Chapter 1

Multimodal images in the brain

Stephen M. Kosslyn, Giorgio Ganis,
and William L. Thompson

Multimodal images in the brain

Mental imagery is like perceiving, but in the absence of an immediate appropriate sensory stimulation. As such, imagery is often identified with specific phenomenology, such as the experience of 'seeing with the mind's eye', 'hearing with the mind's ear', and so on. However, the experience itself is not the image; and, in fact, it is not even clear that mental images must always be accompanied by a specific experience. Rather, mental images consist of internal representations of the same types as those that arise during the early phases of like-modality perception. Mental images are internal representations that are based on information stored in memory. In contrast, perception occurs when information is registered directly from the senses.

This conception of mental imagery leads us to characterize many sorts of imagery. First, each perceptual modality should, in principle, be accompanied by the ability to generate images in that modality. And, in fact, people commonly report visual, auditory, and kinaesthetic images (e.g., Kosslyn *et al.* 1990). Second, not all forms of imagery need give rise to distinct phenomenology. For example, spatial images may give rise to only the most impoverished sense of 'where things are'. Third, mental images need not be simply the recall of previously perceived objects or events; they also can be created by combining and modifying stored perceptual information in novel ways.

Mental imagery has played a central role in theories of mental function at least since the time of Plato. It has fallen in and out of fashion, in large part because it is inherently a private affair – by definition restricted to the confines of one's mind. (In this context, by 'mind' we mean brain function.) Thus, imagery has been difficult to study. In fact, in 1913 the founder of Behaviourism (the school of psychology that focused solely on observable stimuli, responses, and the consequences of responses), John B. Watson, denied that mental images even existed. Instead, he suggested, thinking consists of subtle movements of the vocal apparatus (Watson 1913).

Nevertheless, clever researchers developed empirical methods for studying imagery. Notably, Alan Pavio and his colleagues (see, for example, Paivio 1971) were able to show that the use of imagery dramatically improves memory. However, even in the face of such findings, some researchers were not convinced that imagery is a distinct form of thought. Indeed, Watson's position was echoed 60 years later by Zenon Pylyshyn, who championed the view that mental images are not 'images' at all, but rather rely on mental descriptions no different in kind from those that underlie language. According to Pylyshyn (1973), the pictorial aspects of imagery that are evident to conscious experience are entirely epiphenomenal, like the heat from a light bulb when you read (which plays no role in the reading process). That is, according to this descriptivist view, the fact that we experience visual images as akin to pictures in the mind's eye says nothing about the nature of the underlying mental representation.

The emergence of cognitive neuroscience has opened a new chapter in the study of mental imagery. An enormous amount has been learned about the neural underpinnings of visual

perception, memory, emotion, and motor control. Much of this information has come from the study of animal models. Unlike language and reasoning, these more basic functions have many common features among higher mammals, including humans. In addition, neuroimaging technologies, especially positron emission tomography (PET) and functional magnetic resonance imaging (fMRI), have allowed theories of imagery to be tested objectively in humans. Researchers have taken advantage of these developments to show that mental imagery draws on much of the same neural machinery as perception in the same modality, and can engage mechanisms used in memory, emotion, and motor control.

In this chapter we draw on results from a variety of methods, including studies of the effects of selective brain damage on behaviour, neuroimaging, and studies examining the effects of transcranial magnetic stimulation (TMS). Each method has its strengths and weaknesses, but they are complementary. Thus, for example, neuroimaging provides only correlational data (when engaged in a particular task, a particular set of brain areas is activated) but can monitor the entire brain; TMS can be used to establish causal roles of distinct areas (e.g., by showing that performance in a task that draws on a specific brain area is impaired following TMS to that area), but must be targeted to a specific location. To the extent that the same conclusions are reached using different methods, these conclusions can be taken increasingly seriously.

We briefly review three main classes of research: evidence that imagery engages brain mechanisms that are used in perception and action; evidence that visual mental imagery engages even the earliest visual cortex (Areas 17 and 18); and evidence that imagery engages mechanisms that control physiological processes such as heart rate and breathing, having effects much like those that occur with the corresponding perceptual stimuli.

Mental imagery, perception, and action

We begin with visual imagery, which is by far the most intensively studied modality, and then turn to auditory and motor imagery.

Visual mental imagery

Well over 100 years ago, researchers described brain-damaged patients who had lost the ability to form visual mental images after they became blind (for review, see Farah 1984; however, see also Chatterjee and Southwood 1995). Methods from cognitive psychology have allowed researchers to characterize such deficits in imagery with increasing precision, typically by building on knowledge about perception. For example, some patients have perceptual deficits in only one of the two major cortical visual functions. One major visual pathway runs from the occipital lobe down to the inferior temporal lobes (the so-called 'object properties processing' pathway; see Ungerleider and Mishkin 1982). This pathway in turn can be broken down into two sub-pathways, which subserve shape and colour. Depending on the nature of brain damage, the animal or person cannot easily recognize shape or colour. The other major visual pathway runs from the occipital lobe to the posterior parietal lobes (the so-called 'spatial properties processing' pathway); when damaged, the animal or person cannot easily register location. As we summarize in the following, such detailed knowledge about perception has guided much research on imagery.

Imagery and perception

Typically, parallel deficits appear in mental imagery and perception: damage to the occipital-temporal pathway disrupts the ability to visualize shape (as used, for example, to recollect whether George Washington had a beard) and/or colour (as used, for example, to determine the colour of the inside of a cantaloupe), whereas damage to the occipital-parietal pathway disrupts the ability

to visualize locations (as used, for example, to indicate the locations of furniture in a room when one's eyes are closed; see, for example, Levine *et al.* 1985). Indeed, very subtle deficits can occur in imagery that parallel the deficits found in perception. For example, some brain-damaged patients can no longer distinguish colours perceptually or in imagery (De Vreese 1991) and others can no longer distinguish faces perceptually or in imagery (Young *et al.* 1994)**.**

However, although the deficits in imagery and perception often parallel each other, this is not always the case. In a seminal literature review and analysis, Farah (1984) showed that some patients have selective problems in generating visual mental images (i.e. producing them on the basis of information stored in long-term memory) even though they are able to recognize and identify comparable perceptual stimuli (for a review, see also Ganis *et al.* 2003). In addition, patients have been reported who could visualize but had impaired perception (e.g., Behrmann *et al.* 1992; Jankowiak *et al.* 1992). In short, the results from research with brain-damaged patients suggest that visual mental imagery and visual perception share many common mechanisms, but do not draw on identical processes. Although shape, location, and surface characteristics are represented and interpreted in comparable ways during both functions, the two differ in key ways: imagery, unlike perception, does not require low-level organizational processing; and perception, unlike imagery, does not require us to activate information in memory when the stimulus is not present (see Behrmann 2000).

The results of neuroimaging studies, that compare imagery and perception have dovetailed nicely with those from studies of brain-damaged patients (for a review, see Kosslyn and Thompson 2003). One study, for example, found that of all the brain areas activated during perception and imagery, approximately two-thirds were activated in common (Kosslyn *et al.* 1997). Another study reported that the amount of overlap is considerably greater, over 90 % (Ganis *et al.* 2004). But it is clear that imagery and perception do not activate identical neural systems. Presumably, lesions in the areas not activated in common produce the dissociations, where imagery or perception is disrupted independently; whereas lesions in the areas activated in common produce the more frequently reported parallel deficits in imagery and perception.

Structure of visual mental imagery

Finally, studies of deficits following brain damage have underscored the fact that 'imagery' – like all other cognitive functions – is not a single, undifferentiated ability. Rather, it is a collection of abilities, each of which can be disrupted independently. For example, some patients can make imagery judgements about the shape or colour of objects but have difficulty imagining an object rotating (e.g., when trying to decide whether the letter 'p' would be another letter when rotated 180°, or whether 'Z' would be another letter when rotated 90° clockwise). Other patients have the reverse pattern of deficits. Indeed, when participants perform different imagery tasks while their brain activity is monitored, different patterns of activation are observed while they process images in different ways. For example, when participants mentally rotate patterns, their parietal lobes (often bilaterally) and right frontal lobes typically are strongly activated (e.g., Cohen *et al.* 1996; Kosslyn *et al.* 1998; Richter *et al.* 2000; Jordan *et al.* 2001; Ng *et al.* 2001; for a review, see Zacks 2008). In contrast, if they are asked to visualize previously memorized patterns of stripes and judge which are longer, wider, and so on (all on the basis of their mental images, with eyes closed), these areas are not activated, but other areas in the occipital lobe and left association cortex are activated (Kosslyn *et al.* 1999; Thompson *et al.* 2001).

Depending on the precise task, different sets of processes are activated (O'Craven and Kanwisher 2000; Downing *et al.* 2006; Kanwisher and Yovel 2006). Indeed, brain activation during mental imagery may vary according to the type of object that is visualized. Using fMRI, O'Craven and Kanwisher (2000) found activation in the fusiform face area (FFA) when participants

visualized faces. Conversely, when participants visualized indoor or outdoor scenes depicting a spatial layout, these researchers found activation in the parahippocampal place area (PPA). There was no hint of activation of the PPA during face imagery or of the FFA during place imagery. These results are similar to what was observed when participants actually perceived faces and places. The findings underscore that imagery and perception share very specific, specialized mechanisms.

Visual mental imagery and early visual cortex

A large portion of research on the neural bases of imagery focuses on whether early visual cortex is activated during imagery (for a review, see Kosslyn and Thompson 2003; Kosslyn *et al.* 2006.). Early visual cortex consists of Areas 17 and 18, the first two cortical areas to receive input from the eyes. Researchers have wanted to know whether visual imagery activates these early areas for three main reasons. First, these areas are known to be topographically organized; that is, they preserve (roughly) the local spatial geometry of the retina – and thus patterns of activation in them serve to depict shape. If these areas are activated during imagery, and such activation plays a functional role, this would be evidence that imagery relies on representations that depict information, not describe it. In other words, this would be evidence that mental imagery relies on actual images.

Second, such findings cannot be explained by appeal to 'tacit knowledge', which Pylyshyn (1981) used to explain away the findings from earlier behavioural experiments that attempted to demonstrate that imagery relies on depictive representations. According to this view, participants in imagery experiments may have unconsciously tried to imitate what they thought they would have done in the corresponding perceptual situation (such as by taking more time to scan farther distances across an imaged scene). But such tacit knowledge, stored as descriptions, would not explain why early visual cortex would be activated when participants had their eyes closed during imagery.

Third, if imagery can alter the activation of early visual cortex, this suggests that one's beliefs and expectations can (at least under some circumstances) modulate what one actually sees during perception. And this finding would have clear-cut implications for the reliability of eyewitness testimony and the veracity of visual memory, more generally.

More than 50 neuroimaging studies have examined activation in early visual cortex (for reviews, see Thompson and Kosslyn 2000; Kosslyn and Thompson 2003). The following studies seem to provide the strongest support for activation in early visual cortex during visual mental imagery. The participants had their eyes closed during all of the neuroimaging tasks, and thus activation of early visual cortex could not have been caused by seeing visual stimuli.

In one study (Kosslyn *et al.* 1995), participants were asked to visualize line drawings of objects at different sizes (as if they fit into different-sized boxes that were memorized before the PET scan). Not only was Area 17 activated, compared to a control condition in which identical auditory cues were provided but no imagery was used, but also the specific locus of activation depended on the size of the imaged object. Even though their eyes were closed, the mere fact of visualizing an object at a larger size shifted the activation to more anterior parts of the calcarine sulcus (the major anatomical landmark of Area 17) – just as is found in perception proper (e.g., Sereno *et al.* 1995). This result was replicated by Tootell *et al.* (1998) with fMRI and using a precise method to localize Area 17; there is no doubt that varying the size of objects in mental images shifts the locus of activation along Area 17 comparably to what occurs in perception.

In addition, Klein *et al.* (2000) used event-related fMRI to chart activation in Area 17 when visual mental images were formed. They found clear activation in every participant, with a clear-cut temporal pattern; activation began about 2 seconds after an auditory cue, and peaked around

4–6 seconds later, before dropping off during the next 8 seconds or so. But is such activation playing a functional role in imagery? In another study (Kosslyn *et al.* 1999), participants memorized four quadrants, each with black-and-white stripes (which varied in length, width, orientation, and separation), and later had to visualize them and make subtle shape comparisons, such as deciding which set had longer or wider stripes. PET scanning revealed that Area 17 was activated during this task. Moreover, when repetitive TMS was applied to Area 17 (in a separate group of participants) prior to the task, every participant subsequently required more time to make these judgements than when repetitive TMS was applied so that it did not affect Area 17. Indeed, the magnitude of the decrement in performance was the same when participants had their eyes closed and visualized the stripes as when they had their eyes open and made judgements based on visible stripes. This makes sense if Area 17 is critical in both the imagery and perceptual versions of the task. These findings are consistent with those of Farah *et al.* (1992) who found that after one occipital lobe was surgically removed from a patient (as part of a medical treatment), the apparent size of images decreased by approximately half – as expected if each occipital lobe represents the contra-lateral part of space.

In another PET study (Kosslyn *et al.* 1996), participants closed their eyes and visualized named letters of the alphabet, in upper case form. Four seconds after forming the image, they were asked to judge whether the letter had a specific characteristic (such as any curved lines); the response times and error rates were recorded at the same time that their brains were scanned. Not only were variations in the level of activation in Area 17 significantly correlated with the time participants required to make the judgements, but this correlation was present even after all other correlations between variations in regional cerebral blood flow and response time were statistically removed.

Finally, Slotnick *et al.* (2005) designed a study to examine whether mental imagery could evoke cortical activation with precise retinotopy. Participants took part in a standard retinotopic mapping procedure with three conditions: perception, imagery, and attention. In the perception condition, participants viewed two wedges with a checkerboard texture rotating around a central point. In the imagery condition, participants merely viewed the arcs (edges) of the wedge stimuli and filled in the rest of the figure using visual imagery. In the attention condition, participants also viewed the arcs of the wedge stimuli, but now they paid attention to where the stimulus wedges would have been, without having learned the appearance of the wedges; thus it was not possible for them to visualize the wedge stimuli. The perceptual retinotopic mapping activation was taken as the standard to which the imagery and attention conditions were compared. Statistical analyses revealed that imagery did activate retinotopic maps, and did so (at least for some participants) more strongly than attention alone. These results lend support to the view that mental imagery relies on the same early visual cortical areas as perception.

These results, taken together, indicate that: (1) Activation in early visual cortex is systematically related to spatial properties of the imaged object; (2) if Area 17 is impaired, via TMS or brain damage, so is the use of visual imagery; and (3) the activation in early visual cortex is not likely to be an artefact of activation in other areas, which is merely incidentally sent (via neural connections) to early visual cortex.

Given these positive results, why have many studies failed to find activation in early visual cortex? Kosslyn and Thompson (2003) report a meta-analysis that led to three conclusions: First, if a task requires participants to find a high-resolution detail in an image (such as by evaluating the shape of an animal's ears or comparing two similar sets of stripes), activation in early visual cortex is likely. Second, if a task requires a spatial judgement (which may be mediated by the parietal lobe), activation is less likely. Indeed, many of the studies that did not report activation in early visual cortex used spatial tasks (Mellet *et al.* 1995, 1996, 2000). Third, not surprisingly, the more

sensitive the neuroimaging technique, the more likely the researchers were to detect activation in early visual cortex.

A second puzzle is why some brain-damaged patients continue to have some use of imagery, in spite of the fact that early visual cortex has been severely damaged (see, for example, Chatterjee and Southwood 1995). Probably the most straightforward account for this finding is that early visual cortex is not necessary for all forms of visual imagery. Indeed, Crick and Koch (1995) make a good case that the experience of visual perception does not arise from early visual cortex, but rather from later areas that receive input from the earlier ones. The same is probably true in imagery: if later areas are activated in the absence of the appropriate immediate sensory input, one may experience visual imagery. However, such later areas do not make fine spatial variations accessible to later processes, and hence one apparently needs to reconstruct the local geometry in earlier areas (which have much smaller receptive fields, and hence higher resolution) if one must extract fine-grained details from the imaged object (for a review of imagery abilities in brain-damaged patients, see Ganis *et al.* 2003).

Auditory imagery

Do the first three notes of the children's song 'Three blind mice' ascend or descend? Most people report that they 'hear' the song in the process of deciding (that the three notes ascend). Such phenomenology has been taken to signal the presence of modality-specific internal representations, which correspond to auditory images. Research on auditory imagery has been far less extensive than on visual imagery. Zatorre and Halpern (1993) studied brain-damaged patients to find out whether specific brain areas are critical for auditory imagery. They studied a group of patients who had had the left or right temporal lobe removed (for the treatment of otherwise intractable epilepsy) and compared them to similar control participants. In one condition, the participants heard a familiar song while also reading the lyrics, and judged which of two particular words had the higher pitch. In another condition, the participants saw the lyrics and made the same judgements, but did not actually hear the song – and thus had to rely on their mental imagery. The patients with right-temporal lesions were impaired in both conditions, compared to both other groups. These findings demonstrate that at least some of the neural structures that play a key role in pitch discrimination in perception also play a comparable role in imagery.

Most research on auditory imagery has focused on imagery for music (for a review, see Zatorre and Halpern 2005). Zatorre *et al.* (1996) asked whether auditory imagery draws on the same mechanisms used in auditory perception. The participants either listened to songs and judged the relative pitch of pairs of words, or imagined hearing songs and made the same judgements. No auditory stimulation was present during the baseline condition, which required the participants to judge the relative length of visually presented words. PET revealed that many of the same areas were in fact activated in common in auditory imagery and perception. Although activation was stronger during perception than imagery, it was located in comparable regions in the temporal lobes in both conditions. The activated areas included bilateral associative auditory cortex (BA 21/22, in spite of the fact that the left temporal lobe has often been identified with the perception of language and the right with music or environmental sounds), bilateral frontal cortex (BA 45/9 and 10/47), left parietal cortex (BA 40/7), and supplementary motor cortex (BA 6). The bilateral activation in associative auditory cortex may reflect the fact that these researchers used verbal melodies.

Indeed, in a subsequent study, Halpern and Zatorre (1999) asked musically trained participants to listen to the opening notes of familiar (non-verbal) melodies and then continue 'hearing the melody with the mind's ear'. Again using PET, they found activation in two regions of the right temporal lobe (the superior and inferior temporal cortex), which is consistent with their earlier

study of brain-damaged patients; both of these areas are involved in storing and interpreting nonverbal sounds. Moreover, auditory imagery of a melody that required retrieval from memory also activated two right-hemisphere regions, in the frontal lobe and superior temporal gyrus (which is critical for auditory perception). Finally, the supplementary motor area (SMA) was also activated by auditory imagery, regardless of whether the melody was retrieved or simply rehearsed on-line. This is interesting because no overt behaviour was required. Halpern and Zatorre believe that stored movements are used in this sort of imagery – which makes sense for melodies, where one can subvocalize the tune as part of the process of retrieving the information.

Finally, Griffiths (2000) reports a novel study of patients who became deaf and then hallucinated hearing music. These patients were neither psychotic nor beset with an obvious neurological problem, such as epilepsy. Griffiths was able to perform PET while the patients had such hallucinations, and reports that the posterior temporal lobes, in auditory cortex, as well as several other areas (specifically, the right basal ganglia, the cerebellum and the inferior frontal cortices) were activated.

In short, auditory imagery appears to draw on most of the neural structures used in auditory perception. However, unlike visual imagery, there is little evidence that the first auditory cortical area to receive input from the ears, Area A1, is activated during auditory imagery (see Kleber *et al.* 2007).

Motor imagery

When people are asked to imagine walking to a specific goal placed in front of them and to indicate when they would have arrived, their estimates of transit time are remarkably similar to the actual time they subsequently require to walk that distance (Decety and Jeannerod 1995). In such tasks, people report that they imagine moving; and such imagery typically is referred to as 'motor imagery'. However, in our view the term 'motor imagery' may be slightly misleading. It is likely that participants do not activate the motor commands alone, but also activate representations of kinaesthetic feedback. To be sure, there is a difference between imagining moving one's own arm and imagining having somebody else move it for you in the same way. Nevertheless, both sorts of imagery involve kinaesthetic perceptual representations, along with representations of any motor commands that may accompany such perceptual feedback.

Many studies have now been carried out to investigate the neural bases of such motor imagery, and to distinguish motor imagery from purely visual mental imagery. Although visual imagery may often accompany motor imagery, researchers have documented that motor imagery relies on distinct mechanisms. Specifically, many researchers have shown that cortex used in movement control also plays a role in motor imagery. Indeed, in a classic study, Georgopoulos *et al.* (1989) recorded activity in individual neurons in the motor strip of monkeys while the animals were planning to move a lever along a specific arc. They found that these neurons fired in a systematic sequence, depending on their orientation tuning. Specifically, at first, only neurons tuned for orientations near the starting position of the lever fired, followed by those tuned for orientations slightly farther along the trajectory, and so on. All of this occurred before the animal actually began moving. These findings do not, however, show that mental imagery of movement occurs in the motor strip itself; it is possible that the computation takes place elsewhere in the brain (e.g., the posterior parietal lobes), and that the results of such computation are simply being executed in the motor strip.

Indeed, a host of neuroimaging studies on 'mental rotation' have now been reported, all of which have shown that multiple brain areas are activated during mental rotation. For example, Richter *et al.* (2000) measured brain activation with fMRI while participants mentally rotated the three-dimensional multi-armed angular stimuli invented by Shepard and Metzler (1971) (which

look as if they had been constructed by gluing small cubes together to form the arms). Participants were shown pairs of such shapes in which one member was rotated relative to the other; the participants were asked to report whether the figures in each pair were the same or mirror-reversed. Richter *et al.* report that the superior parietal lobules (in both hemispheres) were activated during this task, as well as premotor cortex (in both hemispheres), supplementary motor cortex, and also the left primary motor cortex.

Other neuroimaging studies have provided strong support for the role of motor processes in mental transformations. For example, Parsons *et al.* (1995) showed participants a picture of a hand, which could be rotated to various degrees; the pictures were presented in the left visual field (so the image was registered first by the right hemisphere) or in the right visual field (so the image was registered first by the left hemisphere). The participants were to decide whether each picture was a left or right hand. Parsons *et al.* expected motor cortices to be activated in this task if participants imagined rotating their own hand into congruence with the stimulus. And, in fact, not only was supplementary motor cortex activated bilaterally, but also prefrontal and insular premotor areas were activated in the hemisphere contralateral to the stimulus handedness – suggesting that participants did in fact imagine the appropriate movements. Many other regions, including areas in the frontal and parietal lobes, and basal ganglia and cerebellum, were active, as was Area 17.

Is motor imagery used only to rotate parts of one's body? Some researchers (Jeannerod 1994; Jeannerod and Decety 1995; Decety 1996) have suggested that people often transform images by imagining what they would see if the objects were manipulated in a specific way. One PET study (Kosslyn *et al.* 1998) directly compared rotation of hands versus inanimate objects, again using the three-dimensional multi-armed angular stimuli invented by Shepard and Metzler (1971). The participants compared pairs of drawings and decided whether they were identical or mirror images (using the task and stimuli from the original Shepard and Metzler study). In the experimental condition, the figures were presented at different relative orientations, and one had to be 'mentally rotated' into congruence with the other; in the baseline condition, the figures were presented at the same orientation, and thus no mental rotation was necessary. The comparison of the two conditions revealed the areas that were activated specifically by mental rotation. The corresponding design was used for drawings of hands, but now the participants decided whether the two hands in a pair were both left or both right, or whether one was a left hand and one a right hand.

In this study, several motor areas were activated when participants mentally rotated hands, including primary motor cortex (Area M1), premotor cortex, and the posterior parietal lobe. None of the frontal motor areas were activated when the Shepard-Metzler figures were mentally rotated. However, Cohen *et al.* (1996) used fMRI to study mental rotation of exactly the same inanimate objects and found that premotor cortex was activated in this task, but only in half the participants.

The fact that only some participants had activation in a motor area during mental rotation of inanimate objects suggests that there may be two strategies for performing such rotations. One strategy involves imagining what you would see if you manipulated an object; the other involves imagining what you would see if someone else (or an external force, such as a motor) manipulated an object. To test this idea, Kosslyn *et al.* (2001) asked participants to perform the same mental rotation task used by Cohen *et al.* (1996), but with a twist: Immediately prior to the task, the participants saw a wooden model of that type of stimulus (one not actually used in the task) either being rotated by an electric motor or they themselves physically turned the stimulus. They were told that during the task they should imagine the stimuli being rotated just as they had seen the model rotate at the outset. In this experiment, Area M1 was activated when participants mentally rotated stimuli after having themselves physically rotated the stimulus (and then imagined themselves doing so), and not when they saw the electric motor rotating the stimulus at the outset.

Similarly, Wraga *et al.* (2003) examined activation when participants mentally rotated images of inanimate objects. They found that activation in motor regions of the brain was greater when participants had just completed mental rotation of body parts (hands) than when they had just completed another session of rotating inanimate objects. In this study, the participants were never instructed to use a motor strategy, but this method of accomplishing the mental rotation task apparently transferred from having just rotated images of hands.

These results showed that imagining oneself manipulating an object is one way in which mental transformation of objects, in general (not just body parts), can take place – and also show that humans can voluntarily adopt this strategy or use a strategy in which they imagine what they would see if an external force transformed an object.

Finally, one can ask whether primary motor cortex plays a functional role in allowing participants to manipulate objects in images. It is possible that the actual computation is taking place in another area that incidentally sends activation to primary motor cortex. To test this hypothesis, Ganis *et al.* (2000) disrupted function in the left primary motor cortex (M1) by administering TMS while participants mentally rotated pictures of hands and feet (with the to-be-rotated stimulus appearing in the right visual field). The TMS was time-locked so that it disrupted neural processing only a specific amount of time after the stimulus appeared. Participants required more time to perform this task if a single magnetic pulse was delivered to the motor strip (roughly over the 'hand area') 650 ms after the stimuli were presented (but not at the other temporal delays tested); moreover, rotation of hands was impaired more than rotation of feet, as expected if this area is specialized for controlling the hand per se. Within the limits of the spatial resolution afforded by the TMS technique, these results suggest that activation in this area reflects processing used to perform the task. As in the case of TMS stimulation of area 17, we cannot be entirely sure, however, that M1 is the primary site of processing because the information could be computed elsewhere in the brain. However, the finding that primary motor cortex is involved in the mental rotation of hands has been replicated by Tomasino *et al.* (2005), using similar materials and paradigms.

In short, mental imagery can engage the motor system. This finding may help to explain why 'mental practice' can improve actual performance (Maring 1990; Driskell *et al.* 1994; Weiss *et al.* 1994; MacIntyre *et al.* 2002; Guillot and Collet 2008; Guillot *et al.* in this volume; MacIntyre and Moran in this volume). In this case, to imagine making movements may not only exercise the relevant brain areas, but also may build associations among processes implemented in different areas – which in turn facilitate complex performance.

Simulating the social world

The great Behaviourist B. F. Skinner (1977, p. 6) wrote, 'There is no evidence of the mental construction of images to be looked at or maps to be followed. The body responds to the world, at the point of contact; making copies would be a waste of time'. We hope that the reader is convinced that the first part of this claim is incorrect; images are in fact internal representations. We now briefly consider the second part, whether having such representations is a 'waste of time'. We focus on a relatively new area, the use of imagery in simulating social interactions.

Mirror neurons and 'mental simulations'

Mental imagery has many possible uses, ranging from helping one to memorize new information to visual problem solving. Among such functions, researchers have suggested that images can function as 'mental simulations' of a possible real-world event. Why take the trouble of lugging furniture around your living room if you can get a sense of how an arrangement will look simply by visualizing it?

One important role of such simulations is in anticipating the consequence of someone's performing an action – or of your performing it. Such simulations apparently depend not simply on the neural machinery used to recognize objects or to situate them in space. In addition, an important role may be played by a subpopulation of neurons in the frontal lobe (area F5 of the monkey brain, which is part of premotor cortex). These neurons respond selectively not only when the animal performs specific actions with the hand and/or mouth, but also when the animal merely observes the same actions being performed by another monkey (or human; Rizzolatti *et al.* 1998). Because of this property, such neurons have been labelled 'mirror neurons'.

Neuroimaging and TMS studies have shown that human premotor cortex is activated when humans observe other people's actions (e.g., Fadiga *et al.* 1995; Grafton *et al.* 1996; Rizzolatti *et al.* 1996; Hari *et al.* 1998; Gangitano *et al.* 2001), which is consistent with the existence of mirror neurons in the human brain. The likely homologue of Area F5 in humans is Broca's area (typically characterized as being involved in speech production), which has prompted some authors to theorize that the mirror neurons in humans may have a crucial role not only in imitation, but also in language acquisition. Mirror neurons may also play a role in motor imagery, consistent with the idea that people often transform images by imagining what they would see if the objects were manipulated in a specific way.

Imagery and emotion

One reason that simulating other people may be useful is that those simulations allow us to anticipate emotional responses. In fact, many findings indicate that imagery of emotional events activates the autonomic nervous system and (as also evident in single-cell recordings in humans) the amygdala. That is, visualizing an object has much of the same effects on the body as actually seeing the object. For example, Lang *et al.* (1993) showed that skin conductance increases, as do heart rate and breathing rate, when participants view pictures of threatening objects. And the same result occurs when they merely visualize the objects. Indeed, Kosslyn *et al.* (1996) found that mental images of aversive stimuli activate the anterior insula, the major cortical site of feedback from the autonomic nervous system. In addition, Kreiman *et al.* (2000) recorded from single cells in the human brain (hippocampus, amygdala, enthorinal cortex, and parahippocampal gyrus) while participants were shown pictures or formed mental images of those same pictures. Some of the cells that responded selectively when participants viewed specific visual stimuli (e.g., faces) also responded selectively when those same stimuli were visualized. Of particular interest, this pattern was seen in the amygdala, which is known to play a key role in certain emotions, especially fear and anger (LeDoux 1995, 1996). Thus, imagery can engage neural structures that are also engaged in perception, and these in turn can affect events in the body itself.

Conclusions

Mental imagery is not a single function. Rather, like all other cognitive activities, mental imagery arises from the joint action of numerous systems. Moreover, there are different types of imagery, and each type can be used in the service of performing many types of tasks. Researchers agree that most of the processes underlying like-modality perception are also used in mental imagery, and imagery in many ways can 'stand in' for a perceptual stimulus or situation. Imagery can not only engage the motor system, but also affect the body much as can actual perceptual experience.

Nevertheless, many questions remain. For example: Why do people differ so much in their imagery abilities? Does genetics affect some aspects of imagery more than others? How does

semantic content in images engage specific mechanisms? How do different types of imagery interact? And, the perennial favourite question, What is the relationship between information processing during imagery and conscious experience? Unlike 25 years ago, questions such as these can now begin to be answered.

Acknowledgements

References

Behrmann, M. (2000). The mind's eye mapped onto the brain's matter. *Current Directions in Psychological Science,* **9**(2), 50–4.

Behrmann, M., Winocur, G., and Moscovitch, M. (1992). Dissociation between mental imagery and object recognition in a brain-damaged patient. *Nature*, **359**, 636–37.

Chatterjee, A. and Southwood, M.H. (1995). Cortical blindness and visual imagery. *Neurology,* **45**(12), 2189–95.

Cohen, M.S., Kosslyn, S.M., Breiter, H.C., *et al.* (1996). Changes in cortical activity during mental rotation: a mapping study using functional MRI. *Brain,* **119**, 89–100.

Crick, F. and Koch, C. (1995). Are we aware of neural activity in primary visual cortex? *Nature,* **375**(6527), 121–3.

Decety, J. (1996). Neural representation for action. *Reviews in the Neurosciences.* **7**(4), 285–97.

Decety, J. and Jeannerod, M. (1995). Mentally simulated movements in virtual reality: does Fitts's law hold in motor imagery? *Behavioral Brain Research,* **72**(1–2*)*, 127–34.

De Vreese, L.P. (1991). Two systems for colour-naming defects: verbal disconnection vs colour imagery disorder. *Neuropsychologia,* **29**(1), 1–18.

Downing, P.E., Chan, A.W., Peelen, M.V., Dodds, C.M., and Kanwisher, N. (2006). Domain specificity in visual cortex. *Cerebral Cortex*, **16**(10), 1453–61.

Driskell, J., Copper, C., and Moran, A. (1994). Does mental practice enhance performance? *Journal of Applied Psychology,* **79**(4), 481–92.

Fadiga, L., Fogassi, L., Pavesi, G., and Rizzolatti, G. (1995). Motor facilitation during action observation: a magnetic stimulation study. *Journal of Neurophysiology,* **73**(6), 2608–11.

Farah, M.J. (1984). The neurological basis of mental imagery: a componential analysis. *Cognition,* **18**, 245–72.

Farah, M.J., Soso, M.J., and Dasheiff, R.M. (1992). Visual angle of the mind's eye before and after unilateral occipital lobectomy. *Journal of Experimental Psychology: Human Perception and Performance,* **18**(1), 241–6.

Gangitano, M., Mottaghy, F.M., and Pascual-Leone, A. (2001). Phase-specific modulation of cortical motor output during movement observation. *NeuroReport,* **12**(7), 1489–92.

Ganis, G., Keenan, J.P., Kosslyn, S.M., and Pascual-Leone, A. (2000). Transcranial magnetic stimulation of primary motor cortex affects mental rotation. *Cerebral Cortex,* **10**, 175–80.

Ganis, G., Thompson, W.L., and Kosslyn, S.M. (2004). Brain areas underlying visual mental imagery and visual perception: an fMRI study. *Cognitive Brain Research,* **20**, 226–41.

Ganis, G., Thompson, W.L., Mast, F.W., and Kosslyn, S.M. (2003). Visual imagery in cerebral visual dysfunction. *Neurologic Clinics of North America,* **21**, 631–46.

Georgopoulos, A.P., Lurito, J.T., Petrides, M., Schwartz, A.B., and Massey. J.T. (1989). Mental rotation of the neuronal population vector. *Science,* **243**, 234–6.

Grafton, S.T., Arbib, M.A., Fadiga, L., and Rizzolatti, G. (1996). Localization of grasp representations in humans by positron emission tomography: 2. Observation compared with imagination. *Experimental Brain Research,* **112**(1), 103–11.

Griffiths, T.D. (2000). Musical hallucinosis in acquired deafness. Phenomenology and brain substrate. *Brain,* **123**(Pt 10), 2065–76.

Guillot, A. and Collet, C. (2008). Construction of the motor imagery integrative model in sport: a review and theoretical investigation of motor imagery use. *International Review of Sport and Exercise Psychology,* **1***,* 31–44.

Guillot, A. *et al.* (2009). Motor imagery in sports sciences: an overview, in A. Guillot and C. Collet (eds), *The Neural Foundations of Mental and Motor Imagery.* Oxford, UK: Oxford University Press.

Halpern, A.R. and Zatorre, R.J. (1999). When that tune runs through your head: a PET investigation of auditory imagery for familiar melodies. *Cerebral Cortex,* **9**, 697–704.

Hari, R., Forss, N., Avikainen, S. Kirveskari, E., Selenius, S., and Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America,* **95**(25), 15061–5.

Jankowiak, J., Kinsbourne, M., Shalev, R.S., and Bachman, D.L. (1992). Preserved visual imagery and categorization in a case of associative visual agnosia. *Journal of Cognitive Neuroscience,* **4**(2), 119–31.

Jeannerod, M. (1994). The representing brain: neural correlates of motor intention and imagery. *Behavioral and Brain Sciences,* **17**(2), 187–245.

Jeannerod, M. and Decety, J. (1995). Mental motor imagery: a window into the representational stages of action. *Current Opinion in Neurobiology,* **5**(6), 727–32.

Jordan, K., Heinze, H.J., Lutz, K., Kanowski, M., and Jancke, L. (2001). Cortical activations during the mental rotation of different visual objects. *Neuroimage*, **13**(1), 143–52.

Kanwisher, N. and Yovel, G. (2006). The fusiform face area: a cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **361**(1476), 2109–28.

Kleber, B., Birbaumer, N., Veit, R., Trevorrow, T., and Lotze, M. (2007). Overt and imagined singing of an Italian aria. *NeuroImage,* **36**(3), 889–900.

Klein, I., Paradis, A.-L., Poline, J.-B., Kosslyn, S.M., and Le Bihan, D. (2000). Transient activity in human calcarine cortex during visual imagery. *Journal of Cognitive Neuroscience,* **12**(6), 15–23.

Kosslyn, S.M., Segar, C., Pani, J., and Hillger, L.A. (1990). When is imagery used in everyday life? A diary study. *Journal of Mental Imagery,* **14**, 131–52.

Kosslyn, S.M., Shin, L.M., Thompson, W.L., *et al.* (1996). Neural effects of visualizing and perceiving aversive stimuli: a PET investigation. *NeuroReport,* **7**, 1569–76.

Kosslyn, S.M., Pascual-Leone, A., Felician, O., *et al.* (1999). The role of area 17 in visual imagery: convergent evidence from PET and rTMS. *Science,* **284**, 167–70.

Kosslyn, S.M., DiGirolamo, G., Thompson, W.L., and Alpert, N.M. (1998). Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. *Psychophysiology,* **35**, 151–61.

Kosslyn, S.M. and Thompson, W.L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin,* **129**, 723–46.

Kosslyn, S.M., Thompson, W.L., and Alpert, N.M. (1997). Neural systems shared by visual imagery and visual perception: a positron emission tomography study. *NeuroImage,* **6**, 320–34.

Kosslyn, S.M., Thompson, W.L., and Ganis, G. (2006). *The Case for Mental Imagery*. New York: Oxford University Press.

Kosslyn, S.M., Thompson, W.L., Kim, I.J., and Alpert, N.M. (1995). Topographical representations of mental images in primary visual cortex. *Nature,* **378**, 496–8.

Kosslyn, S.M., Thompson, W.L., Kim, I.J., Rauch, S.L., and Alpert, N.M. (1996). Individual differences in cerebral blood flow in area 17 predict the time to evaluate visualized letters. *Journal of Cognitive Neuroscience,* **8**, 78–82.

Kosslyn, S.M., Thompson, W.L., Wraga, M., and Alpert, N.M. (2001). Imagining rotation by endogenous and exogenous forces: distinct neural mechanisms for different strategies. *NeuroReport,* **12**, 2519–25.

Kreiman, G., Koch, C., and Fried, I. Imagery neurons in the human brain. (2000). *Nature,* **408**(6810), 357–61.

Lang, P.J., Greenwald, M.K., Bradley, M.M., and Hamm, A. O. (1993). Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology,* **30**(3), 261–73.

LeDoux, J.E. (1995). Emotion: Clues from the brain. *Annual Review of Psychology,* **46**, 209–35.

LeDoux, J.E. (1996). *The Emotional Brain: The Mysterious Underpinnings of Emotional Life.* New York: Simon and Schuster.

Levine, D.N., Warach, J., and Farah, M.J. (1985). Two visual systems in mental imagery: dissociation of 'what' and 'where' in imagery disorders due to bilateral posterior cerebral lesions. *Neurology,* **35**, 1010–8.

MacIntyre, T. and Moran, A. (2009). Meta-imagery processes among elite sport performers, in A. Guillot and C. Collet (eds), *The Neural Foundations of Mental and Motor Imagery.* Oxford, UK: Oxford University Press.

MacIntyre, T., Moran, A., and Jennings, D.J. (2002). Are mental imagery abilities related to Canoe-Slalom performance? *Perceptual and Motor Skills,* **94**, 1245–50.

Maring, J.R. (1990). Effects of mental practice on rate of skill acquisition. *Physical Therapy,* **70**(3), 165–72.

Mellet, E., Tzourio, N., Crivello, F., Joliot, M., Denis, M., and Mazoyer, B. (1996). Functional anatomy of spatial mental imagery generated from verbal instructions. *Journal of Neuroscience,* **16**(20), 6504–12.

Mellet, E., Bricogne, S., Tzourio-Mazoyer, N., *et al.* (2000). Neural correlates of topographic mental exploration: the impact of route *versus* survey perspective learning. *NeuroImage,* **12**, 588–600.

Mellet, E., Tzourio N., Denis, M., and Mazoyer, B. (1995). A positron emission tomography study of visual and mental spatial exploration. *Journal of Cognitive Neuroscience,* **4**, 433–45.

Ng, V.W., Bullmore, E.T., de Zubicaray, G.I., Cooper, A., Suckling, J., and Williams, S. C. (2001). Identifying rate-limiting nodes in large-scale cortical networks for visuospatial processing: an iIllustration using fMRI. *Journal of Cognitive Neuroscience*, **13**(4), 537–45.

O'Craven, K.M. and Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience,* **12**(6), 1013–23.

Paivio, A. (1971). *Imagery and Verbal Processes.* New York: Holt, Rinehart and Winston.

Parsons, L.M., Fox, P.T., Downs, J.H., *et al.* (1995). Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature,* **375**, 54–8.

Pylyshyn, Z.W. (1973). What the mind's eye tells the mind's brain: a critique of mental imagery. *Psychological Bull*etin, **80**, 1–24.

Pylyshyn, Z.W. (1981). Psychological explanations and knowledge-dependent processes. *Cognition,* **10**(1–3), 267–74.

Richter, W., Somorjai, R., Summers, R., *et al.* (2000). Motor area activity during mental rotation studied by time resolved single-trial fMRI. *Journal of Cognitive Neuroscience,* **12**(2), 310–20.

Rizzolatti, G., Fadiga, L., Matelli, M., *et al.* (1996). Localization of grasp representations in humans by PET: 1. Observation versus execution. *Experimental Brain Research,* **111**(2), 246–52.

Rizzolatti, G., Luppino, G., and Matelli, M. (1998). The organization of the cortical motor system: new concepts. *Electroencephalography and Clinical Neurophysiology,* **106**(4), 283–96.

Sereno, M.I., Dale, A.M., Reppas, J.B., *et al.* (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, **268**(5212), 889–93.

Shepard, R.N. and Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science,* **171**, 701–3.

Skinner, B.F. (1977). Why I am not a cognitive psychologist. *Behaviorism*, **5**, 1–10.

Slotnick, S.D., Thompson, W.L., and Kosslyn, S.M. (2005). Visual mental imagery induces retinotopically organized activation of early visual areas. *Cerebral Cortex,* **15**, 1570–83.

Thompson, W.L. and Kosslyn, S.M. (2000). Neural systems activated during visual mental imagery. A review and meta-analyses, in A. W. Toga and J. C. Mazziotta (eds), *Brain Mapping II: The Systems,* pp. 535–60. San Diego: Academic Press.

Thompson, W.L. Kosslyn, S.M., Sukel, K.E., and Alpert, N. M. (2001). Mental imagery of high- and low-resolution gratings activates Area 17. *NeuroImage,* **14**, 454–64.

Tomasino, B., Borroni, P., Isaja, A., and Rumiati, R. I. (2005). The role of the primary motor cortex in mental rotation: a TMS study. *Cognitive Neuropsychology,* **22**, 348–63.

Tootell, R.B.H., Hadjikani, N.K., Mendola, J.D., Marrett, S., and Dale, A.M. (1998). From retinotopy to recognition: fMRI in human visual cortex. *Trends in Cognitive Sciences,* **2**, 174–83.

Ungerleider, L.G. and Mishkin, M. (1982). Two cortical visual systems, in D.J. Ingle and R.J.W. Mansfield (eds), *Analysis of Visual Behavior,* pp. 549–86. Cambridge, MA: MIT Press.

Watson, J.B. (1913). Psychology as the behaviorist views it. *Psychological Review,* **20**, 158–77.

Weiss, T., Hansen, E., Rost, R., and Beyer, L. (1994). Mental practice of motor skills used in poststroke rehabilitation has own effects on central nervous activation. *International Journal of Neuroscience,* **78**(3–4),157–66.

Wraga, M.J., Thompson, W.L., Alpert, N.M., and Kosslyn, S.M. (2003). Implicit transfer of motor strategies in mental rotation. *Brain and Cognition,* **52**, 135–43.

Young, A.W., Humphreys, G.W., Riddoch, M.J., Hellawell, D.J., and de Haan, E.H. (1994). Recognition impairments and face imagery. *Neuropsychologia,* **32**(6), 693–702.

Zacks, J. (2008). Neuroimaging studies of mental rotation: a meta-analysis and review. *Journal of Cognitive Neuroscience*, **20**(1), 1–19.

Zatorre, R.J. and Halpern, A.R. (1993). Effect of unilateral temporal-lobe excision on perception and imagery of songs. *Neuropsychologia,* **31**(3), 221–32.

Zatorre, R.J. and Halpern, A.R. (2005). Mental concerts: musical imagery and auditory cortex. *Neuron,* **47**, 9–12.

Zatorre, R.J., Halpern, A.R., Perry, D.W., Meyer, E., and Evans, A.C. (1996). Hearing in the mind's ear: A PET investigation of musical imagery and perception. *Journal of Cognitive Neuroscience*, **8**, 29–46.