expansion of $\gamma\delta$ T cells in response to MT-priming (*16*).

By all criteria of activation—high density IL-2R expression, response to IL-2, and in situ proliferation—the $\gamma\delta$ T cell subset appears to be roughly ten times as active as the $\alpha\beta$ T cell subset in the primary response to MT. This finding, together with the large amounts of IL-2 produced by isolated $\gamma\delta$ T cells in response to MT stimulation, indicates that $\gamma\delta$ T cells are important in generating lymphokines necessary for initiating the immune response to MT. An intriguing hypothesis is that $\gamma\delta$ T cells have been evolutionarily selected to respond to certain common microbial antigens, thus enabling this population to respond quickly while the population of antigen-specific $\alpha\beta$ T cells begins to expand. The secondary response may involve a switch in receptor usage ($\gamma\delta$ early in the response, then $\alpha\beta$ eventually taking over). Consistent with this notion is the virtual absence of expansion of the $\gamma\delta$ T cell population after secondary MT immunization (*17*).

Among the many potential mycobacterial antigens, certain proteins have been identified as common to all the mycobacterial species and, furthermore, are homologous to various *Escherichia coli* heat shock proteins. A number of these proteins are important in the cell-mediated response to mycobacteria (*18*). A panel of unselected thymocyte TCR $\gamma\delta$ hybridomas has been found to react with the 65-kD mycobacterial heat shock protein (*19*).

The failure of antibodies to MHC class II proteins to block the MT response of $\gamma\delta$ T cells contrasts with the response of $\alpha\beta$ T cells, whose recognition of soluble exogenous antigens (as confirmed in this study) generally requires MHC class II presentation. This result indicates that $\gamma\delta$ T cells and $\alpha\beta$ T cells recognize antigen differently and implies that they have distinct roles in the primary immune response. It will be of interest to determine the in vivo responses of $\gamma\delta$ T cells to other bacterial pathogens.

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Neural Integration of Information Specifying Structure from Stereopsis and Motion

MARK NAWROT AND RANDOLPH BLAKE

When one views a two-dimensional parallel projection of dots on the surface of a rotating globe, the direction of rotation is ambiguous, and the perceived direction of rotation of the two-dimensional figure is unstable over time. Stability can be temporarily induced by adaptation to a three-dimensional globe with a direction of rotation unambiguously specified by stereo disparity; adaptation causes the two-dimensional figure to appear to rotate in the direction opposite that experienced during stereoscopic adaptation. This adaptation effect is selective for axis of rotation but is not shape-specific. It does depend on simultaneous stimulation by multiple depth planes defined by elements moving in different directions. Evidently information about stereopsis and information about structure from motion are integrated within a common neural site in the brain.

THE HUMAN VISUAL SYSTEM HAS SEVERAL sources of information for recovering three-dimensional (3D) shape from two-dimensional (2D) images. One source is stereopsis, which arises from slight horizontal disparities between the two eyes' views. Indeed, so effective is stereopsis that it can extract depth and shape information from monocular images entirely devoid of recognizable form (*1*). A comparably effective source of information about 3D structure is relative motion (*2*). An object that has a shape that is ill-defined when stationary can be immediately perceived when that object moves (*3*). Both stereopsis and relative motion rely on multiple views of a scene to recover 3D structure; in the case of stereopsis the multiple views are provided by the two retinal images, whereas with relative motion the views are integrated over time. It has been proposed that stereopsis and relative motion are processed in common visual pathways (*4*). Here we report direct evidence that the visual nervous system integrates retinal disparity and relative motion information in the processing of 3D shape.

When one views a 2D parallel projection of dots on the surface of an object rotating about an axis, the direction of rotation is ambiguous; for instance, when rotation is about the vertical axis, observers experience a bistable percept whereby the figure's direction of rotation alternates over time between clockwise (CW) (that is, dots on the front surface move from right to left) and coun-

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Department of Psychology, Vanderbilt University, Nashville, TN 37240.

terclockwise (CCW). The perceptual instability when viewing a kinetic 2D image can be eliminated by presenting stereoscopic views of the kinetic 2D figure (*5*). In this case, observers reliably see rotation in just one direction or the other, dependent on the geometry of the retinal disparities. We have used an adaptation procedure to discover whether prolonged exposure to unambiguous 3D motion from stereopsis can bias the perceived direction of rotation of an ambiguous 2D figure. We reasoned that adaptation, a useful strategy for isolating sensory processes (*6*), should be effective if information about structure from stereopsis and information about structure from motion are integrated within common pathways.

The 2D and 3D displays were generated by a Macintosh II computer on two matched video monitors viewed through a mirror stereoscope. In the initial experiment, each monocular display consisted of the parallel projection of a rotating, transparent globe with a shape defined by 200 small (2-min arc) dots scattered randomly over its surface (Fig. 1A). The diameter of the globe was 2.5°, and it rotated 2° about its vertical axis every 33.4 ms; at this framerate, the globe appeared to rotate smoothly and continuously at ten revolutions per minute. By presenting to the right eye a view of the globe one frame in advance of or one frame behind the view of the globe seen by the left eye (*5*), the direction of rotation was unambiguously specified as CW or CCW. When the rotation angle was identical to the two eyes, the direction of rotation was ambiguous. In all experiments, a trial consisted of a 90-s period of adaptation followed by a 15-s period of exposure to a test display. During adaptation and test, the observer stared at a small cross, 6 min by 6 min, located at zero disparity in the center of the globe. The observer's task was to indicate by a key press which direction the ambiguous 2D test figure appeared to rotate, CW or CCW. Rest periods between test episodes were of sufficient duration to dissipate any effects of prior adaptation. Four observers participated in formal testing, and the main phenomena have been confirmed by informal testing of other people.

When identical versions of the 2D rotating figure were viewed by the two eyes, reversals in the perceived direction of rotation were readily experienced (*7*), confirming the ambiguity of the rotation of the 2D figure. Adaptation to a globe with a direction of rotation that was rendered unambiguous by stereopsis caused the nonstereoscopic 2D figure to appear to rotate in the direction opposite that experienced during stereoscopic adaptation. Thus, adaptation to 3D CW rotation caused the 2D figure to appear to rotate CCW, whereas adaptation to 3D CCW rotation caused the 2D figure to rotate CW (Fig. 1A). The aftereffect of stereoscopic adaptation lasted no longer than approximately half a minute. Moreover, adaptation and test displays had to be imaged on the same retinal location for one to bias the other. We found the same pattern of results when the stereoscopic adapting globe and the ambiguous 2D figure rotated about the horizontal axis. Without prior adaptation, the ambiguous 2D figure sometimes appeared to be rolling forward and other times appeared to be rolling backward. Unambiguous stereoscopic adaptation to forward roll now caused the 2D figure to appear to roll backward, and vice versa. Adaptation is specific to rotation about a given axis since adaptation to stereoscopic rotation about the vertical axis did not affect perception of 2D rotation about the horizontal axis (Fig. 1B).

Having established the robustness and selectivity of this adaptation effect, we tested its generality under various stimulus conditions. We found that adaptation to the stereoscopic globe also biased the direction of rotation of a 2D figure viewed monocularly. Of course, binocular viewing is required for stereoscopic adaptation, but evidently those neural elements activated during binocular adaptation are also stimulated during monocular viewing. We also found that a rotating 3D cube (defined by dots scattered over its surface) was an equally effective adapting stimulus (*8*), in that it strongly biased the subsequent direction of rotation of the 2D figure (Fig. 1C). Even adapting stereoscopically to a "wire" figure constructed from randomly oriented lines (*9*) significantly biased perception of the ambiguous 2D figure (Fig. 1D). These last two conditions imply that stereopsis influences relative motion even when the shape of a stereoscopic adaptation object differs from that of a test object defined by relative motion.

We tried adapting observers to a flat plane of dots moving in a single direction. This stimulus had no effect on perception of the 2D figure, regardless if the plane appeared in front of, on, or behind the fixation cross. However, adapting simultaneously with two sheets of dots that were stereoscopically segregated into separate depth planes in front of and behind the fixation point did

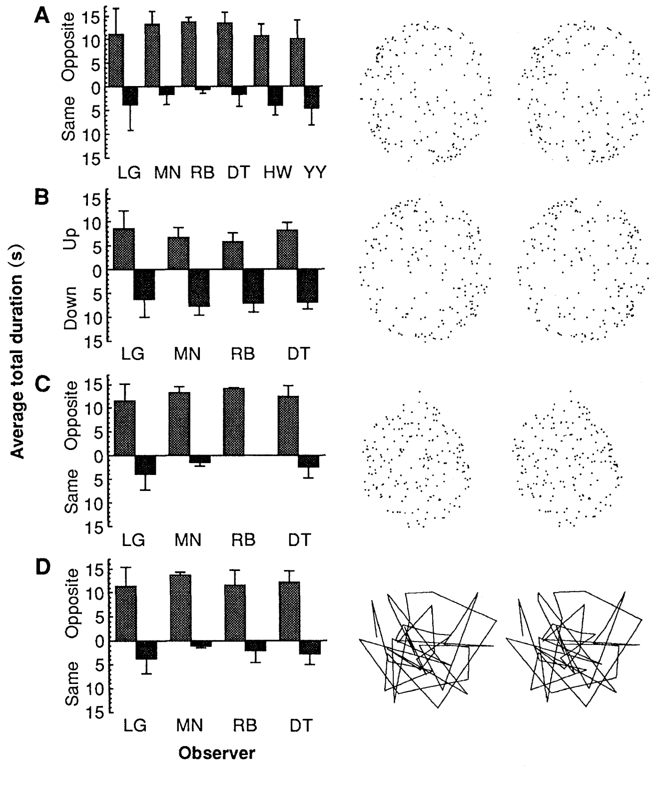

Fig. 1. Total duration of perceived direction of rotation of a 2D figure after different conditions of adaptation. For duration values labeled "opposite" (histograms above the horizontal axis), the test globe appeared to rotate in a direction opposite that experienced during adaptation; for values labeled "same" (histograms below the horizontal axis), the test globe appeared to rotate in the same direction as that experienced during adaptation. Each value is an arithmetic average based on at least eight observations; the bars denote ±1 SD. (**A**) The observer viewed a 3D globe and then tracked the direction of rotation of the ambiguous 2D figure. Both directions of rotation (CW and CCW) were randomly intermixed over conditions of adaptation; results for these two conditions are pooled. (**B**) The observer adapted to the 3D stereoscopic globe rotating either CW or CCW and was tested on a 2D figure with a horizontal axis of rotation; the test figure appeared either to roll forward ("down") or backward ("up"). Perceived direction of rotation of the 2D figure was independent of rotation of the 3D adaptation globe. (**C**) Direction of 2D rotation about the vertical axis following adaptation to unambiguous rotation of a 3D cube. (**D**) Direction of 2D rotation about the vertical axis after adaptation to unambiguous rotation of a 3D wire figure.

influence perceived rotation of the 2D figure. Specifically, when the front plane of dots moved rightward and the back plane moved leftward, the 2D figure appeared to rotate CW; reversing the conditions of adaptation reversed the direction of the aftereffect. Evidently the necessary condition for adaptation of motion by stereopsis is the presence of complex disparity fields carrying information about different directions of motion. In this respect, the present adaptation effect represents a more complex version of the disparity specific motion aftereffect studied by others (*10*).

For a final set of experiments, we devised a 2D figure which, though ambiguous in principle, nearly always appeared to rotate in one direction only. This figure was generated by restricting the display to just those 100 dots moving in a single direction, such that their frame-to-frame trajectories corresponded to one-half of the rotating 2D figure. In principle, this display could correspond to the forward-facing convex surface of a globe rotating in one direction or the rearward-facing concave surface of a globe rotating in the opposite direction. However, in fact, observers nearly always perceived the 2D figure as convex, the percept consistent with viewing a solid (that is, nontransparent) rotating globe; perceiving the textured surface of the globe as concave would imply a peculiar object, that is, a globe with an invisible front surface. With no prior adaptation, observers reliably saw this opaque 2D figure rotating in the direction specified by the dot motion. Adaptation to a full 3D stereo globe rotating in that direction, however, now caused the opaque 2D figure to appear to rotate in the opposite direction, such that its perceived surface curvature was concave, not convex. Thus stereoscopic adaptation forced the 2D figure to assume a direction of rotation and a transparency seldom experienced in the absence of adaptation.

Lastly, we determined whether adaptation to the 2D opaque globe would subsequently bias the perceived direction of rotation of the ambiguous 2D figure. To the extent that unambiguous motion per se is sufficient for adaptation, the 2D opaque globe should be an effective adapting stimulus. For the opaque 2D globe, like the stereo 3D globe, maintains a single direction of rotation throughout the adaptation period, but, unlike the 3D globe, it relies on nonstereoscopic information for disambiguation. We found that perception of the 2D figure remained unstable after adaptation to the opaque globe. This indicates that disambiguation of motion per se is insufficient to produce adaptation; evidently it is the confluence of stereo and motion information that enpowered the 3D globe in the previous experiments.

Considered together, our results demonstrate that extended exposure to structure from stereopsis subsequently influences the perception of structure from motion. It follows, therefore, that information for stereopsis and for relative motion is integrated somewhere within the nervous system. It is tempting to conjecture that this integration occurs in the middle temporal visual area (MT), a site in the brain known to be specialized for analysis of relative motion (*11*). After all, a large percentage of neurons in MT, besides being selective for direction of motion, respond only within limited ranges of horizontal retinal disparity and, hence, can signal stereoscopic depth (*12*). Moreover, MT neurons show an enhanced responsiveness to their preferred direction of motion after exposure to motion in the opposite direction (*13*), an effect that could parallel the adaptation phenomenon described here. Whatever the locus of the mechanisms implicated by our findings, it makes sense from a computational standpoint to embody these two processes in the same neural network, since motion information can resolve ambiguities inherent in stereopsis and vice versa (*14*).

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9. A random wire figure was generated by drawing 40 continuous and connected lines, random in length and orientation, within the coordinates of the cube surface. The wire figure rotated at the same rate as the globe and the cube, and its direction of rotation was specified unambiguously by phase shifting the angle of rotation 2° in one eye relative to the other.
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