation was bilateral for both males and females. In addition, these analyses confirmed that the case-line subtraction (which isolates orthographic processing) more strongly activates extrastriate sites whereas the rhyme-case subtraction (which isolates phonological processing) more strongly activates the IFG region (Fig. 3).

The regions of interest examined encompass those areas traditionally considered to be critical for language[26–28]. We recognize, however, that our study does not provide information about every possible brain region and that there may be other sites relevant to phonological processing which may not show gender differences. Although we do not want to claim that phonological processing makes no demand on right hemisphere sites in males, we wish to emphasize that in a site uniquely serving phonological processing, the IFG, females devote greater right hemispheric resources to the task.

Our results indicate that it is now possible to isolate specific components of language and, at the same time, to relate these language processes to distinct patterns of functional organization in brain in neurologically normal individuals. Using this strategy, we have demonstrated remarkable differences in the functional organization of a specific component of language, phonological processing, between normal males and females. Future studies designed to examine either gender differences in language function or the neural mechanisms related to language, for example, should be specific for the component of language assessed and determined in both males and females. □

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Integration of motion and stereopsis in middle temporal cortical area of macaques

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THE primate visual system incorporates a highly specialized subsystem for the analysis of motion in the visual field[1–6]. A key element of this subsystem is the middle temporal (MT) cortical area, which contains a majority of direction-selective neurons[1–3]. MT neurons are also selective for binocular disparity (depth), which is perplexing given that they are not sensitive to motion through depth[7]. What is the role of disparity in MT? Our data suggest an important link between disparity and transparent motion detection. Motion signals in different directions tend to inhibit each other within a given MT receptive field[8]. This inhibi-

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tion has an averaging effect which minimizes MT responses to random motion signals created by light intensity changes and other non-motion stimuli (motion noise)[9]. But, in the absence of disparity cues, inhibition may also occur between surfaces moving in different directions through the same part of the visual field (transparent motion), thus impairing the detection of either surface. Here we show that inhibition in MT occurs mainly between motion signals with similar disparities. Transparent surface movements at different depths are thus represented independently in MT (that is, without inhibiting each other) whereas spurious motion signals from a given surface tend to cancel out. To our knowledge, these results provide the first evidence for a functional integration of motion and disparity in MT.

We used the stimuli shown in Fig. 1*b* and *c* to study the effect of binocular disparity on motion-opponent inhibition in MT. Each stimulus consisted of a 'preferred' random dot pattern, which moved in the preferred direction and at the preferred depth (disparity) for a given cell, and an 'antipreferred' pattern, which moved in the opposite direction and could assume a variety of depths. The preferred and antipreferred patterns were superimposed to form a transparent motion stimulus (Fig. 1*b*) in which opposite motions were interspersed. We also created two-panel, 'motion border' stimuli to study inhibition between movements in different parts of the receptive field (Fig. 1*c*).

Results were similar for the two stimulus types. In general, both suppressed MT firing rates relative to responses elicited by preferred-direction motion alone. In nearly two-thirds of the neurons, however, the amount of suppression depended on the depth of the antipreferred pattern (Figs 1 and 2). In many neurons (~40% of all tested), suppression was strongest when the antipreferred pattern was at or near the depth of the preferred pattern (Fig. 1). Thus, in these neurons the disparities that caused the strongest excitation in the preferred direction also caused the strongest inhibition in the antipreferred direction. We refer to these as 'planar opponent' cells. In other cells, suppression was strongest when the antipreferred pattern was either in front of or behind the preferred pattern ('near/far opponent' cells; about 15%). Finally, in a small percentage of cells, suppression was weakest when the opponent patterns were at similar depths ('additive' cells; about 4%). The remaining third of the neurons were strongly suppressed regardless of the depth of the antipreferred pattern (Fig. 2*b*, *e*). The distribution of response types is detailed in Table 1.

TABLE 1 Classification of MT neurons according to responses to transparent and motion border stimuli

	Number of cells (% modulation ± s.d.)			
	Planar opponent	Near/far opponent	Additive	No apparent tuning
Transparent stimuli ($n=127$)	41 (49 ± 29%)	22 (48 ± 48%)	6 (38 ± 9%)	58 (NA)
Motion border stimuli ($n=124$)	53 (41 ± 22%)	21 (47 ± 25%)	3 (27 ± 4%)	47 (NA)

In each stimulus, the preferred direction pattern was held at the cell's optimal disparity, whereas the antipreferred direction pattern assumed a variety of disparities. Cells were then classified according to the disparity tuning curve for the antipreferred direction (see for example, Fig. 1*b* and *c*). If this curve showed a well defined minimum within 0.2° of the cell's optimal disparity, the cell was classified as 'planar opponent'. If there was a well defined maximum within 0.2° of the optimal disparity, the cell was 'additive'. If these criteria were not met, but responses were imbalanced on either side of the optimal disparity (such that the antipreferred pattern produced stronger suppression in front of or behind the preferred pattern), the cell was termed 'near/far opponent'. Cells not clearly satisfying these criteria were said to be without apparent tuning. Data shown represent numbers of neurons in each class. Values in parentheses give the per cent modulation; that is, the range of responses due to different antipreferred disparities, normalized in each case to the response to a preferred pattern alone. Data shown are from two cerebral hemispheres in 2 rhesus monkeys. A total 146 MT neurons were studied with either transparent or motion border stimuli (about half with both stimulus types).

Figure 2*a* and *d* shows averaged data for the planar opponent neurons. These cells were suppressed by ~40% (relative to preferred motion alone) when preferred and antipreferred patterns had the same disparity, and this suppression decreased by more than half to 10–20% (on average) when the patterns were separated by ±0.8°. Most of the suppression could thus be relaxed

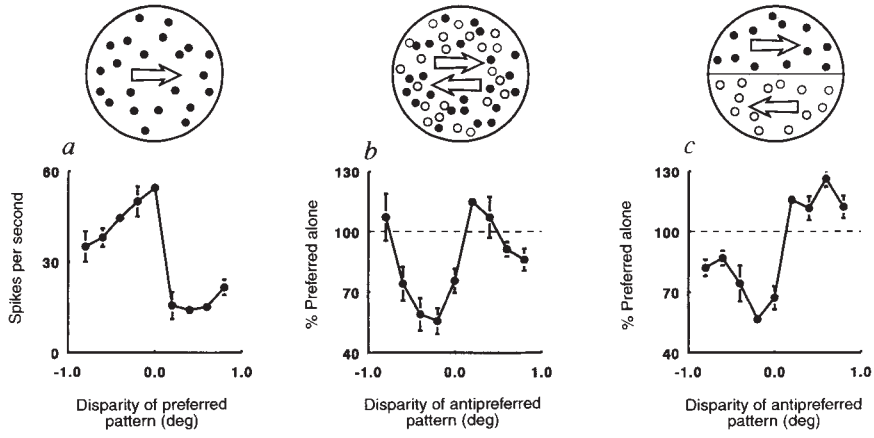

FIG. 1 Data from a 'planar opponent' neuron. The schematics across the top show the stimuli. Left: a single random dot pattern moving in the preferred direction (in this case three o'clock); middle: two superimposed patterns moving in opposite directions (transparent stimulus); right: two adjacent patterns moving in opposite directions (motion border stimulus). Solid circles represent dots moving in the preferred direction; open circles represent the antipreferred direction. Stimuli were 4° diameter and dot density was 5 dots per cm^2. Dots were rendered in stereoscopic depth using colour separation[4]. Disparity tuning curves are shown below: for the preferred pattern alone (left), for the antipreferred pattern in a transparent stimulus (middle), and for the antipreferred pattern in a motion border stimulus (right). For the transparent and motion border stimuli, the preferred pattern was always at 0° disparity (the optimal disparity for this cell). Responses to the two-pattern stimuli were normalized to responses to a preferred pattern alone. The data show that disparity tuning for the antipreferred direction is roughly opposite to tuning for the preferred direction. Error bars give standard error of the mean.

METHODS. Male rhesus monkeys were trained to fixate a point of light while stimuli were presented in the desired portion of the visual field. Eye position was monitored with a scleral search coil[19]. MT neurons were accessed on long, dorso–ventral penetrations with tungsten microelectrodes. After a neuron was isolated, its receptive field mapped, and its preferred direction and disparity determined, a series of motion-opponent stimuli were presented in the centre of the receptive field. Each stimulus lasted one second and was repeated (on average) 5 times; responses are expressed as the average firing rate over the last 800 ms of the stimulus periods. Additional experimental details may be found elsewhere[8,9].

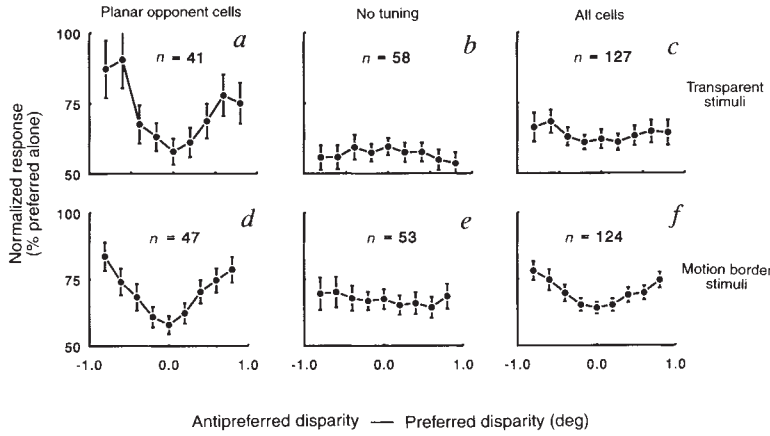

FIG. 2 Average responses to transparent and motion border stimuli. Graphs show firing rates (normalized to responses to preferred motion alone) as a function of the difference between preferred and antipreferred disparities (reflecting the apparent depth between the opponent surfaces). Top row: data for transparent stimuli. Bottom row: data for motion border stimuli. Left column: average responses for cells classified as 'planar opponent' (Table 1). Middle column: average responses for cells without apparent suppression tuning (Table 1). Right column: average responses for all cells. Values are means ± standard error. The planar opponency trend seen in the population data for motion border stimuli (*f*) was highly significant ($P < 0.001$; linear regression of normalized firing rate versus absolute antipreferred–preferred disparity difference). For the planar opponent cells (left column), the average tuning width for half-maximal effect (estimated graphically) was 1.0° for transparent stimuli and 0.9° for motion border stimuli.

by placing the opponent patterns at different depths. In fact, more than a third of the planar opponent cells (14/42 for transparent stimuli, 30/53 for motion border stimuli) did not respond significantly better to a single, preferred pattern than to an opponent stimulus with preferred and antipreferred patterns at different depths ($P > 0.05$, *t*-test). Thus in these cells inhibition depended strongly on the disparity associated with the antipreferred direction. However, we also found a sizeable group of cells in which inhibition did not vary with antipreferred disparity (Fig. 2*b*, *e*), suggesting that the planar opponent neurons represent a distinct group. When the data from all neurons are considered together (Fig. 2*c*, *f*), the planar opponent trend remains visible, at least in the motion border data (Fig. 2*f*) where the trend was highly significant ($(P < 0.001)$; see legend for details).

Our data thus show that motion-opponent inhibition in MT tends to occur within a given disparity channel; that is, between motion signals from similar stereoscopic depths. This finding suggests a physiological basis for recent psychophysical observations on the role of disparity in transparent motion perception[10]. Motion detection thresholds are elevated for opponent motion stimuli such as those used here[11–13], and it has been shown that coherent motion perception is almost completely suppressed if dots are 'paired' so that each small spatial region contains two opposite motions[10]. But when these paired stimuli contain disparity cues, such that opponent motions occur in different depth planes, observers readily perceive two moving surfaces: that is, transparent motion[10]. These findings are closely paralleled by our present data, which show strong MT suppression by opponent patterns at similar depths but little or no suppression by stimuli incorporating a disparity differential (Fig. 2*a*, *d*). These observations, taken with other studies linking MT activity to motion perception[14–16], suggest that disparity cues facilitate transparent motion detection by limiting inhibition in MT between motion signals from different visual depths.

Transparent motion detection might seem simpler if opponent inhibition did not occur in the first place. Directional V1 neurons in the macaque in fact show much less inhibition[8] and might thus seem better suited than MT neurons for detecting transparent motion. But because of the absence of opponency, V1 neurons respond well to motion noise[9] and therefore do not reliably report coherent motion. Most MT neurons, on the other hand, respond best to coherent motion[9] and continue to do so under transparent conditions as long as disparity (or other) information is sufficient to dissociate individual surface movements. Thus, by integrating motion and disparity cues, MT succeeds in representing transparent motion while retaining essential noise reduction properties.

It should be clarified that even without disparity cues, the opponent stimuli used here appear to be transparent; that is, two independently moving surfaces are perceived. One might infer from this that disparity cues are not important in transparent motion perception, given that transparency is already detectable without them. We must re-emphasize, however, that motion detection, measured psychophysically, is in fact substantially impaired for these and other opponent stimuli[10–13]. Moreover, we showed that motion perception is only possible in such stimuli because of small regions containing unbalanced (unopposed) motion signals[10]. If these unbalanced regions are prevented, coherent motion perception is lost entirely[10]. Under such conditions, the importance of disparity, which is sufficient to render even these balanced stimuli fully transparent, is unequivocal. We therefore believe that the effects of disparity elucidated here contribute to an important mechanism for transparent motion detection.

Our data provide evidence for a function for binocular disparity in MT. In an early demonstration of disparity tuning in MT[7], it was found that individual MT neurons do not respond selectively to motion in stereoscopic depth (although population coding cannot be excluded). The role of disparity in MT has since remained unclear. Perhaps disparity allows a more detailed description of moving objects; that is, depth and velocity rather than simply velocity. However, all the visual qualities of moving objects need not be represented in MT simply because they are moving; other aspects, such as colour and texture, could be represented in other cortical areas[17,18]. Why should disparity be represented in MT? Our data suggest that disparity plays an intrinsic role in MT motion computation by providing a means of distinguishing motion signals from different surfaces. Like disparity, other surface characteristics, such as speed, colour and spatial frequency, may also facilitate transparent motion detection by placing constraints on opponent inhibition in MT. □

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