Research Article

Neural Synergy Between Kinetic Vision and Touch

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ABSTRACT—*Ambiguous visual information often produces unstable visual perception. In four psychophysical experiments, we found that unambiguous tactile information about the direction of rotation of a globe whose three-dimensional structure is ambiguous significantly influences visual perception of the globe. This disambiguation of vision by touch occurs only when the two modalities are stimulated concurrently, however. Using functional magnetic resonance imaging, we discovered that touching the rotating globe, even when not looking at it, reliably activates the middle temporal visual area (MT+), a brain region commonly thought to be crucially involved in registering structure from motion. Considered together, our results show that the brain draws on somatosensory information to resolve visual conflict.*

People's daily activities are guided by an amalgam of sensory inputs from different modalities. These sensory modalities, although typically segregated in textbooks, function together to specify behaviorally important objects and events. To give just a few examples, sound and vision interact to influence speech perception (McGurk & MacDonald, 1976) and to specify the nature of dynamic events such as collision (Sekuler, Sekuler, & Lau, 1997). Similarly, sound can influence the perceived roughness of a touched surface (Guest, Catmur, Lloyd, & Spence, 2002), and touch can influence visual perception of surface texture (Heller, 1982) and surface slant (Ernst, Banks, & Bulthoff, 2000).

In the work reported here, we sought to extend the analysis of multimodal perception to an aspect of visual perception—structure from motion—about which there is some evidence concerning possible underlying neural mechanisms. In particular, we exploited the kinetic depth effect: the perception of a three-dimensional (3D) object on the basis of differential optic flow (Doner, Lappin, & Perfetto, 1984; Wallach & O'Connell, 1953). When viewing the 2D parallel projection of a rotating 3D object, one may experience spontaneous reversals in the perceived direction of rotation (Fisichelli, 1947; Howard, 1961; Leopold, Wilke, Maier, & Logothetis, 2002; Miles, 1931; Nawrot & Blake, 1991a). The bistability of motion perception when viewing these kinds of animations is not surprising, for the available stimulus

information is ambiguous. Regarding underlying neural mechanisms, several lines of evidence, both psychophysical (Nawrot & Blake, 1989, 1993; Petersik, 2002; Petersik, Shephard, & Malche, 1984) and neurophysiological (Bradley, Chang, & Andersen, 1998; DeAngelis & Newsome, 1999; Dodd, Krug, Cumming, & Parker, 2001), point to the involvement of fluctuating neural activity within a network of disparity-selective, motion-sensitive neurons (Nawrot & Blake, 1991b), most likely including neurons in the middle temporal visual complex (MT +). By exploiting the bistability of 3D motion perception from optic flow, we have discovered that haptic information strongly influences visual perception of structure from motion. In addition, using functional magnetic resonance imaging (fMRI), we confirmed that tactile stimulation activates MT+, a brain area importantly involved in visual motion perception. These psychophysical and brain-imaging results point to robust interactions between visual motion areas and brain areas activated during haptic exploration of objects.

METHOD

Psychophysical Experiments

Apparatus

Figure 1 shows a schematic of the apparatus used in our four psychophysical experiments. Cinematograms portraying a rotating visual globe were generated by an Apple G4 computer on a pair of matched video monitors (600 × 800 resolution, 75-Hz frame rate) viewed through a mirror stereoscope; animations were programmed in MatLab running in conjunction with the Psychophysics Toolbox (Brainard, 1997). The globe itself was defined by 240 small (3.44 arc min) white dots positioned randomly over the surface of the virtual globe. The diameter of the globe was $7.60°$, and from frame to frame of the animation (i.e., every 13.3 ms), the globe rotated $1.19°$ about its vertical axis, producing the appearance of smooth rotational motion (15 rpm).

Located 24.1 cm directly behind the two stereoscope mirrors was a Styrofoam globe punctured with approximately 100 small pins whose round, protruding heads gave the globe an irregular, textured feel. The size of the tactile globe matched that of the visual globe, and, although invisible to the observer, the tactile globe coincided in location with the apparent location of the visual globe (which appeared directly in front of the midline between the two stereoscope mirrors). The tactile globe was mounted on a rigid shaft and could be smoothly rotated clockwise or counterclockwise by a motor. Located comfortably

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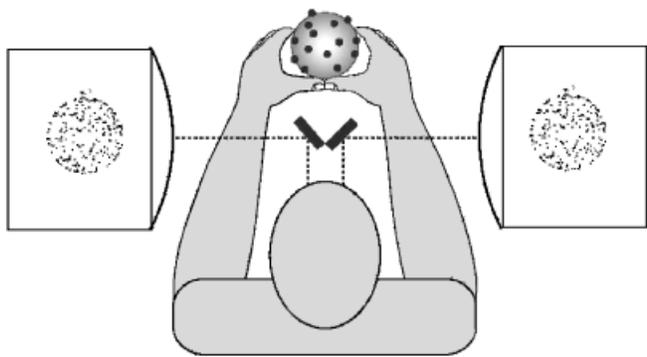
Fig. 1. Schematic (viewed from above) of the apparatus used to present a visual globe and a tactile globe in the same apparent location in space. With the head comfortably restrained by a chin rest, the observer looked through a mirror stereoscope that presented visual animations (random-dot cinematograms) separately to the two eyes, each image generated on a video monitor under computer control. When binocularly fused, the dynamic images portrayed a globe rotating about its vertical axis. The direction of rotation was ambiguous, unless disparity was used to create unambiguous surface structure and rotation direction. The tactile globe was located out of sight, in the same virtual space as the perceived location of the visual globe. The tactile globe could rotate about its vertical axis, either clockwise or counterclockwise, at the same speed as the visual globe. Small ''pimples'' on the tactile globe gave it a textured feel that coincided with the dots defining the visual globe.

underneath one foot of the observer was a computer mouse that could be depressed and released simply by flexing the ball of the foot.

Procedure

In Experiment 1, observers pressed and released the mouse (using the foot) to track the direction of rotation of the visual globe during 60-s observation periods; a minute or more of rest intervened between successive tracking periods. Tracking using the foot was measured under four conditions: (a) visual only (hands not touching the tactile globe), (b) hands touching the tactile globe while it was stationary, (c) hands touching the tactile globe while it rotated clockwise, and (d) hands touching the tactile globe while it rotated counterclockwise. Each condition was repeated four times, and the order of conditions was randomized for each of 5 observers (2 naive).

In Experiment 2, observers pressed and held the mouse using the foot for the entire duration of a single episode of perceived rotation of the visual globe. First, without touching the tactile globe, the observer viewed the ambiguous visual globe until it appeared to rotate in a prespecified direction (either clockwise or counterclockwise), at which time the observer lightly grasped the tactile globe, which was either stationary or rotating clockwise or counterclockwise. On some trials, the tactile globe rotated in the same direction as that being currently experienced visually (consistent condition); on other trials, the tactile globe rotated in the direction opposite that being visually experienced (inconsistent condition). At the same time that the observer grasped the tactile globe, he or she depressed the mouse with the foot. The observer released the mouse when the perceived direction of rotation of the visual globe reversed, ending that trial. At this time, the duration of the trial was recorded, the visual display disappeared, and the observer released the tactile globe. A total of 60 trials was administered to each of 5 observers (2 naive).

In Experiment 3, the observer started each trial by lightly grasping the rotating tactile globe while at the same time keeping the eyes closed; on half the trials, the tactile globe rotated clockwise, and on the remaining trials it rotated counterclockwise, with the order of rotation of the tactile globe randomized over trials. After 5 s (signaled by a tone), the observer released the tactile globe and, simultaneously, opened his or her eyes to view the visual globe for 1 s. At the end of this period, the observer reported the initial perceived direction of rotation of the visual globe. A total of 40 trials was administered to each of 5 observers (2 naive).

In Experiment 4, 4 observers (2 naive) tracked the direction of rotation of the ambiguous globe for 15 s by operating the mouse with the foot; prior to this tracking period, observers were adapted to one of two conditions: (a) a stereoscopically defined globe rotating unambiguously in a single direction (clockwise or counterclockwise) for 90 s or (b) a tactile globe rotating in a given direction (clockwise or counterclockwise) for 90 s.

Brain-Imaging Experiment

For brain imaging, participants lay supine within the scanner with their head in the head coil. Visual stimuli were presented on two small LCD screens mounted within a Visuastim XGA goggle system (MRI Devices Inc., http://www.mrivideo.com) worn by the participant. Each screen had a virtual size of 76.2 cm × 57.2 cm, and the screens were viewed at a virtual distance of 120 cm. The same stereoscopic visual rotating-globe stimulus used for the psychophysics experiments was used in the imaging experiment, except that under the different viewing conditions in the scanner, the diameter of the globe was $7.2°$. In each run during the visual condition, participants viewed a rotating globe, a stationary globe, and a fixation dot (rest) in a repeating, prespecified sequence.

In the tactile condition, instead of viewing a globe participants grasped a plastic ball that was 8.6 cm in diameter and covered with molded plastic nodules. The ball (tactile globe) was attached to the end of a wooden rod that was supported by a base held between the participant's legs. The rod was suspended horizontally such that the participant could hold the tactile globe comfortably in both hands while the experimenter (standing outside the scanner) rotated the rod. Through headphones, the experimenter received instructions indicating the beginning of motion, stationary periods, and rest periods. The experimenter signaled the onset and offset of rest periods to the participant with a tap on the rod. This signal directed the participant to remove his or her hands from the globe at the start of rest periods and to return his or her hands to the globe at the end of rest periods. Thus, there was no tactile stimulation during rest periods.

During the imagery condition, participants were asked to imagine the same globe used in the visual condition. They received auditory instructions directing them to imagine a rotating globe or a stationary globe, again in an alternating prespecified sequence with interleaved rest periods. During rest periods for the imagery condition, participants clasped the stationary tactile globe with their hands.

A standard MT+ localizer stimulus (Huk, Dougherty, & Heeger, 2002; Tootell et al., 1995) was always presented in the first run of a session. After that, eight 4-min runs were acquired, four runs for each of two conditions. Each participant completed only two different conditions during any one scanning session. Runs of a particular condition were presented in pairs, and the condition that was presented as the first pair of runs was counterbalanced across participants;

for each participant, whether a run began with the motion stimulus or the stationary stimulus was alternated across runs.

All imaging was done using a 3-T whole-body GE Signa MRI system with birdcage head coil, located at the Vanderbilt University Medical Center (Nashville, Tennessee). The field of view was $24 \times 24 \times 9.0$ cm with an in-plane resolution of 64×64 pixels and 18 contiguous coronal scan planes per volume, resulting in a voxel size of $3.75 \times 3.75 \times 5.0$ mm. Coronal slice locations were selected in the posterior cortex, with the first slice intersecting the occipital pole and the last slice intersecting the midpoint of the corpus callosum. Images were collected using a T2*-weighted echo-planar-imaging acquisition (TE = 25 ms, TR = 2,000 ms, flip angle = 70°) for blood-oxygen-level-dependent (BOLD) based imaging. High-resolution T1-weighted anatomical volumes were also acquired using a 3D fast spoiled grass (FSPGR) acquisition (TI = 400 ms, TE = 4.18 ms, TR = 10 ms, flip angle = 20°). Data were analyzed using the Brain Voyager (Brain Innovation, Maastricht, The Netherlands) 2D analysis tools. Functional data were spatially smoothed using a Gaussian filter (full width at half maximum = 4 mm). Statistical maps for MT+ localization were calculated using Brain Voyager's Single-Study General Linear Model tool.

RESULTS AND DISCUSSION

Psychophysical Experiments

Experiment 1

In this experiment, observers tracked fluctuations in perceived direction of rotation of the ambiguous visual globe during 1-min observation periods (Fig. 2). On trials involving visual stimulation only, perceived 3D visual motion fluctuated between clockwise and counterclockwise, with neither direction dominating during the viewing period; this result simply replicates earlier findings (e.g., Nawrot & Blake, 1991a). The same pattern of results was found when observers tracked perceived direction of motion while touching the stationary tactile globe, which is to be expected. But on trials when observers touched the rotating tactile globe throughout the observation period, all 5 observers saw the visual globe rotating in the direction the tactile globe rotated for significantly more than half of the total viewing period. It is worth noting that haptic information, although potent, did not completely eliminate reversals in perceived direction of rotation. This is not too surprising in view of the fact that compelling visual depth information (specified by luminance gradients) also fails to disambiguate completely the perception of rotation in structure-from-motion displays (Dosher, Sperling, & Wurst, 1986). Moreover, our finding is consistent with the reliable but relatively weak influence of touch on visual perception of slant portrayed by conflicting depth cues (Ernst et al., 2000). Finally, all observers in our study, including those naive about the hypothesis, knew that the tactile globe and visual globe were not one and the same, simply from the layout of the apparatus, which they inevitably saw when entering the room—this knowledge, too, might weaken the linkage between touch and vision.

Experiment 2

This experiment examined the influence of touch on individual durations of perception of a given direction of rotation. For all observers tested, the average duration of perception of a given direction of visual motion was significantly longer on consistent trials (tactile globe rotating in the same direction as the ambiguous visual globe) than on
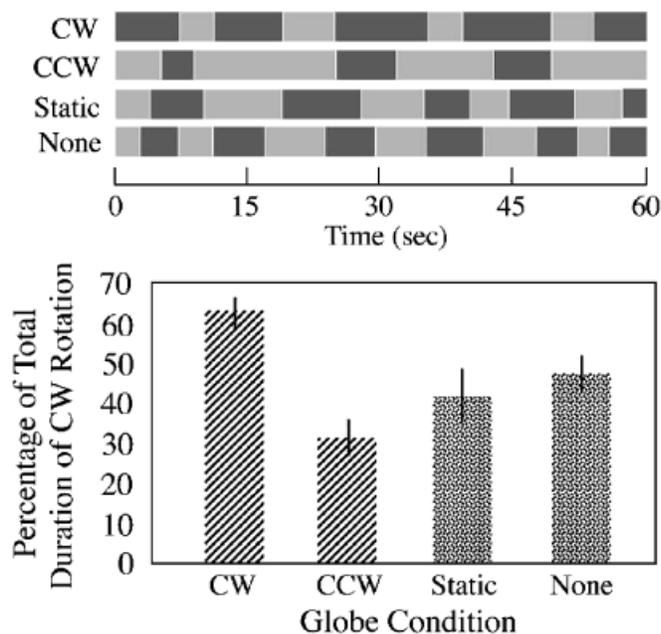
Fig. 2. Results from Experiment 1. The upper panel shows successive durations of perceived clockwise (dark gray) and counterclockwise (light gray) rotation of an ambiguous globe during a 60-s viewing period during which the observer touched a tactile globe that was rotating clockwise (CW), touched a tactile globe that was rotating counterclockwise (CCW), touched a tactile globe that did not rotate (Static), or did not touch the tactile globe at all (None). The lower panel shows the average (across 5 observers, 2 of whom were naive) percentage of the total viewing period during which clockwise rotation was experienced in these four conditions; error bars show ± 1 *SEM*.

inconsistent trials (Fig. 3). This pattern of results dovetails with the tactile globe's ability to boost the dominance of a given direction of motion (Experiment 1). For 3 of 5 observers, touch lengthened the average duration of perception of a given direction of motion on consistent trials and reduced average duration on inconsistent trials; for the other 2 observers, touch primarily affected perception on consistent trials.

Experiments 3 and 4

To learn whether the perceived direction of motion of the ambiguous visual globe could be influenced by prior exposure to the unambiguous rotating tactile globe, in Experiment 3 we employed a priming procedure similar to that used successfully in the study of other ambiguous figures (Long, Topino, & Mondin, 1992; Wilton, 1985). Unlike in the first two experiments, the tactile globe had no influence on the perceived direction of the visual globe for any of the 5 observers tested—responses were approximately equally divided between the two categories for all observers. For several observers, the perceived direction of globe rotation remained unchanged for many successive trials, regardless of the direction of rotation of the tactile globe. This pattern of results—extended persistence in perception of an intermittently presented ambiguous stimulus—also has been described by Leopold, Wilke, Maier, and Logothetis (2002). These authors interpreted this temporary "stabilization" of perception as evidence for the involvement of some form of implicit perceptual memory. Whatever produces this bias in favor of one perceptual interpretation, our
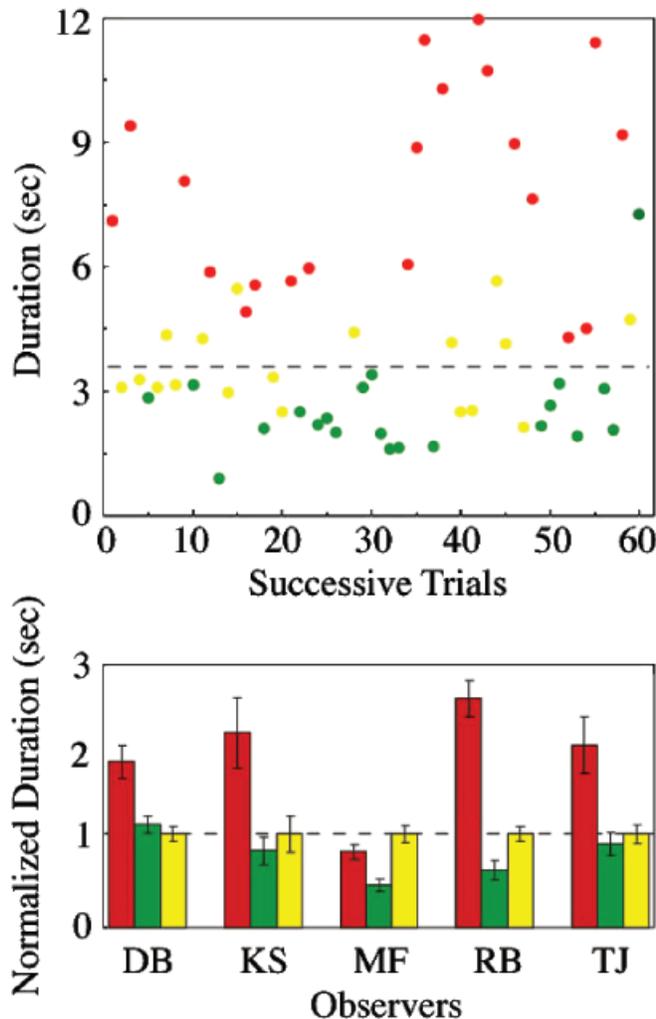
Fig. 3. Results from Experiment 2. The upper panel presents trial-by-trial results for 1 observer. Each dot shows how long the visual globe appeared to rotate in a given direction of motion once the observer began touching the tactile globe. Red symbols denote trials on which the tactile globe was rotating in the same direction as the visual globe (consistent trials), and green symbols indicate trials on which the tactile globe rotated in the opposite direction (inconsistent trials); yellow symbols indicate trials on which the globe was stationary. The dotted line shows the average duration for the stationary trials for this observer. The lower panel shows average results across the 5 observers for consistent (red) and inconsistent (green) trials, normalized relative to each observer's durations on stationary trials (yellow dots and dotted line). Vertical bars show ± 1 *SEM*.

findings show that unambiguous information provided by another modality—touch in our case—is insufficient to counteract it.

Given the negative results from Experiment 3, we wondered whether 5 s of tactile stimulation alone might be too brief to influence subsequent perception of the ambiguous globe. This possibility led us to perform a final experiment in which observers were exposed for 90 s either to a tactile globe rotating in a given direction (tactile globe only) or to a visual globe whose direction of rotation (either clockwise or counterclockwise) was unambiguously specified by retinal disparity (stereoscopic globe only). Immediately following adaptation to the tactile globe or to the stereoscopic globe, observers tracked the

perceived direction of rotation of an ambiguous globe for 15 s. Results showed a robust stereoscopic visual adaptation effect, replicating earlier results (Nawrot & Blake, 1989), but no effect of adaptation to a rotating tactile globe. These results run counter to the argument that the influence of touch on visual structure from motion is mediated only by imagination or attention, either of which should have worked effectively when the globe was first touched and then viewed immediately afterward.

To summarize, these four psychophysical experiments show that touch can influence perception of ambiguous visual motion, but only when the two modalities are stimulated simultaneously. It is worthwhile to consider our results in the context of the multisensory integration model advanced recently by Ernst and Banks (2002). According to that model, cue information specifying a given object property is combined across sources in a manner that minimizes the variance in the final estimate. Thus, in situations involving multiple cues, all cues will have an influence, but the source with the least variance will dominate perception. In their successful test of the model, Ernst and Banks manipulated variance by introducing different amounts of noise into the stimulus. In contrast, we utilized motion stimuli that are inherently variable in appearance and, therefore, are analogous to noisy stimuli. Consequently, our data do not lend themselves to the kind of maximum likelihood estimates required to derive quantitative fits to Ernst and Banks's integration model. Still, the influence of touch on visual perception of an ambiguous stimulus like ours follows naturally from their model. Moreover, as Ernst and Banks pointed out, one implementation of the maximum likelihood estimator can be realized by integrating activity among neurons responsive to vision and touch, an operation that would require simultaneous activation of the two modalities in the manner we found. It is natural to wonder where in the nervous system multimodal integration is accomplished, and toward that end, we performed our brain-imaging experiment.

Brain-Imaging Experiment

Given that touch can disambiguate 3D structure from motion, where would one expect to find neural circuitry underlying this bisensory interaction? Neurophysiological experiments have shown that area MT contains neurons selective both for direction of visual motion and binocular disparity (Bradley et al., 1998; DeAngelis & Newsome, 1999; Dodd et al., 2001) and that microstimulation of these neurons influences perception of 3D surface layout defined by motion (DeAngelis, Cumming, & Newsome, 1998). Moreover, brain-imaging work has demonstrated that the MT+ complex in humans can be activated by brush strokes along the arm and hand (Hagen et al., 2002), suggesting the existence of projections to MT+ from brain areas activated by somatosensory stimulation. It is tempting to conclude, therefore, that the neural interactions mediating the influence of touch on 3D shape from motion include activity within MT+. To learn whether touching a rotating globe can indeed activate MT+, we used fMRI to measure a correlate of neural activity—the BOLD signal—within MT+.

After localizing MT+ using standard techniques (Huk et al., 2002; Tootell et al., 1995), we measured BOLD signals throughout a series of 4-min stimulation periods during which participants looked at or imagined a stereoscopically defined globe or touched an actual globe (see Method). The results from this experiment are presented in
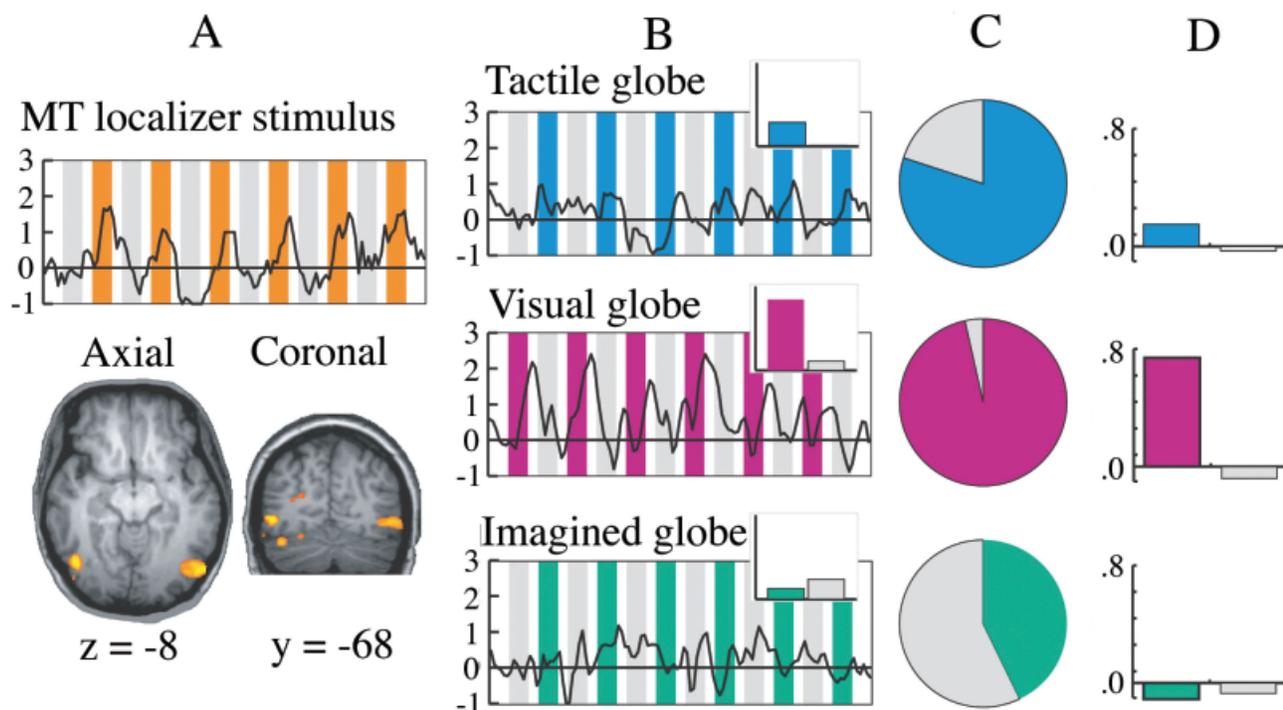
Fig. 4. Results from the brain-imaging experiment: blood-oxygen-level-dependent (BOLD) activation in the middle temporal visual complex (MT+) as a function of stimulus modality. The maps in (a) indicate the location of the MT+ complex on axial and coronal brain slices for 1 representative participant. These statistical maps were calculated from the 234-s time course shown above them. The stimulus-presentation protocol consisted of 12-s intervals of expanding-contracting dot patterns (orange) and 12-s intervals of static dots (gray) interleaved with 6-s intervals of rest (white). The horizontal axis represents time, and the vertical axis represents percentage signal change relative to resting baseline. The graphs in (b) show time courses from MT+ for three experimental conditions for 1 representative participant. Each time course shows that participant's data from a single 234-s run with 12-s intervals of the rotation condition (colored: blue, magenta, green) and 12-s intervals of the static condition (gray) interleaved with 6-s intervals of rest (white). The horizontal axis represents time, and the vertical axis represents percentage signal change relative to baseline. Each inset bar graph shows mean percentage signal change for rotation (colored) and static (gray) intervals for that one representative run. The pie charts in (c) present the percentage of runs for each condition that produced a higher percentage signal change for the rotation than for the static condition. Sample sizes (number of runs) were 20, 28, and 7 for the tactile, visual, and imagery conditions, respectively. The histograms in (d) show mean percentage signal change relative to baseline in MT+ for rotation (colored) and static (gray) intervals across all participants.

Figure 4. Reliable MT+ activation was indeed obtained while participants touched the rotating globe (blue pie chart in Fig. 4c), although the level of activation was substantially weaker than that measured in response to the visually defined globe (compare blue and magenta histograms in Fig. 4d). BOLD signals measured during the imagination of rotating and stationary globes did not differ significantly from those measured during rest, implying that tactile activation of MT+ is not attributable solely to visual imagery, at least when test conditions are sequenced in the manner used here (Goebel, Khorram-Sefat, Muckli, Hacker, & Singer, 1998). This finding is not particularly surprising, because the psychophysical results from Experiments 3 and 4 point to the same conclusion.

Our brain-imaging results clearly show that MT+ is differentially activated when touching a rotating versus a stationary 3D object; this, of course, is the same pattern of activation produced by viewing a rotating versus a stationary object. Our psychophysical results show that haptic information influences perceived 3D shape (Experiments 1 and 2), but only when paired simultaneously with visual stimulation (Experiments 3 and 4). Moreover, haptic information, even when paired with vision, has limited potency: Perceived direction of rotation of the visually ambiguous globe was never entirely governed by

touching the unambiguous tactile globe. Evidently, then, touch can modulate vision, but its influence is modest and too weak to produce significant visual adaptation on its own. These psychophysical results make sense in light of our brain-imaging data showing that MT+ activation produced by touch was considerably weaker than that produced by vision.

CONCLUSIONS

When it comes to identifying objects, people are remarkably adept at judging size, shape, and mass on the sole basis of the haptic information afforded by handling objects. Indeed, a case can be made for the primacy of the tangible over the visible, a case forcefully argued centuries ago by Bishop Berkeley (1709/1992) in his "Essay Towards a New Theory of Vision." Contemporary work in cognitive neuroscience now speaks directly to this issue. Single-unit recording experiments (Maunsell, Sclar, Nealey, & DePriest, 1991) and brain-imaging studies (Amedi, Malach, Hendler, Peled, & Zohary, 2001; James et al., 2002) have disclosed the existence of tactile input to neurons in object-selective visual areas within the ventral stream. The discoveries reported here reveal that high-fidelity haptic information substantially

influences perceived 3D object rotation specified by ambiguous 2D optic flow. Our brain-imaging results strongly suggest that at least some of the neural interactions underlying this influence occur within visual area MT+. At the same time, those results imply that touch influences visual perception only when subsets of MT+ neurons are already selectively activated by visual input. Touch, in other words, can modulate MT+ but cannot, on its own, sculpt distinct patterns of activity within MT+.

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