Do Visual and Tactile Object Representations Share the Same Neural Substrate?

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Objects can be recognized using any of our sensory modalities. For instance, a bumblebee can be recognized by seeing its characteristic yellow and black colors, by hearing its distinctive buzzing sound, by feeling the fuzzy surface of its body as it walks across our hand, by experiencing the pain as it stings our finger, or by any combination of these cues. But, it is only by using vision and touch that the complex three-dimensional (3-D) geometric properties of particular objects can be recognized. Of these two senses, vision is the one we use most often to identify objects—although the tactile system (or haptics) is also useful, particularly in situations where the objects cannot be seen. Haptics can also provide information about the weight, compliance, and temperature of an object—as well as information about its surface features, such as how sticky or slippery it is—information that is not readily available by merely looking at the object. But, by the same token, vision can provide information about an object's color and surface patterns—features that cannot be detected by haptics. Moreover, even though both haptics and vision provide information about an object's volumetric shape, there are clear differences in the way in which that information is garnered by the two systems. The haptic system can operate only on objects that are located within personal space, that is, on objects that are within arm's reach. The visual system, however, can analyze not only objects that reside within personal space but also those that are at some distance from the observer. Of course, when objects are at a distance, only the surfaces and parts of an object that face the observer can be processed visually (although it is possible, in some cases, for the observer to walk around the object and take in information from multiple viewpoints). When objects are within reach, however, they can be manipulated, thus revealing the structure and features of the previously unseen surfaces and parts to both the visual and the haptic system.

The receptor surfaces of both systems have regions of low and high acuity. For vision, the high-acuity region of the retina is the fovea; for haptics, the high-acuity regions are the fingers, lips, and tongue. Although both systems are able to bring these high-acuity surfaces to bear on an object, vision has a decided speed advantage. After all, a saccadic eye movement can be planned and executed in under 200 ms, whereas moving the fingers to a new location of an object takes much longer. But even though the visual system is much more efficient in this regard, both systems perform their high-acuity analysis of an object in a serial fashion. The visual system, however, is capable of carrying out a coarse-grain analysis using the peripheral retina simultaneous with the fine-grained analysis carried out with the fovea. In contrast, except for extremely small objects, it is difficult for the haptic system to carry out a coarse-grained analysis using the palms (or even enclosure by the arms) simultaneous with a fine-grained analysis with the fingers.

Despite these differences between the two systems, the fact remains that vision and haptics are the only two sensory systems that are capable of processing the geometrical structure of objects. It is perhaps not surprising, therefore, that higher order processing of objects by the two systems appears to deal with their respective inputs in much the same way. For example, in many situations, particularly those in which differential information about surface features such as color and visual texture are not available, visual recognition of objects is viewpoint dependent. In other words, if an object is explored visually from a particular viewing angle, recognition will be better for that view of the object than for other views (Harman & Humphrey, 1999; Humphrey & Khan, 1992; Tarr, 1995). The concept of "viewing angle" in haptic exploration of objects is not as well defined as it is in vision—in part because objects, particularly ones that can be manipulated, are rarely explored from one "viewpoint." Nevertheless, work by Newell, Ernst, Tjan, and Bulthoff (2001) has shown that haptic recognition of 3-D objects that are fixed to a surface is much better when the "views" of the objects during the test phase of the experiment are the same as they were during the study phase. Although this finding may be somewhat artificial, it does suggest that information about an object's structure, which could be considered a higher order representation of that object, is encoded and stored in a similar way by the visual and haptic systems. Also in support of this idea are data suggesting that perspective is important for the successful perception of haptically apprehended tangible 2-D drawings of 3-D objects (Heller et al., 2002). Accuracy for matching a tangible drawing to its 3-D counterpart haptically was better when the drawing was depicted with perspective, despite the fact that distortions of perspective, such as foreshortening, are associated with visual processing, not haptic processing.

Indeed, because the characteristics of the visual and haptic object representations are so similar, there is some speculation that the two modalities actually share the same underlying representation. For example, several studies (Easton, Greene, & Srinivas, 1997; Easton, Srinivas, & Greene, 1997; Reales & Ballesteros, 1999) have used cross-modal priming between vision and haptics to show that exposure to real objects in one modality affected later naming of the objects when they were presented using the other modality. The term *priming* in this context refers to the facilitative effect that prior exposure to a stimulus has on responses to that stimulus during a subsequent encounter, a facilitative effect of which people are usually quite unaware. In a cross-modal priming experiment, then, subjects would first be exposed to objects in one modality and then would be required to identify or discriminate between the same objects presented in the other modality. Interestingly, in at least three experiments (Easton, Greene, & Srinivas, 1997; Easton, Srinivas, & Greene, 1997; Reales & Ballesteros, 1999), cross-modal priming and within-modality priming resulted in similar effect sizes, suggesting that a "visual" representation of an object can be activated as much by a haptic presentation of the object as by a visual presentation of the object (and vice versa). One possible explanation of this finding is that there is, in fact, a single representation of the object that can be equally activated by both modalities. A second possibility is that there are two representations, one visual and one haptic, but each representation is able to co-activate the other. For this latter explanation to work, however, an assumption must be made that the co-activation is efficient enough to produce complete transfer of the relevant information delivered by the two modalities. In fact, if the transfer were that complete and transparent, then in many ways the second explanation reduces to the first—and the only difference is how distributed are the two representations. A third possibility, of course, is that the cross-modal priming and the within-modality priming are both mediated by verbal or semantic processing of the object. In other words, the two modality-specific representations are re-activated by feedback from verbal processing systems. The fact, however, that babies as young as 2 months of age, as well as chimpanzees (Streri, 1993), show evidence of transfer in cross-modal (visual-to-haptic) matching tasks, suggests that interactions between the systems are not mediated by only verbal representations.

As was mentioned earlier, there is evidence that if only one view of an object is studied, then during later testing the object will be recognized more quickly if that view rather than another is presented—and this is true in both the visual as well as the haptic domain. What is interesting is that this viewpoint-specificity is also true for cross-modal presentations. In other words, an object studied haptically from one particular "viewpoint" will be better recognized in a visual presentation if the same rather than a different view of the object is presented (Newell et al., 2001). Like the cross-modal priming results described earlier, this finding also suggests that vision and haptics share a common object representation. Moreover, the viewpoint-specificity of the cross-modal transfer lends support to the argument that this shared representation encodes the 3-D structure of the object rather than a more abstract conceptual or verbal description of the object.

In short, there is reasonably good behavioral evidence to suggest that vision and haptics encode the structure of objects in the same way—and use a common underlying representation. This conclusion finds additional support in a number of neuroimaging studies that have demonstrated overlap between visual and haptic processing within the human brain. This overlap appears to occur in regions of the brain that are usually considered visual, such as extrastriate areas in the occipital cortex. Several investigators (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; Amedi, Malach, Hendler, Peled, & Zohary, 2001; Deibert, Kraut, Kremen, & Hart, 1999) have found that haptic object identification tasks show activation in visual areas when measured using functional magnetic resonance imaging (fMRI). In other words, compared to a control task, identifying objects haptically produced greater activation in the extrastriate cortex (in addition to other regions). The involvement of visual areas in haptic processing has also been demonstrated using transcranial magnetic simulation (TMS), a technique in which a brief magnetic pulse is applied to the brain to disrupt the processing occurring in a localized region of the cortex. This is sometimes referred to as a "transient lesion," because processing is suspended temporarily in the target region. TMS was applied to different regions of the cortex while subjects were asked to identify the orientation of a grating that was placed on their finger (Zangaladze, Epstein, Grafton, & Sathian, 1999). When TMS was applied to the occipital cortex contralateral to the hand being used, subjects were not able to perform the task, but when TMS was applied to the ipsilateral occipital cortex, they performed normally.

The fact that the application of TMS to the occipital cortex disrupts tactile discriminations (coupled with the fact that visual areas within this region show activation to haptic identification of objects) could be construed as evidence that extrastriate cortex is not devoted entirely to the processing of visual information—but is also involved in haptic processing. Indeed, one might even speculate that the extrastriate cortex is the neural substrate of the shared bimodal object representation suggested by the behavioral studies. Another, perhaps more straightforward explanation, of course, is that the activation in the extrastriate cortex is simply a reflection of visual imagery. In other words, when one uses touch to explore an object, a mental image of the object is constructed and this process of constructing a mental image recruits the extrastriate cortex. There is no doubt that mental images of objects are constructed when they are haptically explored for the purposes of recognition; there is also no doubt that these mental images are predominantly visual. But, the question is not whether or not visual imagery occurs during haptic exploration, but whether or not such imagery drives the activation in the extrastriate cortex. It has certainly been argued that the reason that TMS applied to the occipital cortex interferes with haptic recognition is that it disrupts visual imagery (Zangaladze et al., 1999). Nevertheless, it is not clear that haptic recognition depends on visual imagery, nor is it clear that the extrastriate areas activated during haptic exploration tasks are the same areas that are activated during visual imagery.

In an attempt to address these questions, Amedi et al. (2001) compared the activation produced in the extrastriate cortex when subjects were presented visually or haptically with objects, or when objects were only imagined. They found that an object-selective area of the extrastriate cortex, the lateral occipital complex (LOC), responded preferentially when objects were explored visually or haptically, but did not respond when objects were only imagined. In a follow-up study (Amedi et al., 2002), objects were again presented visually and haptically, but in addition auditory sounds were presented that were diagnostic for particular objects. The LOC did not show differential activation (compared to baseline levels) when objects were identified by their sounds. As before, however, the LOC responded preferentially when objects were identified using either vision or touch. This study makes three important points. First, it confirms the idea that a common area within the extrastriate cortex (LOC) can be driven both by visual and by haptic information about an object's structure. Second, it shows that the LOC is probably bimodal not multimodal in nature, because auditory cues associated with a particular object did not produce activation there. And finally, it shows that the mental image of an object evoked by associated auditory cues was also insufficient to activate the LOC. Taken together, these findings suggest that the mental (visual) image of an object that might be evoked during haptic exploration is not responsible for the activation observed in LOC—unless one assumes that visual images invoked by tactile cues are different from the visual images invoked by auditory cues, or the visual images invoked by deliberate imagination. For instance, the visual imagery induced by an auditory cue may not be as detailed or specific as that induced by tactile exploration—and may be more difficult to sustain. Nevertheless, even indistinct visual imagery would be expected to produce activation in the LOC. Furthermore, if one postulates that a special kind of visual image is invoked by haptic cues, then this is tantamount to suggesting that haptics and vision enjoy a special relationship (perhaps a bimodal representation) that is independent of any overarching visual image that might be generated by other means.

The behavioral and neuroimaging evidence we have described so far suggests that haptics and vision share a common bimodal representation of objects. To explore this hypothesis further, in a recent study (T. W. James et al., 2002), we combined the cross-modal priming method used in previous behavioral studies with high-field fMRI. As we have seen, priming paradigms are a good tool for investigating the nature of object representations (Reales & Ballesteros, 1999), because they involve the use of an implicit task, in which earlier exposure to an object can affect (or not affect) current processing of the same object. Any observed effect of the priming manipulation must be attributed to residual activation of the object representation or to some form of permanent change to that representation.

Because we wanted to look directly at cross-modal priming of the geometric structure of objects, we used a set of 3-D novel objects that were made out of clay and spray-painted white (Fig. 7.1). By using objects that were both novel and meaningless, we hoped to limit the use of semantic or verbal encoding. Importantly, we also used a passive viewing paradigm, in which subjects were simply required to look at the objects and to do nothing else. They did not have to identify, name, or explicitly recall the objects in any way. It was expected that this "task" would ensure the implicit activation of the object representation on subsequent presentations with as little "explicit contamination" as possible.

We hypothesized that any common region for haptic and visual object processing that we identified would show an equivalent priming effect whether the objects were first studied visually or haptically. This hypothesis is derived directly from the notion that equivalency of brain activation with priming implies that there was no extra processing step that differentiates the study of objects in one condition from the study of objects in the other. That is, if equivalent priming effects were found in the common extrastriate area identified in other studies (Amedi et al., 2002; Amedi et al., 2001; Deibert et al., 1999), then whatever effects earlier visual or haptic study had on processing in this region must also have been equivalent. If such results were indeed obtained, it would be difficult to argue that haptic representations were stored elsewhere (such as in the parietal somatosensory cortex) and had an indirect influence on activation in this occipital region. The extra processing step required for an indirect influence should lead to differences between haptic and visual priming effects. In contrast, if there were observed differences between visual and haptic priming, then this would imply that there were distinct visual and haptic representations.


FIG. 7.1. Examples of novel three-dimensional clay objects.

Before scanning, each participant in our study visually explored a set of 16 objects and haptically explored a separate set of 16 objects. During scanning, participants were presented with visual images of these studied objects on a projection screen together with an additional set of 16 nonstudied objects. Priming effects could therefore be assessed by comparing the pattern of activation that was obtained with the studied objects with the pattern of activation that was obtained with the nonstudied objects. Figure 7.2 illustrates a brain region in the lateral ventral occipital cortex that showed significant haptic-to-visual priming, significant visual-to-visual priming, and showed significant overlap be-

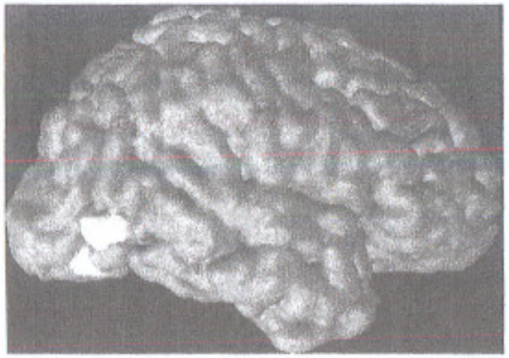

FIG. 7.2. Bimodal lateral occipital cortex activation. The brain image is a rendered representation of the grey-matter surface of the right hemisphere. The white region indicates the location of the LOC. The LOC is equally activated, bilaterally, by visual and haptic exploration of objects and shows equivalent priming effects whether prior exposure was visual or haptic.

tween visual and haptic exploration (T. W. James et al., 2002). This region corresponds to the lateral occipital complex (LOC), a region that has been implicated in the selective processing of visual objects (Kanwisher, Chun, McDermott, & Ledden, 1996; Malach et al., 1995) and often shows evidence of visual priming in imaging studies (for review, see Cabeza & Nyberg, 2000; Schacter & Buckner, 1998; Wiggs & Martin, 1998). Thus, it was not surprising that the LOC was activated by visual exploration of objects or showed significant visual-to-visual priming effects. More recently, the function of the LOC has been reinterpreted as bimodal (Amedi et al., 2002; Amedi et al., 2001). Thus, it was not too surprising that the LOC showed significant haptic-to-visual priming as well. The interesting point to be made, however, is that the effect of haptic priming in the LOC was equivalent to that of visual priming. This can be seen in the activation time courses shown in Fig. 7.3. Visually and haptically studied objects each produced more activation than nonstudied objects, but importantly the time courses for the activation produced with visually and haptically studied objects overlapped almost completely. The increase in activation with studied objects that we observed, although inconsistent with other priming results using *common* objects (for review, see Cabeza & Nyberg, 2000; Schacter & Buckner, 1998; Wiggs & Martin, 1998), was consistent with the results from at least two other priming studies that used *novel* objects (Henson, Shallice, & Dolan, 2000; Schacter et al., 1995).

Our priming experiment (T. W. James et al., 2002), together with results of previous studies (Amedi et al., 2002; Amedi et al., 2001), provides converging evidence that visual imagery does not mediate the haptically produced activation in the LOC. In previous studies, no visual stimulus was present during haptic exploration conditions, and this lack of a visual stimulus should promote the use of visual imagery. Recall that during scanning in our study, participants were always viewing a visual stimulus. What varied from trial to trial was whether or not the object on the screen had been previously explored haptically or visually. Thus, the use of visual imagery during scanning was equally likely (or rather equally unlikely, since there was a real visual image present) during all experimental conditions. In short, visual imagery during scanning could not have been responsible for the increased activation with haptic priming.

The use of the priming paradigm with separate study and test phases raises another question: Could visual imagery during haptic study of the objects have produced permanent changes in occipital cortex that were responsible for the observed differences in activation seen during the test phase? In other words, could the haptic priming effect have been caused by activation of visual cortex through visual imagery instead of through somatosensory input? A widely accepted theory of mental imagery suggests that visual imagery is the endogenous activation of neural mechanisms normally involved in visual perception (Farah, 2000; Kosslyn & Shin, 1994). In other words, invoking some sort of high-level semantic or abstract representation of an object feeds back onto early areas in visual cortex and activates perceptual representations by "normal" feedforward processing. As a consequence, there is perception of visual images without vi-

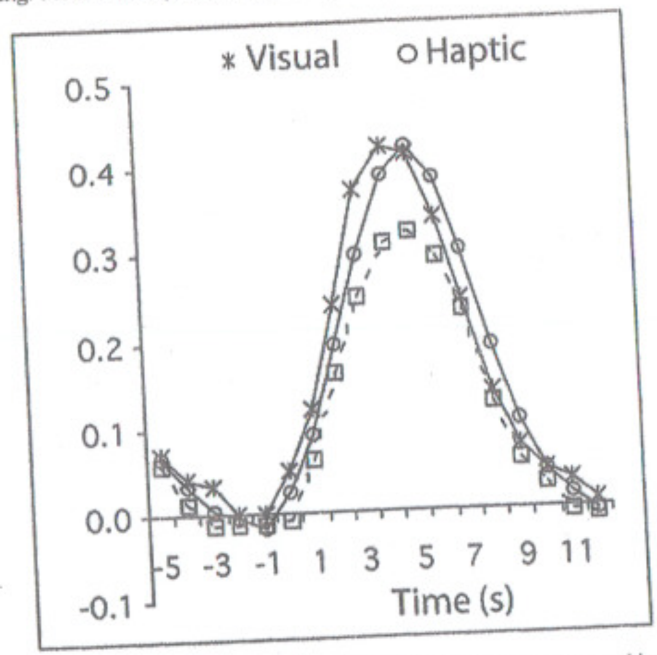

FIG. 7.3. Time course of activation from the LOC. Time courses are averaged hemodynamic responses from 32 visually primed, 32 haptically primed and 32 nonprimed (squares) trials per participant ($N = 8$). Vertical axis indicates percent signal change from a rest baseline.

sual input. It is possible that the visual imagery elicited by haptic exploration of objects during the study phase of the experiment could unfold in the same way, that is, by activating an abstract representation, which in turn activates a perceptual representation. But it is also possible that haptic exploration could directly activate the perceptual object representation, without activating an abstract representation. As we saw earlier, young infants and chimpanzees (Streri, 1993), who presumably have a limited capacity for abstract or symbolic representation, show efficient transfer of training between haptics and vision, suggesting that abstract representations are not necessary for cross-modal transfer. In addition, our study was designed to limit abstract encoding of the objects (by using meaningless novel objects). Furthermore, patient DF, who is described in further detail a bit further on, has preserved visual imagery, despite severe damage to the "normal" feedforward visual processing regions, suggesting that activation of these regions, and thus activation of geometric object representations, is not necessary for visual imagery. Finally, the fact that we found equivalent effects of visual and haptic priming on activation in visual areas such as the LOC suggests that no extra computational step, such as utilizing an abstract representation, was implemented. These findings, combined with the results of experiments using auditory-cued mental imagery (Amedi et al., 2002; Amedi et al., 2001), provide strong converging evidence that occipital cortex activity during haptic exploration of objects is not produced because of an endogenous cue to visually imagine the object, but instead is produced by direct haptic input to bimodal object representations in the LOC. Activation of the LOC may in turn produce activity in other occipital regions that are involved in the production of visual images, but these activations would likely be much more unspecified than those produced by direct haptic input, causing a much smaller priming effect. This is in fact what happens with cross-modal auditory-to-visual priming: priming effects are smaller across modalities than within modalities (e.g., see Greene, Easton, & LaShell, 2001). This is presumably because interactions between vision and audition can only occur if the incoming information is first transformed into a sufficiently abstract representation—a requirement made necessary because vision and audition do not share a common representation at a lower level of processing such as geometric structure.

Although there was no behavioral data collected in our experiment, the fact that levels of activation were the same for both kinds of priming is consistent with the results of earlier behavioral experiments (Easton, Greene, & Srinivas, 1997; Easton, Srinivas, & Greene, 1997; Reales & Ballesteros, 1999). In these studies, cross-modal priming effects between haptics and vision were of the same magnitude as the within-modal priming effects observed with either vision or haptics, even with novel objects. In both neural activation and behavior, then, cross-modal priming is no less "efficient" in its effect than within-modal priming. Taken together, these findings suggest that no extra computational step is required to prime visual processing of object shape using a representation based on previous haptic input than is required to prime visual processing of object shape using a representation based on previous visual input. Indeed, we would argue that cross-modal priming makes use of a common haptic and visual representation. One candidate region for the neural substrate of this common representation is the LOC, which not only showed equivalent within-modality and across-modality priming, but was also equally activated by haptic and visual exploration of objects in our study and in other studies (Amedi et al., 2002; Amedi et al., 2001). The common representation, we would argue, is not semantic or verbal in nature. In our priming study, we used novel objects instead of common objects to minimize the chances of semantic or verbal mediation of any priming effects that were observed. The fact that priming effects were found with these novel objects that are difficult to label verbally suggests that cross-modal priming can occur "below" the level of semantic or verbal representations of objects. Thus, one might speculate that the common visual and haptic representation of objects occurs first at the level of shape processing, and not at a more abstract or associative level, such as semantic or lexical processing.

Evidence from neuropsychological studies of patients with visual agnosia also supports the idea that haptic and visual signals may converge at the level of geometric representations of objects. In a recent report, a patient with prosopagnosia, who could not recognize faces visually, was also found to have difficulty learning to recognize faces using the sense of touch (Kilgour, de Gelder, & Lederman, 2004). Further evidence for haptic and visual convergence comes from investigations in our own lab of a patient (DF) with visual form agnosia (for original report, see Milner et al., 1991). DF is able to recognize objects using information from surface properties like color and texture, but is unable to recognize objects based on contour or form information (Humphrey, Goodale, Jakobson, & Servos, 1994). In short, she is unable to generate geometric structural representations of objects (Milner & Goodale, 1995). Neuroimaging shows that DF has bilateral lesions in area LOC (T. W. James, Culham, Humphrey, Milner, & Goodale, 2003), in the same region of the occipital cortex that we have shown to underlie bimodal geometric structural representations of objects (T. W. James et al., 2002). This would suggest that DF should not only have difficulty recognizing the shape of an object from vision, but should also have difficulty recognizing the shape of an object from her sense of touch. Preliminary findings from our laboratory indicate that this is the case.

When given a tactile recognition memory test using objects like the ones shown in Fig. 7.1, DF was able to recognize only 7 of 12 (58%). This performance is just above chance level, and is significantly worse than that of an age-matched con-trol. But more importantly, when DF was tested with similar objects in a visual ecognition test, she actually performed slightly better, recognizing 8 of the 12 objects (67%). Given DF's pronounced deficit in recognizing objects visually, one might have expected her to do better with tactile information.

We explored DF's haptic object recognition skills further, using a paired-as-ociates task in which letter names were paired with a new set of novel objects hat were explored haptically. As can be seen in Fig. 7.4 (right axis), a healthy ontrol participant was able to learn the letter names A through L for 12 dif-erent objects within three blocks of trials. DF was unable to perform this task, managing only one correct response out of twelve after four blocks of trials.

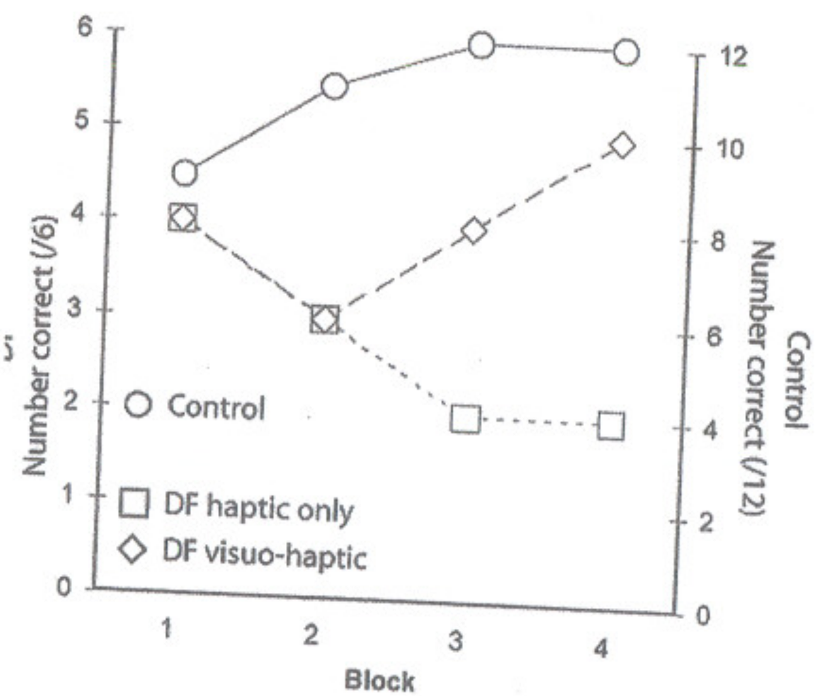

FIG. 7.4. Paired associates learning for DF and one healthy control participant. Data are shown across blocks of either 6 (DF) or 12 (control) trials. The control participant performed only the haptic paired associates (circles), whereas DF performed the haptic (squares) and the visuohaptic (diamonds) paired associates.

We then reduced the number of objects and had DF learn the letter names A through F paired with six haptically explored objects. As Fig. 7.4 (left axis) shows, DF's average performance on this easier task was not only much poorer than the control participant, but she actually did worse over time. This is particularly surprising because feedback was given after every trial. In a final task, DF performed the same paired-associates task with six objects but this time used both vision and touch together. We assumed that exploring the objects using multiple sensory inputs should maximize her ability to identify the objects. DF's performance on this task (Fig. 7. 4; diamonds), although again much worse than the control participant's haptic-only performance, did show some improvement over time. In fact, with even more training on the combined vision and haptic task (not shown in Fig. 7.4), she reached an asymptote of five out of six correct. The fact that DF was able to perform the paired associates task under bimodal sensory conditions suggests that her deficit was not entirely a memory problem, but was a problem in using haptics to learn about the geometrical structure of new objects. Although the better performance in the bimodal learning condition suggests that the two systems can bootstrap one another despite the damage to the LOC, the performance in this condition was still well below normal.

DF is also poor on sequential matching tasks using these same objects. In this task, she was allowed to explore a sample object for 3 sec and was then immediately given a test object and was asked if it was the same or different. Whether she performed this task haptically (with her eyes closed) or visually, she was equally poor (scoring 67% and 72% correct, respectively). Healthy controls find this task exceedingly easy. Again this suggests that her LOC lesion has interfered with her ability to learn the geometric structure of objects both visually and haptically.

DF's poor haptic performance at encoding the structure of new objects contrasts with her excellent haptic recognition of familiar objects. Like many individuals with visual form agnosia, DF is able to recognize objects, such as kitchen utensils and tools, as soon as they are placed in her hands—even though she is unable to identify them by sight alone. But the fact that she does so poorly in learning to recognize new objects using haptics suggests that area LOC, which is damaged bilaterally in her brain, may play an important role in enabling the haptic system to acquire information about the geometrical structure of new objects. This may be particularly true when the set of objects to be discriminated share many parts in common, as was the case for the novel objects in this particular study. In the case of haptic recognition of familiar objects, haptic information about object structure may be able to bypass LOC and make contact with higher order object representations. Visual information about object structure, however, must be processed by the LOC, which is why DF has great difficulty recognizing the form of objects, even when they are familiar. Taken together, the results from DF (and the prosopagnosia patient discussed earlier) suggest that lesions of visual areas in the occipitotemporal cortex that disrupt the visual recognition of object form can also interfere with haptic recognition of objects. The deficit appears to be most apparent when encoding the structure of objects that have not been encountered before.

It is important to note that although we have shown here that vision and haptics are intimately interrelated when it comes to representing the geometric structure of objects, there can also be no doubt that haptics and vision are integrated even more seamlessly when providing feedback for the successful execution of visuomotor commands. For instance, during movements of the arm and hand, a proprioceptive representation of the hand's position in space is automatically and effortlessly referenced to the visual calculation of the hand's position. Whether these calculations are carried out in isolation, or whether they share computational and neural overlap are questions that are beginning to be addressed. For instance, activation in regions of the parietal and occipital cortex are known to be influenced by the position of the eye (DeSouza et al., 2000; DeSouza, Dukelow, & Vilis, 2002). Haptics and vision also appear to be integrated during the processing of motion (Hagen et al., 2002) and it is likely that this is due to a direct somatosensory input into the middle temporal motion complex (Blake, Sobel, & James, 2004), an area specialized for the processing of object motion and optic flow. In addition, there is a growing body of evidence suggesting that vision, haptics, and also audition can all be influenced by each other during the allocation of attention to specific regions of space (Butter, Buchtel, & Santucci, 1989; Macaluso, Frith, & Driver, 2000, 2002; Maravita, Spence, Kennett, & Driver, 2002).

In most studies of haptic or visual object recognition, the objects are fixed and are studied with a single sensory modality; this is not the way that we normally interact with objects when we are trying to recognize or encode them. Interactions between vision and proprioception, between visual and tactile motion perception, and between visual and tactile allocation of attention, would all be involved in the active exploration of an object that is held and manipulated in our hands. In fact, for optimum representation of the geometric structure of an object it may be necessary to exploit all of these visuohaptic and visuomotor interactions (Harman, Humphrey, & Goodale, 1999; K. H. James et al., 2002). More regions in the brain may be multisensory than was previously thought and consequently, demonstrating that area LOC is bimodal may be only the first step toward realizing the bimodal nature of much of what up to now has been regarded as exclusively "visual" cortex.

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e processed by theOC, which is why DF has great difficulty orm of objects, everhen they are familiar. Taken together, the (and the prosopagnia patient discussed earlier) suggest that reas in the occipitmporal cortex that disrupt the visual rec-t form can also infere with haptic recognition of objects. rs to be most appait when encoding the structure of objects en encountered bee.

: to note that althgh we have shown here that vision and itely interrelated wn it comes to representing the geometric ts, there can also ho doubt that haptics and vision are inte-seamlessly when pviding feedback for the successful execu-r commands. For iance, during movements of the arm and ptive representati of the hand's position in space is auto-rtlessly referenced the visual calculation of the hand's posi-ese calculations ararried out in isolation, or whether they nal and neural ovep are questions that are beginning to be tance, activation iegions of the parietal and occipital cor-e influenced by thosition of the eye (DeSouza et al., 2000; w, & Vilis, 2002). ıptics and vision also appear to be inte-processing of moti(Hagen et al., 2002) and it is likely that rect somatosensomput into the middle temporal motion obel, & James, 200 an area specialized for the processing of optic flow. In adcbn, there is a growing body of evidence ion, haptics, and a audition can all be influenced by each allocation of attenn to specific regions of space (Butter, cci, 1989; MacalusFrith, & Driver, 2000, 2002; Maravita, & Driver, 2002).

of haptic or visuabject recognition, the objects are fixed th a single sensorydality; this is not the way that we nor-objects when we atrying to recognize or encode them. In-n vision and propception, between visual and tactile , and between vil and tactile allocation of attention, ed in the active exration of an object that is held and ma-ands. In fact, for dmum representation of the geometric ct it may be necesy to exploit all of these visuohaptic and tions (Harman, Hphrey, & Goodale, 1999; K. H. James regions in the brairay be multisensory than was previously quently, demonsting that area LOC is bimodal may be oward realizing thimodal nature of much of what up to ded as exclusivelyisual" cortex.

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