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6.19 Cross-Modal and Multisensory Interactions between Vision and Touch

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Glossary

g9000	amodal Devoid of sensory modality reference.	
g9005	cross-modal Reflecting the effect of a stimulus in one sensory modality on processing in another.	
g9010	encoding With respect to memory, the process of storing information at initial exposure.	
g9015	extrastriate visual cortex Nonprimary visual cortex.	
g9020	functional magnetic resonance imaging (fMRI) A method for measuring brain activity using MRI.	
g9025	haptic Sensing by touch through active manual exploration.	
g9030	multisensory Reflecting processing of inputs from more than one modality.	
	positron emission tomography (PET) A method for measuring functional brain activity as indexed by regional cerebral blood flow, using a positron-emitting isotope.	g9035
	priming Unconscious effect of one stimulus on processing of another.	g9040
	retrieval The process of recalling previously encoded and stored information from memory.	g9045
	tactile Sensing by touch through passive stimulation of the skin surface.	g9050
	transcranial magnetic stimulation (TMS) A method for testing the function of discrete brain regions by applying magnetic pulses to the head.	g9055
	visual imagery Mental reconstruction of a pictorial representation (seeing with the mind's eye).	g9060

s0005 6.19.1 Functional Involvement of Visual Cortical Areas in Tactile Perception

s0010 6.19.1.1 Macrosatial versus Microspatial Tasks

p0005 Activation of extrastriate visual cortical areas during tactile perception was first demonstrated in a positron emission tomographic (PET) study from our laboratory (Sathian, K. *et al.*, 1997), in which participants were asked to discriminate the orientation of gratings presented to the immobilized right index fingerpad. When this task was contrasted with a control task requiring discrimination of grating groove width, activation was

found at a focus in the left extrastriate visual cortex, close to the parieto-occipital fissure. Since this focus was known to be active during visual discrimination of grating orientation (Sergent, J. *et al.*, 1992) and spatial imagery (Mellet, E. *et al.*, 1996), it was considered to mediate spatial processes common to vision and touch (Sathian, K. *et al.*, 1997). The location of this activity near the parieto-occipital fissure indicates possible homology with an area in the macaque parieto-occipital fissure known as V6 or PO where a large proportion of neurons appear to be orientation selective (Galletti, C. *et al.*, 1991). Indeed, the focus of activation in our PET study (Sathian, K. *et al.*, 1997) is in the vicinity of the human V6 complex of areas (Pitzalis, S. *et al.*, 2006).

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These results suggested that tactile analogs of visual tasks potentially activate the same cortical areas as the visual tasks and that the visual cortex responds to certain tasks independently of the sensory modality in which the task is presented. A fairly extensive series of studies have since established that cerebral cortical areas previously regarded as exclusively visual are activated by haptic/tactile input in a task- and stimulus-specific manner, as reviewed below.

p0010 A subsequent functional magnetic resonance imaging (fMRI) study from our laboratory (Zhang, M. *et al.*, 2005) confirmed left parieto-occipital cortical activation during discrimination of grating orientation (relative to discrimination of grating groove width) with the right index fingerpad, and also found selective activation in other cortical areas. Among these areas were the right postcentral sulcus (PCS) and the left anterior intraparietal sulcus (aIPS). The PCS corresponds to Brodmann's area 2 (Grefkes, C. *et al.*, 2001) and is considered to be part of S1 (primary somatosensory cortex), while the aIPS has been consistently identified as a multisensory region, as will become increasingly evident as this chapter progresses. Other groups have corroborated the role of the aIPS in tactile discrimination of grating orientation, using fMRI: one group reported bilateral activity in this region during performance of this task with either hand, relative to discrimination of small changes in grating location on the fingerpad (van Boven, R. W. *et al.*, 2005). Activity was greater on the left than the right in this study, regardless of which hand was used. Another group scanned gratings over the fingerpad and found right-lateralized activity in the PCS–aIPS region during discrimination of grating orientation with either hand, relative to discrimination of grating roughness (Kitada, R. *et al.*, 2006). The right aIPS part of this region was directly established as multisensory by the demonstration that it was also activated by visual discrimination of grating orientation, relative to discrimination of grating color.

p0015 At the time we reported cross-modal parieto-occipital cortical activation during tactile discrimination of grating orientation (Sathian, K. *et al.*, 1997) this was an unusual finding and hence we wished to confirm that the finding was not merely epiphenomenal. This possibility was ruled out using transcranial magnetic stimulation (TMS) to test whether disrupting the function of this cortical region was detrimental to performance. Applying single-pulse TMS directly over the parieto-occipital focus and at sites close to it, at the appropriate interval (180 ms after the onset

of tactile stimulation), significantly impaired discrimination of grating orientation but not of grating groove width, whilst TMS at more distant sites did not affect performance on either task (Zangaladze, A. *et al.*, 1999). This allowed us to infer that the activation found in the earlier PET study was not accidental but, in fact, functionally meaningful. A more recent study (Merabet, L. *et al.*, 2004) used repetitive TMS (rTMS) at 1 Hz (hertz, unit of frequency (cycles per second)) to decrease local cortical excitability. This study exploited a known dissociation between subjective magnitude estimates of perceived tactile interdot distance, which increase with physical interdot distance (up to 8 mm), and those of perceived tactile roughness, which peak at intermediate values (around 3 mm). The main finding was that rTMS over S1 disrupted judgments of roughness, but not interdot distance, whereas rTMS over medial occipital cortex impaired distance but not roughness judgments. In addition, a congenitally blind patient with bilateral occipital lesions following a stroke was impaired on tactile judgments of interdot spacing but not roughness (Merabet, L. *et al.*, 2004).

Two conclusions can be drawn from these observations, together with the studies of the grating orientation task reviewed above (Sathian, K. *et al.*, 1997; Zangaladze, A. *et al.*, 1999; Zhang, M. *et al.*, 2005). First, visual cortical activation may be necessary for some tactile tasks because performance on these is disrupted when these cortical areas are deactivated by TMS or damaged by lesions. Second, visual cortical involvement occurs in macrospatial (large-scale) tactile tasks, but not in microspatial (small-scale) tasks where the parameters of interest vary in the range of ≤ 3 mm. This conclusion is consistent with psychophysical studies suggesting that macrospatial tactile tasks are preferentially associated with visual processing (Klatzky, R. L. *et al.*, 1987), and that vision seems to be better than touch for perceiving macrospatial features, the reverse being true for microspatial features (Heller, M. A., 1989).

An fMRI study from our laboratory focused on the macrospatial–microspatial dichotomy (Stoesz, M. *et al.*, 2003). As a macrospatial task, we used a global form condition in which participants were asked to distinguish between the upside-down letters T and V, contrasting this with detection of a 3 to 4 mm gap in a bar as the microspatial task. Activity in the lateral occipital complex (LOC) was greater bilaterally in the form task than in the gap task, in agreement with the studies reviewed so far indicating

that macrospatial tactile tasks are more likely to evoke visual cortical activity during tactile tasks. The LOC is located within the ventral visual pathway, which is specialized for form processing and is a visual object-selective area (Malach, R. *et al.*, 1995) thought to be homologous to macaque inferotemporal cortex (Grill-Spector, K. *et al.*, 1998). A recent fMRI study from our laboratory confirmed the conclusion that visual cortical activation during microspatial tasks is minimal (Stilla and Sathian, unpublished observations). In this study, a three-dot array was presented to the immobilized fingerpad with the array oriented along the long axis of the finger, the central dot in the array being offset to the left or right by <2 mm. Subjects were asked to indicate the direction of offset. Activation in this spatial task was contrasted against that due to discrimination of the duration of stimulation with an array that lacked a spatial offset, thus isolating activity associated with tactile microspatial processing. The key point here is that there was only minimal activation of the LOC bilaterally, although there was strong and extensive activation in multiple parietal cortical areas, including the left PCS, bilateral aIPS, bilateral posterior IPS (pIPS), and bilateral posterior insula (Stilla and Sathian, unpublished observations).

We also found that there was haptic texture selectivity in the right medial occipital cortex, probably in visual area V2. This focus overlapped with a visually texture-selective area that was primarily in area V1 (primary visual cortex), the multisensory overlap being on the border between V1 and V2. This result is interesting not merely because it extends the range of visual areas that respond to tactile tasks into areas quite early in the visual cortical hierarchy, but also because, for the first time, visual areas were shown to be active in a microspatial tactile task. It remains to be seen whether this is an exception to the general rule that microspatial tactile tasks do not recruit visual cortical activity, or whether such tasks might tend to evoke activity in particular early visual cortical areas under the appropriate conditions.

Conversely, the LOC was bilaterally active during p0040 shape perception in both haptic and visual modalities (Stilla and Sathian, submitted), consistent with numerous earlier fMRI studies (Deibert, E. *et al.*, 1999; Amedi, A. *et al.*, 2001; 2002; James, T. W. *et al.*, 2002; Stoeckel, M. C. *et al.*, 2003; Reed, C. L. *et al.*, 2004; Zhang, M. *et al.*, 2004). As mentioned above, we found bilateral activation of the LOC during tactile 2D form discrimination, distinguishing between upside-down Ts and Vs, when this task was contrasted with gap detection (Stoesz, M. *et al.*, 2003). We also found activation of the right LOC in the same form task, relative to bar orientation discrimination, in a PET study (Prather, S. C. *et al.*, 2004). Thus, the LOC appears to be consistently active during tactile perception of either 2D or 3D form. Studies of patients with lesions involving the LOC suggest, moreover, that it is actually necessary for haptic as well as visual shape perception. One patient with visual agnosia (inability to recognize objects), following a lesion of the left occipitotemporal cortex that probably included the LOC, also turned out to have tactile agnosia, although somatosensory cortex and basic somatic sensation were intact (Feinberg, T. E. *et al.*, 1986). Another patient who developed bilateral lesions of the LOC was impaired at learning unfamiliar objects using either touch or vision (James, T. W. *et al.*, 2006a). Multisensory object selectivity in the LOC appears to be confined to a subregion, which responds more strongly to graspable visual objects (such as tools) than to other stimuli (such as buildings or faces) but does not appear to be object selective in the auditory modality (Amedi, A. *et al.*, 2002).

Our study (Stilla and Sathian, submitted) also p0045 found multisensory shape selectivity bilaterally in

s0015 6.19.1.2 Motion, Texture, and Form

p0030 Several studies have shown that an area involved in perception of visual motion, the human MT complex (which is considered to be the human homolog of macaque MT, a visual motion-processing area), is also active during presentation of tactile motion stimuli, even in the absence of any task (Hagen, M. C. *et al.*, 2002; Blake, R. *et al.*, 2004). Psychophysical studies point to a common representation of motion across vision and touch: tactile motion perception can be used to disambiguate the direction of motion in an ambiguous visual motion display (Blake, R. *et al.*, 2004), and facilitates such disambiguation when presentation of the visual motion display is delayed (James, T. W. and Blake, R., 2004). However, when the direction of motion is unambiguous but incongruent between vision and touch, visual motion disrupts tactile motion perception (Craig, J. C., 2006).

p0035 In a recent fMRI study, we contrasted activations during shape and texture perception in both haptic and visual modalities (Stilla and Sathian, submitted). We found somatosensory areas that were selectively activated during haptic texture perception, in the parietal operculum and posterior insula bilaterally.

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the PCS, and at multiple foci within the IPS, including the aIPS, pIPS, and ventral IPS (vIPS). Multisensory shape selectivity had been reported previously in the left aIPS (Grefkes, C. *et al.*, 2002) and in a caudal region of the IPS located between our pIPS and vIPS foci (Saito, D. N. *et al.*, 2003). Multisensory shape processing in the IPS fits with the description of multisensory responses in various parts of the IPS in monkeys (Iriki, A. *et al.*, 1996; Duhamel, J. R. *et al.*, 1998), although the homologies with humans remain uncertain. The demonstration of extensive multisensory overlap in the cortical processing of shape raises the possibility that both visual and haptic shape perception may engage a unitary neural representation, as in the case of motion perception. This is supported by cross-modal priming effects between visual and haptic object presentations in two fMRI studies, although the effects were in opposite directions in the two studies (Amedi, A. *et al.*, 2001; James, T. W. *et al.*, 2002). Additional psychophysical evidence bearing on the issue of a common visuo-haptic representation of shape is considered in the next section. Of some interest is the finding of multisensory shape processing in the PCS, which, as pointed out earlier in this chapter, corresponds to Brodmann's area 2 (Grefkes, C. *et al.*, 2001), part of S1. Along with the finding of multisensory texture selectivity in V2 described above, this underscores the ubiquity of multisensory processing, with its presence even in regions early in the sensory hierarchies.

p0050 Face perception is a special case of form perception. Obviously, sighted humans perform face recognition almost exclusively using vision, but they can also identify faces haptically. Like the patients described in the studies of object perception (see above), a prosopagnosic patient (i.e., one who could not recognize faces visually) was found to be unable to recognize faces haptically (Kilgour, A. R. *et al.*, 2004). Face recognition also occurs cross-modally between vision and touch (Kilgour, A. R. and Lederman, S., 2002), albeit not without a cost relative to within-modal recognition (Casey, S. J. and Newell, F. N., 2007). This cost in cross-modal performance is unrelated to the encoding modality or to differences in encoding procedures and suggests that, unlike object and motion perception, face recognition may not rely on a representation that is common to both vision and touch (Casey, S. J. and Newell, F. N., 2007). Recent fMRI studies fit with this idea: face-selective voxels in ventral and inferior temporal cortex are mostly nonoverlapping between the two modalities (Pietrini,

P. *et al.*, 2004); the left fusiform gyrus is activated during haptic face recognition, whereas the right fusiform gyrus is more active during visual face recognition (Kilgour, A. R. *et al.*, 2005); and left fusiform activity increases when the faces are familiar compared to unfamiliar while the right fusiform remains relatively inactive (James, T. W. *et al.*, 2006b). Differential activation of the left versus right fusiform gyrus for haptic versus visual face perception may reflect processing of modality-specific featural face information, whilst modality-independent configural face information is dealt with elsewhere in the brain (Casey, S. J. and Newell, F. N., 2007). Since imagery of visually presented faces produces greater activation in the left than in the right fusiform gyrus (Ishai, A. *et al.*, 2002), another possibility is that haptic face perception may involve imagery mechanisms, although one study found no correlation between performance on haptic face recognition and imagery ratings (Kilgour, A. R. and Lederman, S., 2002). Further studies are needed to resolve the neural basis of multisensory face perception, and its differences from multisensory object perception.

6.19.2 Visual Imagery and Multisensory Representations

s0020

The studies reviewed so far establish that visual p0055 cortical processing is routinely involved in normal tactile perception in the sighted, especially during macrospatial tasks but potentially during microspatial tasks as well. Such processing is quite task specific, so that extrastriate visual cortical areas known to be specialized for particular visual tasks are involved during performance of the same tasks in touch. So far we have considered whether vision and touch share a common representation (e.g., for objects and motion) or separate representations (e.g., for faces). In this section we consider the nature of these representations in more detail. It was formerly thought that cross-modal performance was mediated by language, but cross-modal abilities have been demonstrated in preverbal infants and in several nonhuman primate and nonprimate species (see Rose, S. A., 1994 for a brief review). However, whilst linguistic competence may not be necessary, it may play a facilitatory role: it is possible to produce a verbal description of unfamiliar objects (Easton, R. D. *et al.*, 1997a) and a verbal secondary task disrupts both visual and haptic encoding of unfamiliar objects such that subsequent

cross-modal recognition is impaired (Lacey, S. and Campbell, C., 2006a).

p0060 A more fundamental explanation for cross-modal recruitment of the visual cortex into nonvisual tasks is that these tasks might involve visual imagery. This is an intuitively appealing explanation, especially since subjects consistently report mental visualization of tactile stimuli during macrospatial tasks such as discrimination of grating orientation or tactile form, which are associated with visual cortical recruitment. This is not true of microspatial tasks such as discrimination of grating groove width or gap detection, which tend to not involve visual cortical activity (Sathian, K. *et al.*, 1997; Zangaladze, A. *et al.*, 1999; Stoesz, M. *et al.*, 2003; Zhang, M. *et al.*, 2005). Visual imagery might be triggered by lack of familiarity with the tactile stimuli or tasks used; indeed, such cross-modal translation may be a general phenomenon, especially during complex information processing (Freides, D., 1974). Consistent with the idea that visual imagery mediates visual cortical activity in touch, an fMRI study from our laboratory (Zhang, M. *et al.*, 2004) found that inter-individual variations in the magnitude of haptic shape-selective activity in the right LOC (ipsilateral to the hand used for haptic perception) were strongly predicted by ratings of the vividness of visual imagery. In contrast, activation strengths in the left LOC were uncorrelated with these visual imagery scores, pointing to an additional role for factors other than visual imagery in cross-modal visual cortical recruitment (Zhang, M. *et al.*, 2004). Left-lateralized activity has, however, been found in the LOC when either geometric or material object properties are retrieved from memory in the absence of visual or haptic input (Newman, S. D. *et al.*, 2005) and in both the blind and the sighted while generating mental images of shape derived from haptic and visual experience, respectively (De Volder, A. G. *et al.*, 2001). (Although this last report did not specifically identify the LOC, the illustrations and coordinates of activation clearly indicate it.)

p0065 If the representation of haptically perceived objects is indeed primarily visual, there should be a relationship between cross-modal memory performance and visual imagery ability. Several studies show that children's visuo-spatial abilities are indeed correlated with cross-modal memory performance for both familiar (Johnson, C. L. *et al.*, 1989) and unfamiliar objects (Stoltz-Loike, M. and Bornstein, M. H., 1987). Furthermore, good imagers (as measured by scores on the Vividness of Visual Imagery Questionnaire,

VVIQ; Marks, D. F., 1973) are better at cross-modal memory than are poor imagers (Cairns, E. and Coll, P., 1977). However, this approach has its limitations. One is that visual imagery is a multicomponent process: images have to be generated and maintained, and once retrieved can be inspected, scanned, rotated, or otherwise manipulated (Kosslyn, S. M., 1980; 1994). Furthermore, individuals may vary in ability on one or more of these components (Kosslyn, S. M. *et al.*, 1990; 1984). Thus, a single test of visual imagery ability may not be appropriate since it may not capture the relevant component and thus may not be sensitive to the relevant individual differences. Secondly, it has been argued that the VVIQ only measures a subjective aspect of the experience of imagery rather than imagery processes and abilities *per se* (Pearson, D. *et al.*, 2001; Dean, G. and Morris, P. E., 2003). Moreover, the superiority of good imagers might stem not from greater proficiency at imagery but from better use of strategically important information (Baddeley, A. D. and Andrade, J., 2000). In addition, different aspects of visual imagery may contribute differentially to cross-modal memory and perceptual representations. For example, spatial recall predicts cross-modal performance whereas mental rotation does not (Stoltz-Loike, M. and Bornstein, M. H., 1987).

Some have argued that the LOC activity observed p0070 during haptic shape perception is not due to visual imagery since visual imagery evoked less activity in the LOC than did haptic object recognition (Amedi, A. *et al.*, 2001). However, this reduced activation might have been due to object familiarity and/or the lack of a requirement to maintain images online during the entire scan. Nonetheless, other possible explanations should be considered for visual cortical recruitment during tactile perception. Vision and touch can both encode object shape, and visual cortical activation during tactile perception might reflect a multisensory representation rather than a specifically visual image. Psychophysical observations indicate, for example, that cross-modal visuo-haptic priming is essentially as effective as within-modal priming (Easton, R. D. *et al.*, 1997a; 1997b; Reales, J. M. and Ballesteros, S., 1999), and that cross-modal shape matching can be quite effective even when the objects are highly similar (Norman, J. F. *et al.*, 2004). An alternative approach to the relationship between visual and haptic representations argues that vision and touch encode object properties common to both modalities into a single representation that is multisensory (Sathian, K., 2004) or amodal (e.g., Lewkowicz, D. J.,

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1994). It is our view that the amodal label is best suited to processing of information that cannot be derived directly from sensory systems and that must be represented linguistically or perhaps propositionally. We prefer instead the term multisensory, referring to a representation that is accessible from multiple sensory systems, but in which the modality tags of the associated inputs are preserved (Sathian, K., 2004). In the case of vision and touch, modality-independent representations can be specified as spatial in format since both these sensory systems can encode spatial information such as size, shape, and the relative positions of different object features. An important question is the precise nature of the modality-independent representation.

p0075 The format of visuo-haptic object representation has been investigated behaviorally using interference tasks in a cross-modal memory paradigm. In one study (Lacey, S. and Campbell, C., 2006a), both visual and verbal interference disrupted encoding of unfamiliar objects, significantly reducing subsequent cross-modal recognition, while haptic interference was ineffective and familiar objects were immune to any form of interference. These results suggested that encoding in both modalities resulted in a common representation linked to a strategy of covert verbal description. Since the visual interference task (dynamic visual noise) is known to disrupt visual imagery mnemonics for recall of word lists (Quinn, J. G. and McConnell, J., 1996) and the use of visual imagery in symbolic comparison tasks (Dean, G. M. *et al.*, 2005), these results suggested that the common representation could be a visual image. Interference might have been more important for the unfamiliar objects because cross-modal memory for familiar objects is probably supported by closely interconnected representations in several formats – for example, visual, verbal, and haptic (Lacey, S. and Campbell, C., 2006a).

p0080 Lacey S. and Campbell C. (2006b) showed that spatial interference disrupted both encoding and retrieval, independent of the modality in which the interference task was presented, whereas nonspatial interference in either modality had no effect. Thus the common representation could be a modality-independent spatial one, rather than visual. It remains uncertain whether this reflects a single, multisensory spatial representation or separately derived visual and haptic spatial representations that are compared cross-modally. A recent neuroimaging study is instructive in this regard, showing that category selectivity within human inferotemporal cortex

is relatively independent of whether the input modality is visual or haptic (Pietrini, P. *et al.*, 2004). Subjects with early-onset blindness had similar patterns of category-selective responses during haptic object perception in this study, although there were some differences in the locations of the category-selective responses between blind and sighted subjects. These findings suggest a single multisensory representation for objects that may be spatially rather than visually based. This interpretation is suggested by the recent work by Kozhevnikov and co-workers (Kozhevnikov, M. *et al.*, 2002; 2005; Blajenkova, O. *et al.*, 2006) showing that visual imagery is of two distinct types. Object imagery refers to images that are more pictorial and detailed in terms of shape, color, brightness, etc., whilst spatial imagery refers to images that are more concerned with the spatial relations of objects and object parts and hence may facilitate spatial transformations. Thus, an interesting question is how these different types of imagery are related to cross-modal performance: for example, are spatial imagers better at haptically deriving representations than object imagers?

If haptic and visual perception engage a modality-independent imagery system, we might expect to see similarities between visually and haptically accessed component processes of this system. For example, scanning times in visual imagery increase with the spatial distance to be inspected in the image, implying preservation of metric spatial information in visual images (Kosslyn, S. M., 1973; Kosslyn, S. M. *et al.*, 1978). The same effect is observed in scanning haptically derived representations, implying that these are also spatial and that similar, if not identical, imagery processes operate in both modalities (Röder, B. and Rösler, F., 1998). Similarly, studies of mental rotation of visual stimuli show that the time taken to judge whether two objects are the same or mirror images increases linearly with increasing angular disparity between the stimuli (Shepard, R. N. and Metzler, J., 1971). This also holds true for haptic and tactile stimuli (Marmor, G. S. and Zaback, L. A., 1976; Carpenter, P. A. and Eisenberg, P., 1978; Hollins, M., 1986; Dellantonio, A. and Spagnolo, F., 1990; Prather, S. C. and Sathian, K., 2002; Prather, S. C. *et al.*, 2004). A PET study from our laboratory (Prather, S. C. *et al.*, 2004) investigated the mental rotation of tactile stimuli – upside-down Js presented in one of two mirror-image configurations. Contrasting a mental rotation condition (stimuli at 135–180° angle with respect to the long axis of the finger) with a pure mirror-image discrimination condition (stimuli at 0°)

revealed activity in the left aIPS, at a focus that is also active during mental rotation of visual stimuli (Alivisatos, S. and Petrides, M., 1997), lending further support to the idea that similar spatial imagery processes operate on both visually and haptically derived representations.

p0090 Interestingly, these similarities between visually and haptically derived representations are observed in both the early-blind and the late-blind as well as the sighted (Carpenter, P. A. and Eisenberg, P., 1978; Röder, B. and Rösler, F., 1998). The blind are reported to be slower than the sighted at haptic mental rotation (Marmor, G. S. and Zaback, L. A., 1976) but Hollins M. (1986) suggests that, after controlling for greater variability in the use of frames of reference by the sighted, this difference is more apparent than real. Taken together, these studies indicate that common processes are engaged when generating, retrieving, and manipulating representations derived from both vision and touch.

s0025 **6.19.3 Top-Down and Bottom-Up Processing**

p0095 If mental imagery underlies tactile activation of the visual cortex, we would expect to find direct, bottom-up somatosensory projections into the visual cortical areas that are implicated in tactile perception, as opposed to the top-down projections from prefrontal into visual cortical areas that would be required to support a process such as visual imagery (Mechelli, A. *et al.*, 2004). These are possibilities that can be tested empirically, either by studying connectivity in experimental animals or by analyzing fMRI data to reveal effective connectivity. A study from our laboratory (Peltier, S. *et al.*, 2007) probed effective connectivity using structural equation modeling, based on the correlation matrix between the time courses of fMRI activity in various regions. This study revealed both bottom-up and top-down paths in a network of haptically shape-selective areas, including foci in the PCS, the IPS, and the LOC. This suggests that potential neural substrates exist for both visual imagery and multisensory representations, in relation to visual cortical involvement during haptic shape perception.

p0100 Neurophysiological and neuroanatomic studies in monkeys have also illuminated understanding of cross-modal visual cortical recruitment. Some neurons in area V4 (a nonprimary area in the ventral visual pathway) were selective for the orientation of a

tactile grating when it served as a cue for matching to a subsequently presented visual stimulus, but not when it was task irrelevant (Haenny, P. E. *et al.*, 1988). The requirement for task relevance implicates top-down, rather than bottom-up, inputs. Multisensory inputs have been reported in early sensory cortical areas that are traditionally considered unisensory, including V1 (Falchier, A. *et al.*, 2002; Rockland, K. S. and Ojima, H., 2003) and auditory association cortex (Schroeder, C. E. *et al.*, 2001; Schroeder, C. E. and Foxe, J. J., 2002; Schroeder, C. E. *et al.*, 2003). Analysis of the laminar profile of these projections suggests that both top-down (Falchier, A. *et al.*, 2002; Schroeder, C. E. and Foxe, J. J., 2002; Rockland, K. S. and Ojima, H., 2003; Schroeder, C. E. *et al.*, 2003) and bottom-up (Schroeder, C. E. and Foxe, J. J., 2002; Schroeder, C. E. *et al.*, 2003) inputs exist. Thus, the sum total of the evidence to date indicates the probable existence of multisensory representations that are flexibly accessible via both vision and touch, with the potential to involve interactions between bottom-up sensory inputs and top-down processes such as visual imagery.

6.19.4 Cross-Modal Conflict, Enhancement, and Perceptual Illusions

p0105 If vision and touch produce separate representations, how do these affect each other? Classic research suggested that vision dominates touch (Rock, I. and Victor, J., 1964). When the visual width of an object was distorted by a lens, individuals who both saw and felt the object were unaware of the cross-modal conflict and reported the distorted width perceived visually, rather than the true width perceived tactually. Thus this sensory conflict was resolved in favor of the visual percept. More recent research has shown the situation to be more complex and to depend on the specific object property (Klatzky, R. L. *et al.*, 1987). For example, under neutral instructions the haptic saliency of object properties is hardness > texture > shape and under haptically biased instructions this changes to texture > shape > hardness. However, in combined visual and haptic perception, and in haptic perception with concurrent visual imagery, this saliency is reversed and changes to shape > texture > hardness/size (Klatzky, R. L. *et al.*, 1987). Visual imagery can therefore influence tactile perception in the absence of visual perception and, moreover, different modalities may be optimal for

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different object properties (Klatzky, R. L. *et al.*, 1993). Thus, there is not a simple dominance of visual over tactile perception.

p0110 Another interesting phenomenon is the asymmetry normally observed in cross-modal memory performance: in general, performance is better when visual encoding is followed by haptic retrieval than the reverse (e.g., Jones, B., 1981; Streri, A. and Molina, M., 1994; Lacey, S. and Campbell, C., 2006a; 2006b). Asymmetric performance appears to be a consistent aspect of cross-modal memory but, while many studies address the difference between within- and cross-modal performance, the difference between the two cross-modal conditions receives less attention (e.g., Easton, R. D. *et al.*, 1997a; 1997b; Reales, J. M. and Ballesteros, S., 1999; Nabeta, T. and Kawahara, J., 2006). It has been suggested that if cross-modal memory relied on a common representation, based on properties that can be represented equally well by different modalities (Lewkowicz, D. J., 1994), then performance should be similar in the two cross-modal conditions (Freides, D., 1974; Streri, A. and Molina, M., 1994). The fact that asymmetric performance occurs suggests otherwise, but given that the basis for the asymmetry still requires explanation, it would be premature to rule out a common representation solely on this basis. One explanation for asymmetry may be that, although vision and touch are both encoding the same information about an object into the same modality-independent format, this information may not be encoded equally well because of competition from other, more salient, modality-specific information. As noted above, visual imagery instructions alter the haptic salience of object properties (Klatzky, R. L. *et al.*, 1987) – without the imagery-biased instructions it might have been more difficult to encode shape because of the more salient hardness and texture information.

p0115 In a study using an *n*-back letter recognition task, Bliss I. and Hämäläinen H. (2005) showed that haptic working memory capacity appears to be limited and variable. A simple explanation for asymmetry may therefore be that haptic working memory is more error prone than visual working memory. An alternative is that haptic representations may simply decay faster than visual representations. Indeed, the decay function in haptic memory, rather than being progressive, appears to occur entirely in a band of 15–30 s poststimulus (Kiphart, M. J. *et al.*, 1992). This suggests that performance might be lower in the haptic–visual condition of the cross-modal memory task because haptically encoded representations have

substantially decayed by the time that visual retrieval is required. However, several cross-modal memory studies show that increasing the delay between encoding and retrieval up to 30 s did not affect haptic–visual performance more than visual–haptic performance (Garvill, J. and Molander, B., 1973; Woods, A. T. *et al.*, 2004) and so it seems that the explanation will be more complicated than a simple function of haptic memory properties alone. Interestingly, asymmetry is also observed in cross-modal studies involving very young infants (e.g., Streri, A. and Molina, M., 1994). These studies attribute asymmetric performance to constraints imposed by different stages of motor development (Streri, A. and Molina, M., 1994), but since asymmetry persists beyond early development into more mature motor systems (Easton, R. D. *et al.*, 1997a; 1997b; Bushnell, E. W. and Baxt, C., 1999; Lacey, S. and Campbell, C., 2006a; 2006b), it is likely that other representationally important factors are involved.

Haptic versions of visual illusions have been used p0120 to investigate the relationship between vision and touch. In the Müller–Lyer illusion, two lines of identical length and endcapped with fins that point either outward or inward are seen as shorter or longer, respectively, than the true length. This visual illusion has also been demonstrated in a haptic format (Heller, M. A. *et al.*, 2002; Millar, S. and Al-Attar, Z., 2002) and appears to be independent of visual experience since blindfolded, normally sighted individuals as well as those with low vision, late-blind subjects, and congenitally blind individuals were all equally susceptible to the illusion (Heller, M. A. *et al.*, 2002). Length distortion is an illusion that was first described haptically and subsequently found to also occur in vision. Length distortion refers to overestimation of the distance between two points as a function of the increasing length of an indirect pathway between them. The same effect can be observed, albeit of a smaller magnitude, in the visual version of the task (Balakrishnan, J. D. *et al.*, 1989). These studies suggest a common visuo-haptic representation of space that may be based on body-centered reference points (e.g., the body midline or the positions of the hands relative to each other), since instructions to use these in judging Müller–Lyer line length virtually eliminated the illusion in both modalities whilst external reference points (a frame surrounding the illusion figure) had no effect (Millar, S. and Al-Attar, Z., 2002). The use of these body-centered reference points may be a common mechanism for integrating spatial information from vision and touch.

p0125 Other approaches have identified interactions between vision and somatosensory representations of the body. One line of research has demonstrated that noninformative vision of the body can improve tactile spatial acuity, as measured using grating orientation discrimination (Taylor-Clarke, M. *et al.*, 2004), and that this cross-modal enhancement is abolished by TMS over S1 (Fiorio, M. and Haggard, P., 2005). In related work, visual stimuli (light flashes from light-emitting diodes (LEDs) on the finger) have been shown to increase the proportion of concomitant electro tactile stimuli that are detected; however, signal detection analyses showed only a small change in perceptual sensitivity – most of the effect apparently arose from criterion shift (Johnson, R. M. *et al.*, 2006). Similarly, a patient with a right hemispheric lesion was reported to perceive touch on the contralesional hand only when viewing the tactile stimulation (Halligan, P. *et al.*, 1996). Another line of research pertains to the rubber hand illusion. When a rubber hand is positioned in alignment with one's own, invisible hand, if one sees the rubber hand being touched, one experiences illusory touch, indicating a feeling of ownership of the synthetic hand (Botvinick, M. and Cohen, J., 1998). Such a feeling of ownership is associated with activity in the ventral premotor cortex (Ehrsson, H. H. *et al.*, 2004), a region where, in monkeys, neurons exhibit visual receptive fields that are anchored to the arm and move with it (Graziano, M. S. *et al.*, 1994).

p0130 Yet another line of work stems from observations that tactile stimuli can be referred ipsilaterally from intact body parts to phantoms of resected body parts (Ramachandran, V. S. and Hirstein, W., 1998; Aglioti, S., 1999). Tactile stimuli applied to the intact hand of arm amputees have been shown to evoke contralateral percepts referred topographically to the phantom hand (Ramachandran, V. S., 1995), and similar contralateral mirror-symmetric referral of sensations also occurs in patients with sensory loss due to neurological lesions (Sathian, K., 2000). The referral is evoked for touch but typically not other kinds of somatosensory stimuli, such as pain or temperature (Ramachandran, V. S., 1995; Sathian, K., 2000). The referred sensations tend to be relatively high threshold, crudely localized, and lacking spatial organization, leading to the conclusion (Sathian, K., 2000) that they are unlikely to depend on neurons in area 3b, which exhibit fine-grained spatial resolution and topographic organization (DiCarlo, J. J. *et al.*, 1998). Also, since the hand representation in area 3b has sparse callosal connectivity (Killackey, H. P. *et al.*, 1983) and normally lacks

neurons with bilateral receptive fields (Pons, T. P. *et al.*, 1987), transcallosal referral probably occurs more posteriorly in S1, in areas 1 and 2, or in the parietal opercular cortex, where bilateral somatosensory responsiveness (Robinson, C. J. and Burton, H., 1980a; 1980b; Iwamura, Y. *et al.*, 1994) and callosal connectivity (Killackey, H. P. *et al.*, 1983; Manzoni, T. *et al.*, 1984) are found in the hand representation. Interestingly, in both amputees (Ramachandran, V. S., 1995) and patients with sensory loss (Sathian, K., 2000), visual input via a mirror tended to strengthen referred percepts, suggesting a role for multisensory convergence. Use of a mirror to create conflict between the vision of touch (present) and the feeling of touch (absent) enhanced subsequent sensitivity to touch; the effect was eliminated by TMS over posterior parietal cortex (Ro, T. *et al.*, 2004). Provision of illusory visual input using a mirror has been exploited as a rehabilitative method to improve arm function affected by strokes (Altschuler, E. L. *et al.*, 1999; Sathian, K. *et al.*, 2000). These studies point to the existence of intricate and multifaceted interactions between visual and tactile processing that may be beneficial during normal perception as well as in neurological rehabilitation – such interactions offer fertile ground for future basic and clinical investigation.

6.19.5 Conclusions

s0035

In this chapter, we have outlined a plethora of cross-modal and multisensory interactions that occur in a variety of circumstances. Such interactions underscore the generality of multisensory processing, and are increasingly being recognized by researchers. The effects of visual deprivation that are reviewed by Burton (see Chapter Visual Deprivation Effects on Somatosensory and Visual Systems: Behavioral and Cortical Changes) should be interpreted in the context of these normal interactions, although a unifying framework is inchoate. The development of this framework remains a major challenge for future work.

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Further Reading

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