

Anke Marit Albers

3021858

Neuroscience & Cognition

July 2011

## Similarities and differences between imagery and perception in early and late visual cortex

### **Abstract**

Mental visual imagery has been suggested to require the same brain areas as visual perception. The extent of this overlap has long been investigated but visual cortex has not consistently been found to be involved during imagery. This review investigates the extent to which visual imagery and perception are similar. Behavioral, patient, and neuroimaging studies are reviewed. Specifically, recent decoding studies are reviewed. Decoding not only allows for investigation of overlapping brain activity between imagery and perception, but also reveals overlap in specific representational content related to both processes.

Patient and behavioral studies indicate that many similar principles govern imagery and perception. Imaging studies show that different parts of visual cortex are activated during imagery. These activations follow the retinotopic and functional organization also observed during perception. Decoding studies show instances where a classifier trained on perceptual data could classify imagery data, and the other way around. This indicates that representational patterns for imagery and perception are highly alike in several visual areas. However, data also suggest a difference between early and later visual areas.

Activity in higher order, functionally organized areas was observed during most imagery tasks. Conversely, activity in early areas depended on task demands. Imagery tasks resulted in V1 activity mostly only when stimulus details such as shape, orientation and retinotopy were important. Differences in specific task demands can strongly influence the extent of overlap between imagery and perception. Previous results should be viewed in light of the differences between task demands and future studies should take into account these differences.

## **Introduction**

Imagine that you are packing your suitcase for a holiday in some nice country. While packing, you might have to decide which size suitcase to take. You also have to find the most efficient way to pack it – how will you make everything fit? This kind of activity requires you to mentally envision the suitcase, as well as the objects you are trying to squeeze in. You must take into account their size and texture, to prevent damage while packing. You might also have to imagine their color, to decide which shirt you will take with you, the blue or the purple. You try to compose a mental picture of yourself: which shirt fits better with your shoes? Both during packing the suitcase, and now, when trying to imagine it, you are likely using mental imagery. Imagery can be also involved when recovering information from memory (Kosslyn, Thompson, & Ganis, 2006). For example, the question of which fruit is bigger, an apple or a kiwi, can be efficiently solved by forming a mental picture of the fruits and comparing them ‘with the mind’s eye’ (Ishai, 2010; Kosslyn, Ganis, & Thompson, 2001).

According to Kosslyn and colleagues (2006, p. 6): “a mental image occurs when a representation of the type created during the initial phases of perception is present but the stimulus is not actually being perceived; such representations preserve the perceptible properties of the stimulus and ultimately give rise to the subjective experience of perception”. These representations are prolonged and voluntary (Kosslyn, et al., 2006), but hard to study due to their private nature. As evident from this definition by Kosslyn et al, mental images are thought to be very close to the experience of perception. Kosslyn actually suggests that perception and imagery share the same neural mechanisms and networks (Kosslyn, et al., 2001; Kosslyn, et al., 2006).

This idea of overlap between imagery and perception has been the topic of a long standing debate (for summaries see Farah, 1988; Kosslyn, et al., 2006; Pylyshyn, 2003b). The original debate considered the format of the mental images (Finke, 1985): are they depictive, or even

photograph-like (Finke, 1980; Kosslyn, 1981; Kosslyn, Ganis, & Thompson, 2003; Kosslyn, et al., 2006), or are they of a conceptual, propositional nature (Pylyshyn, 1981, 2003b). Involvement of primary visual cortex during mental visual imagery is predicted by the depictive account of mental imagery, but not by the propositional account (Slotnick, Thompson, & Kosslyn, 2005). Overlapping brain activity in perceptual areas has generally been taken to indicate that imagery indeed involves top-down activation of perceptual representations. However, this need not indicate that images are necessarily depictive (Farah, 1988): imagery and perception might share neural correlates but do not involve similar kinds of representations (Pylyshyn, 2003b). To truly say that imagery and perception involve the same representations they must not only activate the same areas, but they must do so in a similar way (Marzi, Mancini, Metitieri, & Savazzi, 2006; Pylyshyn, 2002, 2003a; Slotnick, et al., 2005).

For many researchers the exact format of the images is less relevant (Farah, 1988; Finke, 1985; Podgorny & Shepard, 1978). To them, the issue of interest is whether imagery and perception function similarly: to what extent are perceptual areas activated during imagery (Podgorny & Shepard, 1978) and are they activated in the same way (Marzi, et al., 2006; Slotnick, et al., 2005)? Perception might be depictive or propositional (Farah, 1988), but it is a non-static, interpretational process and, if similar, the rules of perception should govern imagery as well (Podgorny & Shepard, 1978). Many studies suggest similar activation patterns between imagery and perception as well as similar behavioral patterns (Farah, 1988; Kosslyn, et al., 2006). Overlap in brain activity has not consistently been found though (for a review, see Kosslyn & Thompson, 2003) and imagery does not always follow perceptual rules either (Mohr, Linder, Dennis, & Sireteanu, 2011). Especially activation of early visual cortex is not consistently observed. Imagery thus does not figure like perception in all aspects and this makes sense. Whereas imagery activity is induced by top-down connections from

prefrontal and parietal cortex (Klein et al., 2004), perceptions are induced by bottom-up sensory information from the eye and Lateral Geniculate Nucleus (LGN) (Farah, 1988). Since images are induced from within, there must be an influence of prior experience or the lack thereof: imagery is based on what has been perceived before. Perception, in contrast, is driven by direct sensory input and should therefore result in a richer and stronger experience.

Investigating the extents and limitations of the overlap between imagery and perception might allow insight into the nature of mental images. Moreover, the extent of overlap between imagery and perceptual processes is highly relevant by itself. If mental representations are of the same kind as perceptual representations and share neural networks, this could allow mutual influences of imagery and perception. And, if imagery can influence subsequent perception, this might have important implications for the idea that perception can be objective

The present review investigates the role of visual areas during visual imagery, as well as the level of overlap with perception in both activity patterns and representational content. Overlap between perception and imagery has been suggested for all sensory domains, but only vision has been extensively investigated. Auditory imagery has been found to activate primary auditory cortex and auditory association cortex (Kraemer, Macrae, Green, & Kelley, 2005; Meyer et al., 2010). Olfactory imagery is also thought to involve the same areas as olfactory perception (Bensafi, Sobel, & Khan, 2007; de Araujo, Rolls, Velazco, Margot, & Cayeux, 2005). For motor imagery, the primary motor cortex might be involved in motor imagery (Annett, 1995), but inconsistent results have also been obtained here (de Lange, Roelofs, & Toni, 2008; Hermes et al., 2011). Due to the extensive research on visual perception and imagery, however, this domain might provide the most insight into the commonalities between imagery and perception.

First, behavioral, neuroimaging and patient studies on mental imagery are reviewed. Subsequently, the relatively new method of fMRI decoding is discussed. This method allows investigation of the representational content of brain activity and might prove valuable when investigating whether imagery activates the same areas *in the same way*. Many conventional fMRI studies aim at this by investigating retinotopic and functional organization during imagery. FMRI decoding allows investigation related to the activation of individual stimuli and therefore goes one step further. This method has already been applied a few times for visual mental imagery and could provide new insights into the nature of mental imagery and its relation to perceptual processing. Together this sketches a picture of the extent of activity in visual areas during mental visual imagery.

### **Similarities between imagery and perception**

The similarities between imagery and perception have since long been investigated. Original studies involved behavioral measures and investigations of brain-damaged patients. More recently, neuroimaging has been applied. The different lines of research have revealed varying results about the visual brain areas activated during visual mental imagery. Together, these studies might provide new insights into the exact nature of mental imagery.

#### *Behavioral studies*

Behavioral studies into mental imagery showed that imagery often obeys the same rules and principles as perception (for a review, see Farah, 1988; Finke, 1985). Podgorny and Shepard (1978) had participants judge whether a probe dot fell on or off a specific stimulus shape. The shapes were letters of the alphabet, constructed from several black-colored squares in a 5x5 grid. The specific reaction times patterns observed were similar when the stimulus shape was

perceived and when the stimulus shape was imagined. Finke and Kosslyn (1980, p. 127) set out to investigate whether the “neural structures that limit peripheral acuity in perception also limit peripheral acuity in imagery”. They had their participants judge whether two dots were still separately visible or became blurred in the periphery of the visual field. Acuity was reduced in peripheral regions during imagery and perception alike.

A recent study examined the effect of eccentricity on reaction times (RTs) (Marzi, et al., 2006). During perception, central stimuli are reacted to faster than peripheral stimuli. This has been suggested to be a result of a retinotopic organization in primary visual areas due to the density of retinal ganglion cells. Marzi and colleagues tested RTs for central and peripheral stimuli that were either perceived or imagined. A similar effect of eccentricity was observed for perceived and imagined stimuli, indicating that even during imagery, stimulus eccentricity might activate visual areas following the retinotopy. A further experiment showed that larger stimuli were also reacted to faster, for both imagery and perception alike. These results indicate overlap between perception and imagery for retinotopic areas. However, whether this involves V1 activity cannot conclusively be determined, as higher areas also show retinotopy. Most behavioral studies suffer the same problem: theories about overlapping brain activity remain suggestive and cannot rule out alternative explanations such as tacit knowledge (Farah, 1988; Finke, 1985; Pylyshyn, 1981) .

### *Patient data*

Patients with all types of selective visual deficits have been described to have selective imagery deficits too (Farah, 1988). People impaired on color perception often also show impairment on color imagery and selective ‘what’ or ‘where’ impairments of perception present with similar impairments of imagery, thus showing either impairment for object imagery or for imagery of location (Farah, 1988). Impaired face imagery has been described

for a patient with face perception difficulties who was unimpaired when imagining buildings and places (Farah, 1988). In a famous study, two patients with unilateral neglect were asked to describe the Piazza del Duomo in Milan, a square with which they were highly familiar, from a particular viewpoint (Bisiach & Luzzatti, 1978). Unilateral neglect results in the patient ignoring one side of the visual field, as if it does not exist. These patients showed a similar neglect when describing the square, ignoring most buildings on their left side. When asked to describe the square from the opposite viewpoint, the other half of the buildings was described, while the buildings currently on the left were ignored. This indicated that they did remember all the buildings, but ignored one side during imagery like they did during perception.

These cases indicate overlap between imagery and perception in higher visual areas. Data on patients with V1 damage present a dissociation between imagery and perception. For example, one patient with cortical blindness due to bilateral infarction of calcarine cortex performed the same as controls on a test that required mental imagery (Zago et al., 2010), suggesting that V1 cannot be critical for mental imagery. The opposite case has also been described: two patients with intact V1, spared perception, normal memory and language, but impaired visual imagery (Moro, Berlucchi, Lerch, Tomaiuolo, & Aglioti, 2008). Both these patients had a lesion in their temporal cortex, indicating that early visual areas were not critically involved. As they had normal performance for imagery in other modalities, their deficits could not be attributed to some general mental imagery regions. This double dissociation suggests that visual mental images do not require projection onto the primary visual areas (Bartolomeo, 2008). However, these are patient data and therefore limited. The extent of lesions is usually large. Furthermore, a one to one mapping of function to lesion sides does not exist in an interconnected network such as the brain (Young, Hilgetag, & Scannell, 2000). While simple lesions might impair functionality, further lesions sometimes

result in restored functionality (Young, et al., 2000). Neuroimaging methods allow investigation of healthy people and allow a more direct means to investigate the involvement of visual areas.

### *Neuroimaging data*

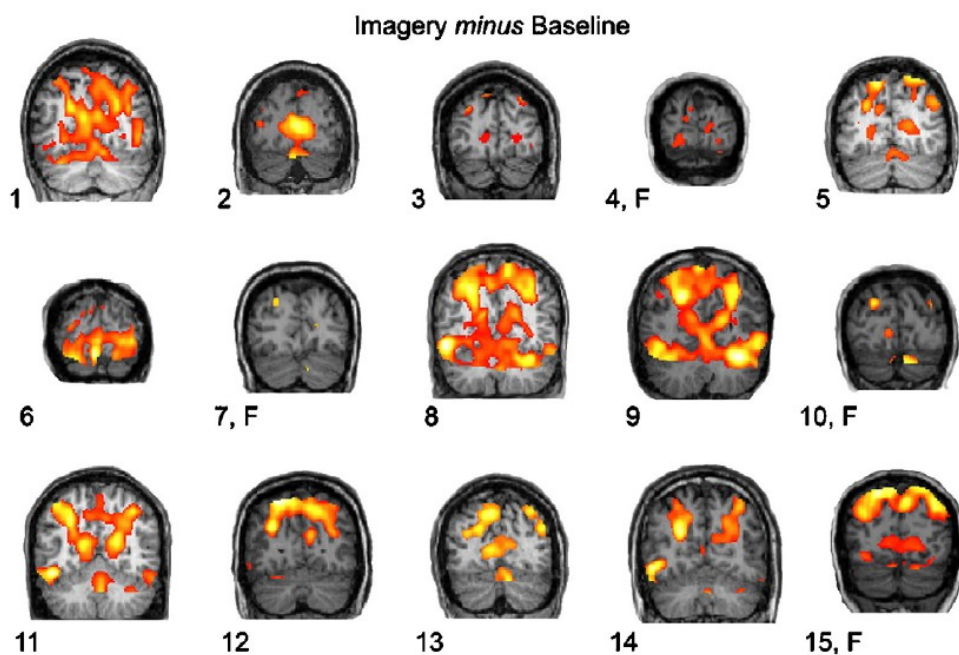
Several researchers report activity in the primary visual cortex during imagery (Klein, et al., 2004; Kosslyn & Thompson, 2003; Slotnick, et al., 2005). Mazard and colleagues (2005) tested participants on perception and imagery for object and non-object drawings. They asked their participants to judge propositions about the perceived or imagined common objects and non-objects, such as '*higher than wide*', to be true or false. This resulted in bilateral activation of early visual areas in the calcarine cortex, although activity was less strong during imagery than during perception. Imagery of objects resulted in a slightly left lateralized activity pattern including left temporal-occipital lobe, what the authors interpret as an effect of semantic processing in response to real objects. There was large individual variability in the extent of imagery related activity (*Figure 1*). Klein and colleagues (2000) asked participants to form a mental image of an animal and subsequently evaluate a concrete or abstract feature of this animal such as 'has pointy ears', or 'is affectionate'. They investigated transient signal changes in the fMRI BOLD time course in calcarine sulcus. Peaks were observed for imagery of the animal, regardless of the type of characteristic to be evaluated.

Others do not find this activity (Kosslyn & Thompson, 2003). Knauff and colleagues (2000) had participants solve a spatial visual imagery task. They did not find significant activity in V1, but only in later areas. They suggest that V1 is not necessary for visual imagery. A recent study even showed a down-regulation of V1-V3 during imagery (Kaas, Weigelt, Roebroek, Kohler, & Muckli, 2010). These researchers eliminated the effect of short-term memory on imagery by letting participants imagine a movement that they had never observed. A meta-



analysis on the involvement of areas 17 and 18 during visual imagery reported nineteen fMRI studies that showed activity in early visual cortex, but also eight studies that did not find this activity (Kosslyn & Thompson, 2003). A similar pattern was observed for other imaging modalities PET and SPECT (Kosslyn & Thompson, 2003).

Several studies reported large individual variability in the amount of activity in calcarine sulcus during imagery (Klein, et al., 2000; Kosslyn & Thompson, 2003; Mazard, et al., 2005). This provides a possible explanation for the variability in results regarding V1 activity during imagery at the group level (Klein, et al., 2000; Kosslyn & Thompson, 2003).



**Figure 1.** Single-subject BOLD responses in the calcarine cortex from the study by Mazard and colleagues (2005) overlaid on each subject's anatomical image. As also reported by others (Klein, et al., 2004; Kosslyn & Thompson, 2003), there was large individual variability in the BOLD response in calcarine cortex during the Imagery condition. Participant number and gender (F=female) are indicated. (*Adapted from Mazard, et al., 2005*).

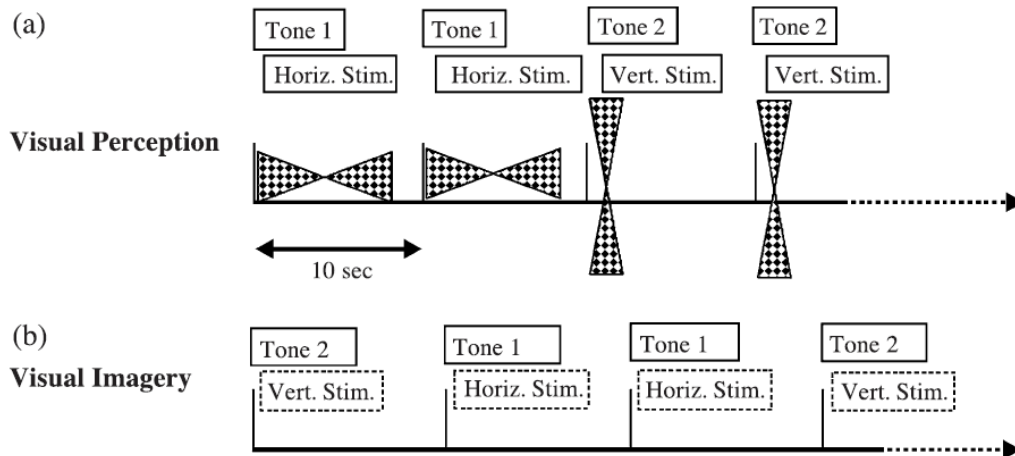
### *Retinotopy during imagery*

Thus, V1 is not simply turned on or off during mental imagery. Moreover, the activity observed might be just an epiphenomenon (Farah, 1988; Pylyshyn, 2002). Some stronger indications for imagery related activity in early visual areas follow from research that shows that imagery does not only activate these regions, but that it does so in a specific manner similar to that observed for perception (Marzi, et al., 2006; Pylyshyn, 2002, 2003a; Slotnick, et al., 2005). As Kosslyn and colleagues (2006, p. 18) stated: “the brain uses space on the cortex to represent space in the world”. According to them, it does so not only for perception, but also for imagery.

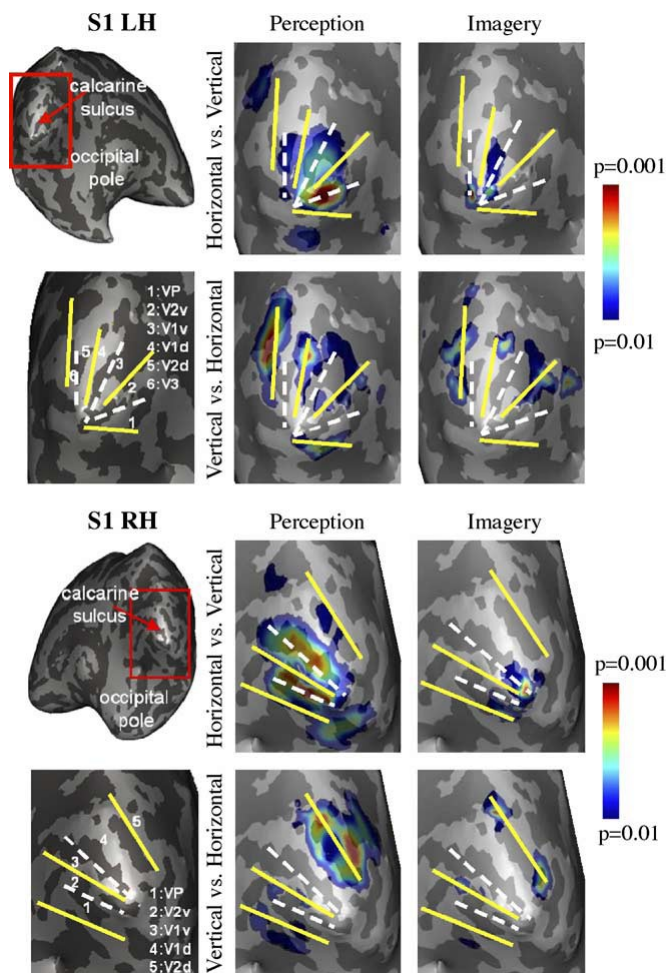
This is most clearly observed in early visual areas that have strong retinotopic organization. That is, cells that are adjacent in the retina also project to neighboring cells in the primary visual cortex. Objects contiguous in the world and hence also on the retina, are thus also bordering on the primary visual cortex. Due to the small receptive fields, a very fine spatial layout is preserved in the early visual cortex. This is important for the visual features that are processed here such as edges, orientations and forms. Later visual areas do have retinotopy too, but cells have much larger receptive fields and spatial information is less strictly preserved. These areas are predominantly organized by function (Engel, Glover, & Wandell, 1997; Tootell, Hadjikhani, Mendola, Marrett, & Dale, 1998), showing sensitivity to specific features such as color or motion, or specific objects such as faces and houses (O’Craven & Kanwisher, 2000).

The previously discussed RT study by Marzi and colleagues (2006) already suggested a retinotopic organization of imagery, with faster RTs for centrally compared to peripherally imagined stimuli. To directly compare retinotopic maps of visual cortex obtained during perception and imagery, Klein and colleagues (2004) had participants imagine flashing bow-tie shaped stimuli that were either horizontally or vertically oriented (*Figure 2*). When

contrasting the activity patterns for the vertical and horizontal stimuli during imagery, retinotopic characteristics were revealed that closely matched those observed during perception (*Figure 3*).



**Figure 2.** The flickering black-and-white bow-tie shaped stimuli used by Klein and colleagues (2004) to investigate whether early visual cortex was retinotopically activated during imagery. (a) In the perceptual condition, the participants received simultaneously an auditory tone and a horizontal or vertical visual stimulus. (b) In the imagery condition, only the auditory cues were delivered and participants were to visualize the corresponding horizontal or vertical flickering stimulus (Klein, et al., 2004).



**Figure 3** Perception and imagery retinotopic maps of the occipital cortex obtained by Klein and colleagues (Klein, et al., 2004). Statistical maps ( $p < 0.01$ , non-corrected, at least four contiguous voxels) of the horizontal/vertical and vertical/horizontal contrasts, for visual perception and imagery, are presented for one participant (Participant #1; LH, left hemisphere; RH, right hemisphere). Maps are projected on individual inflated occipital cortex (red zoomed region defined on the whole hemisphere). The horizontal and vertical meridians were obtained from retinotopic phase-encoded acquisitions (horizontal: dotted white lines; vertical: yellow lines); they define the frontiers between visual areas (Klein, et al., 2004).

Slotnick and colleagues (2005) also set out to investigate whether visual mental imagery might activate topographically organized cortex in a way related to the spatial geometry of the imagined stimulus. They used rotating checkerboard stimulus wedges in order to produce standard retinotopic maps (Engel, et al., 1997). Imagery of the rotating wedges induced a retinotopic map comparable to the map obtained during perception. These two studies (Klein, et al., 2004; Slotnick, et al., 2005) show strong evidence for a retinotopic activation of early visual areas during imagery. At first sight this seems reasonable, because if imagery activates V1 and other early areas, why would it do so differently from perception? However, since during imagery there is no necessary relation to the retina itself, it could also be thought that the most efficient way to imagine is to imagine at the fovea. Attentional processes also often involve saccades in order to place the object of interest in the foveal region of retina. A study by Williams and colleagues (2008) showed that during an object comparison task with two same-category objects located in opposite corners of visual field the activity in the foveal region contained information on the object category. Although this is during object perception, Williams et al suggest that the foveal activity is induced by top-down activity from higher visual regions and reflects a mental representation. Their finding that the foveal information is related to task performance indeed suggests that mental images need not be represented only in assumed peripheral regions, but rather, that image location might be task dependent. In the previous two studies (Klein, et al., 2004; Slotnick, et al., 2005), stimulus location was relevant and hence, retinotopy was observed, whereas in the latter study it was the object itself rather than its spatial layout that was of interest (Williams, et al., 2008).

### *Functionally organized areas during imagery*

Higher visual areas follow a functional organization with stimulus specific areas (Tootell, et al., 1998). One of the nicest examples regards the Fusiform Face Area (FFA) and the

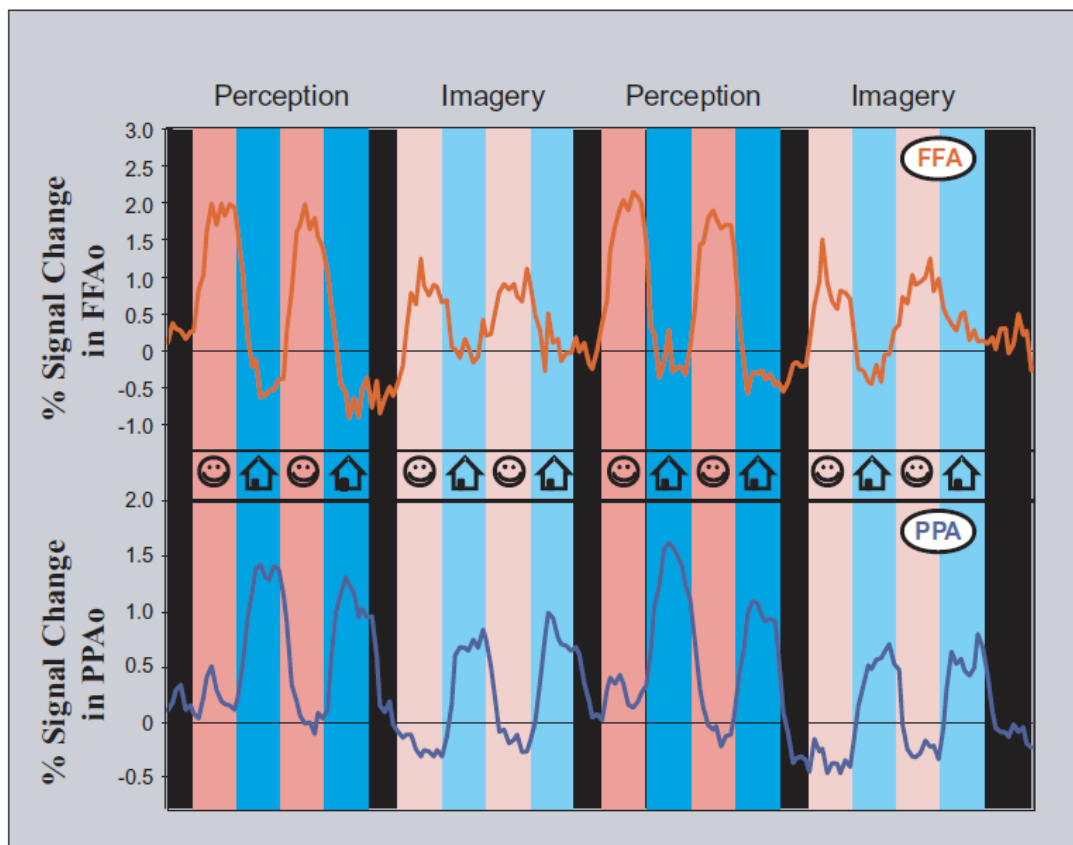
Parahippocampal Place Area (PPA). These areas show a stronger activity in response to respectively face and scene stimuli compared to other stimuli (O'Craven & Kanwisher, 2000). If imagery does obey the same principles as perception in these higher visual areas as well, it must follow this organization and show stimulus specific activity patterns.

Some of the discussed studies suggest such a functional specialization (Mazard, et al., 2005; Slotnick, et al., 2005). The finding that perceived and imagined objects activated left hemisphere more strongly than non-objects was thought to be related to left-lateralized semantic processing (Mazard, et al., 2005). Imagined rotating checkerboard wedges activated the human motion area MT+ (Slotnick, et al., 2005). Other studies confirm these findings of stimulus specificity. Instruction-based motion imagery based on rules also activated MT+ significantly (Kaas, et al., 2010). MT+ was also critically involved during mental rotation tasks, again a form of imagery that involves motion (Seurinck, de Lange, Achten, & Vingerhoets, 2011).

Rich and colleagues (2006) had participants judge which of two objects with the same color (e.g. a banana and a cob of corn) had a darker shade in their original color. The objects, however, were presented as gray scale photographs. The color imagery required to solve the task resulted in consistent activity of V4, a color processing area.

Johnson and colleagues (2007) presented participants a picture of a scene and a picture of a face simultaneously. Immediately after these pictures were shown, either, participants were cued to refresh this picture mentally, or the picture was shown again. During refreshing, it is thought that a mental image is reflexively generated (Johnson, et al., 2007). They found that refreshing the pictures indeed resulted in top-down modulation of stimulus-specific areas: when refreshing a face, the FFA was activated, while scene refreshing resulted in PPA activity. These areas were similarly, but stronger, activated during perception of faces and houses respectively.

Earlier, O'Craven and Kanwisher (2000) already showed a selective involvement of FFA and PPA during imagery. Participants either viewed or imagined famous faces or familiar places (on the MIT campus). This resulted in activity in FFA (for faces) and PPA (for places), albeit less strong during imagery than during perception. In a follow up experiment, participants were instructed every 12 seconds to think of either a place or a face, in a random order. When an observer blind to the order of face and place imagery categorized the single-trial activity, he was able to correctly identify the imagined stimulus for 85% of the trials (Figure 4).



**Figure 4.** Time course of percent signal change (averaged over subjects 1 and 3; four runs each) for the FFAo (top) and PPAo (bottom) for the experiment from O'Craven and Kanwisher (2000). Participants had to imagine face and house stimuli for several seconds. An observer blind to the order of the stimuli could reliably assign the epochs to specific conditions (Adapted from O'Craven & Kanwisher, 2000).

A slightly different study by Sung & Ogawa (2008) reported that indeed the PPA was activated during both perception and imagery of buildings, but that FFA was only activated during perception and not during imagery. They suggested that face imagery appears at a different, more conceptual level of imagery, as it activated frontal regions. Visual areas, on the other hand, were suggested to be involved only for more detailed objects such as buildings. However, their imagery task was relatively unconstrained, as they asked participants to imagine as many familiar faces as possible in the short period of 15 seconds. This indeed could have led participants to imagine familiar faces more conceptually. This thus does not exclude the option that FFA is indeed activated during imagery of faces at a more detailed, depictive level.

Even though many studies report retinotopically and functionally organized imagery-related activations (e.g. Johnson, et al., 2007; Klein, et al., 2004), some studies suggest that activity for imagery and perception are not so similar. Higher order areas, such as prefrontal and parietal cortex, are thought to be similar, but lower order areas not so much (Ganis, 2004). This larger overlap in frontal areas and greater difference between imagery and perception in occipital-temporal regions was also reported by Johnson and colleagues (2007). They did report overlap in earlier visual areas; however, activity was just less strong than during perception. Weaker activation for imagery seems to be a general finding (Johnson, et al., 2007; Klein, et al., 2004; Klein, et al., 2000; O'Craven & Kanwisher, 2000; Reddy, Tsuchiya, & Serre, 2010). This is in accordance with introspective reports that imagery is just a faint version of actual perception from even the earliest psychological writings (O'Craven & Kanwisher, 2000). Rationally this makes sense too: during imagery there is only top-down input in V1, while physical stimuli, that provide bottom-up input, should result in much stronger activations.

### *Mental imagery and perception can mutually influence each other*

The observed overlap between imagery and perception might be of high relevance, as a shared use of brain systems could potentially lead to interaction effects in case both functions require the same area at (more or less) the same moment. Conversely, if interaction between perception and imagery are observed at levels represented by early visual areas, this could indicate that imagery and perception share a neural mechanism for processing this feature (Mohr, et al., 2011). Interaction effects for perception are commonly observed when sequential presentation of certain stimuli influences perception of the subsequent stimuli, for example as in priming. Again, this might happen in retinotopic areas as well as in functionally organized areas.

In retinotopic cortex, the direct Tilt After-Effect (direct TAE) was observed for imagined and perceived gratings in a fMRI study (Mohr, Linder, Linden, Kaiser, & Sireteanu, 2009), and in a subsequent, nicely controlled behavioral experiment (Mohr, et al., 2011). When participants adapted to imagined vertical gratings with an orientation of  $+15^\circ$  or  $-15^\circ$ , subsequent test gratings oriented close to the original vertical orientation were perceived as tilted in the opposite direction, away from the adapted lines. This effect was less strong for imagery than for perception, but significantly present. Neural adaptation was observed after mental imagery of the lines with fMRI in V4 and V3 (Mohr, et al., 2009). As the direct TAE is thought to rely on early visual areas (V3 or V4), as also evident from the fMRI study (Mohr, et al., 2011; Mohr, et al., 2009), this influence of imagery on perception is a strong indication for involvement of these areas during mental visual imagery. It must be noted though, that although the authors found a direct TAE twice, other effects were not always observed likewise (Mohr, et al., 2011; Mohr, et al., 2009). An indirect TAE is the effect that after adapting to tilted vertical gratings, horizontal test lines seem to be oriented more towards the



original, vertical lines than they actually are. This effect was not observed, again indicating that the effect of mental imagery is not in all aspects similar to that of perception.

A study by Yi and colleagues (Yi, Turk-Browne, Chun, & Johnson, 2008) investigated the effect of refreshing a stimulus on fMRI repetition suppression and subsequent memory. Repetition suppression (or fMRI adaptation) is a reduced fMRI signal observed for repeated compared to novel stimuli. This has been observed for visual areas (Grill-Spector, Henson, & Martin, 2006; Grill-Spector & Malach, 2001), as well as higher order cognitive areas (De Baene, Kühn, & Brass, 2011). Yi et al (2008) had participants judge a visual scene, that was either repeated or had to be refreshed right after presentation, as in the study by Johnson et al (2007). During a subsequent presentation of the stimuli, the repetition suppression in the BOLD signal was investigated. Refreshed scenes produced adaptation in the PPA equal to repeated scenes, and differently from novel or once-presented scenes. When memory was assessed after the scanning procedure, refreshed scenes were remembered equally well as repeated scenes, and again better than novel or once-presented scenes. This suggests that thinking of a scene, as during refreshing, is comparable to actually seeing it again (Yi, et al., 2008), providing support for the idea that imagery and perception share neural substrates at least in higher visual areas.

These studies suggest that the brain activity during imagery is actually relevant rather than an epiphenomenon, as it influences subsequent behavior (Farah, 1988; Pylyshyn, 2002). The reverse influence, from perception on imagery, has also been documented. Wais and colleagues (2010) showed that providing visual input during imagery can impair the recollection of the to-be-imagined stimulus. When participants had to recollect details of a prior experiment using mental visualization, they performed better when they had their eyes closed compared to when their eyes were open and irrelevant visual stimuli were shown. This indicates that bottom-up perceptual input can influence the imagery process, indicating that

these might tap into similar systems. Many studies have their participants imagine with eyes closed (e.g. Amedi, Malach, & Pascual-Leone, 2005; Cui, Jeter, Yang, Montague, & Eagleman, 2007; Lee, Marzelli, Jolesz, & Yoo, 2009; Reddy, et al., 2010), circumventing this problem. On the other hand, the meta-analysis by Kosslyn & Thompson (2003) did not show a significant correlation between activation in early visual cortex and having eyes closed or opened.

Having just seen a stimulus might be different from imagining a stimulus that has to be recovered from long-term memory. For recently perceived stimuli more details might still be available, whereas for stimuli retrieved from (long-term) memory details might have been forgotten. Kaas and colleagues (2010) suggest that imagery activity in earlier visual areas might be related to short term memory. Imagery-related activity, according to them, occurs in higher areas, including V4 and higher. In their own study they try to exclude the effect of short-term memory by having participants imagine a never-seen movement of a dot. They reported a negative bold-response during imagery in V1, V2 and V3. Both the refreshing studies (Johnson, et al., 2007; Yi, et al., 2008) as well as several other studies presented the to-be-imagined stimuli right before imagery (Cichy, Heinzle, & Haynes, 2011; Johnson, et al., 2007; Klein, et al., 2004; Reddy, et al., 2010; Stokes, Thompson, Cusack, & Duncan, 2009). Most of these studies do find V1 activity, while two do not report on this (Johnson, et al., 2007; Reddy, et al., 2010). Unfortunately, not many studies require imagery from long-term memory and this limits the interpretability of the results.

## **Decoding**

All together, behavioral research, patient studies, neuroimaging data and interference effects point towards activity in visual cortex during visual imagery. However, not all areas are activated similarly during imagery. Some more complex picture evolves. The involvement of

higher visual areas, or visual association cortex, seems to be rather general. Stimulus specific areas are activated during both imagery and perception and imagery can have effects on behavior. This indicates that imagery might intermix with perception occasionally. However, for the earlier visual areas the data are not so clear. It has been suggested that specific task demands influence the involvement of these areas (Kaas, et al., 2010; Kosslyn, et al., 2006). Consequently, occipital cortex involvement has been mainly found during tasks in which details of the imagined stimulus were required. To further investigate this issue, a recent technique in neuroimaging can be of use: decoding. Decoding allows investigation of the content of representations and mental images directly. It therefore might provide new insights into the involvement of early visual areas during visual imagery.

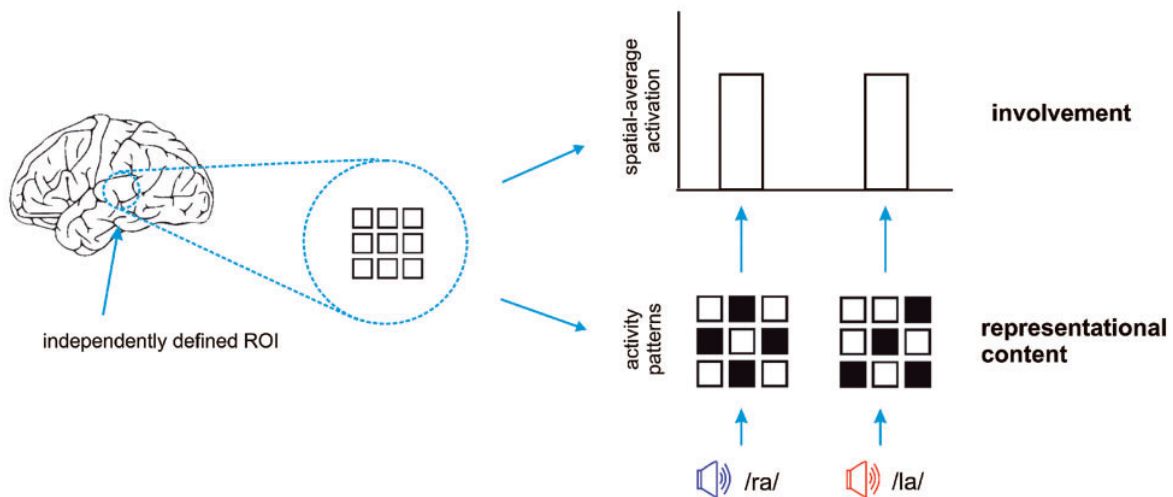
#### *The rationale behind decoding and pattern analysis*

Conventional fMRI analysis aims at finding macroscopic brain regions that are activated as a whole, during a specific task condition. Activation is observed when multiple nearby voxels show effects in the same direction and this brain activity is assumed to reflect the involvement of this area in the specific mental function targeted by the task (Mur, Bandettini, & Kriegeskorte, 2008). Since this usually involves spatial smoothing and/or averaging across voxels, fine-grained spatial pattern information is often lost and only the regional average is observed (Mur, et al., 2008). In certain cases, overall activity is sufficient to infer mental content. For example, in the study by O'Craven & Kanwisher (2000) a naïve observer could determine with 85% accuracy whether the participant was thinking about a face or a scene based on brain activity signal alone (*Figure 4*). This was possible because the stimuli (faces and scenes) are sufficiently different to activate separate brain areas (Haynes & Rees, 2006). The differential activation of FFA and the PPA could easily be observed in several participants (O'Craven & Kanwisher, 2000). However, in many cases the activity related to

distinct stimuli or mental states is much more similar or involves the same region (Haynes & Rees, 2006), as in early visual cortex. There, specific distributed patterns of activation *within* a region are of interest. Pattern-information analysis aims at finding these specific patterns, inferring that they contain representational content and might provide information beyond simply showing activation or not (Mur, et al., 2008). The rationale behind this is that even though overall activity in a region remains the same, individual voxels might change their pattern and these fine-grained patterns of activity can be informative about mental content (*Figure 5*). For example, if in an area a subset of 15 of the 25 voxels is activated by one stimulus and another subset of 15 by another stimulus, the activity patterns are distinct. Yet, overall activity is 15 voxels large in both cases. Pattern-information fMRI involves directly contrasting experimental conditions, with a change in pattern across conditions reflecting a change of activity in the neural population (even though the fMRI signal might not precisely reflect the neural activity patterns). Whenever activity patterns are statistically distinct, thus, conditions A and B are more different than expected by just noise, a condition can be detected above change from the brain activity pattern (Mur, et al., 2008).

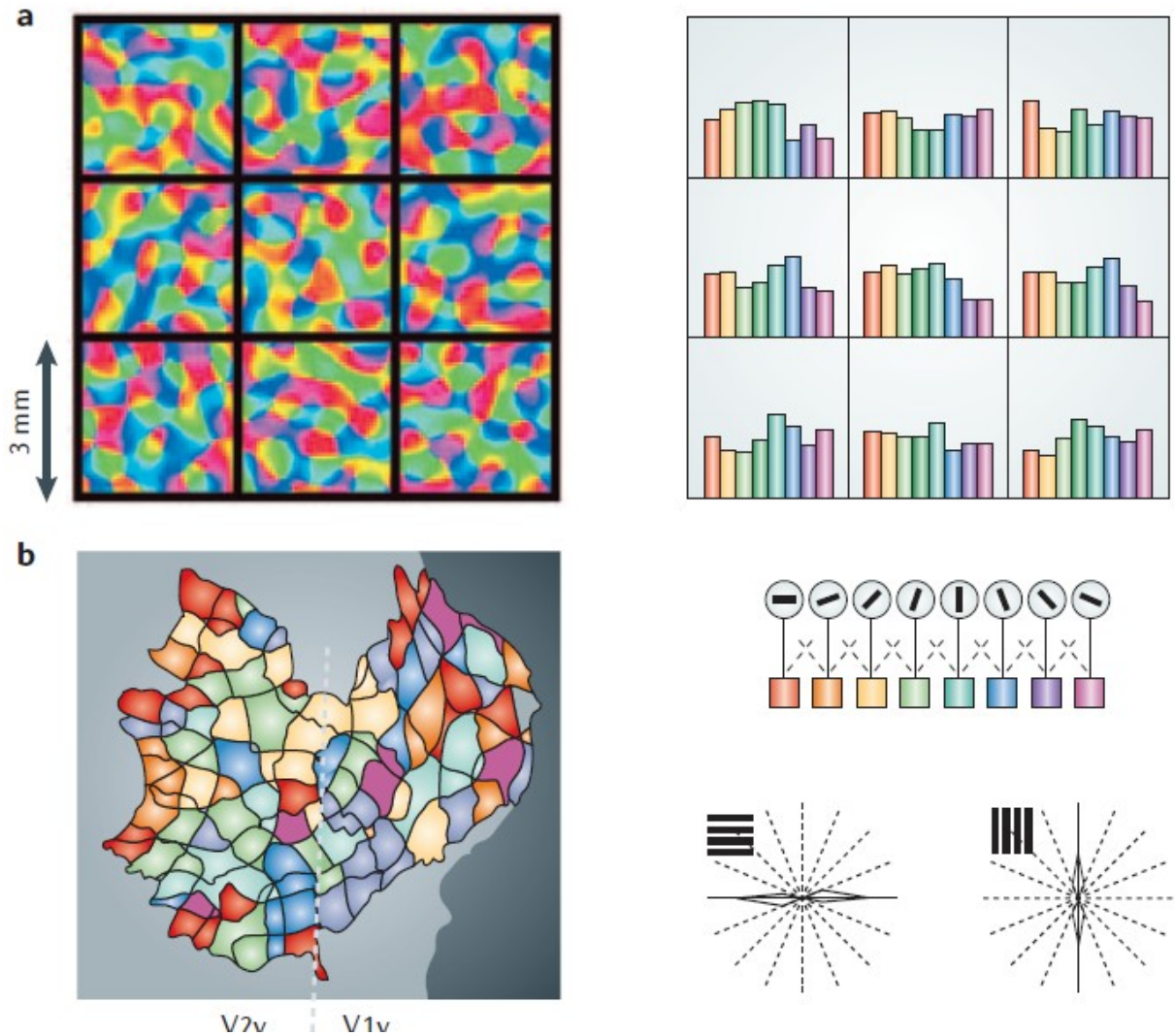
Statistical tests to infer differences between multivariate data might not be applicable for fMRI data. Therefore many studies “approach pattern analysis as a classification problem: if we can classify the experimental conditions (which elicit the representational states we are interested in) on the basis of the activity patterns better than chance, this indicates that the response pattern carries information about the experimental conditions” (Mur, et al., 2008). This approach is called ‘decoding’ or ‘brain reading’ and requires a method to separate patterns belonging to one condition from patterns belonging to the other condition (Mur, et al., 2008). A relatively simple and widespread method is to construct a linear plane that separates the patterns represented in a multidimensional space: linear classification. Several types of linear classifiers exist: the minimum-distance classifier, the Fisher linear discriminant analysis

(FLDA) and the linear support vector machine (SVM), that all have their own advantages and disadvantages (Mur, et al., 2008). Other, less commonly used methods also exist (Stokes, et al., 2009). Decoding is thus classifying a specific pattern as belonging to a specific condition or stimulus.



**Figure 5.** Activation indicates involvement, pattern-information indicates representational content. A specific ROI can show the same spatial-average activation resulting from different patterns encoding different representational content. This figure shows a hypothetical ROI consisting of nine voxels. The ROI’s multivoxel pattern of activity is different for /ra/ than /la/ speech sounds, but these different patterns result in the same spatial-average activation. This difference will go undetected by conventional activation-based analysis. Pattern-information analysis can be used to show that an ROI’s multivoxel activity pattern differs significantly across conditions, i.e. that the region contains information about the experimental conditions. Differences in multivoxel patterns across conditions can be interpreted as reflecting differences in underlying neuronal population activity (Adapted from Mur, et al., 2008).

An interesting application of fMRI pattern analysis is the investigation of orientation coding of stimuli in V1 and V2 (Kamitani & Tong, 2005). Neurons in early visual cortex (V1-V4) show orientation selectivity: neurons’ firing rates differ depending on the object orientation. However, these orientation columns are too small to be detected with fMRI. By assuming that individual voxels might show a slight, but true, preference for a certain orientation, evaluating all these voxels together might display a pattern selective to stimulus orientation (*Figure 6*) (Haynes & Rees, 2006; Kamitani & Tong, 2005). After applying linear



**Figure 6.** Decoding perceived orientation in the early visual cortex as done by Kamitani and Tong (Kamitani & Tong, 2005). (a) In the primary visual cortex (V1) of primates, neurons with different orientation preferences are systematically mapped across the cortical surface (left panel: different colors correspond to different orientations), too closely spaced to be resolved by functional MRI at conventional resolution (voxels indicated by black grid). Due to slight irregularities in the distribution of groups of selective neurons each voxel has a slight preference (right panel). (b) When subjects view images consisting of bars with different orientations, each orientation causes a subtly different response pattern in the early visual cortex<sup>8,9</sup>. The map shows the spatial pattern of preferences for different orientations in V1 and V2 plotted on the flattened cortical surface<sup>8</sup> (ventral). Although the preference of each small measurement area is small, the perceived orientation can be reliably decoded with high accuracy when the full information in the entire spatial response pattern is taken into account (*Adapted from Haynes & Rees, 2006*).

ensemble orientation detectors, Kamitani and Tong could reliably decode the orientation of eight different stimuli. This effect was most strong for V1 and V2, areas sensitive to orientation and edge. It was also selective for the voxels related to the retinotopic location of the stimulus; voxels in other parts of the hemifield did not contain information. This first application of multivariate classification showed that indeed information can be revealed from activity patterns, even below the resolution of fMRI (Haynes & Rees, 2006).

As evident from the above example, pattern analysis can be performed on specific brain regions of interest (ROI). It can also be used to investigate the full brain volume (Mur, et al., 2008). The smaller the voxel size, the more detail can be provided, but smaller voxels might also result in a higher level of noise. Therefore, voxels of 2x2x2 mm at a 3T scanner provide a reasonable alternative. Pattern-information analysis can also detect activity patterns such as measured with conventional fMRI: all voxels changing pattern in the same direction. This is just one of all the changes in brain activity that it can detect.

The potential applications for decoding are unlimited; however, it is questionable whether generalization between participants will ever be possible due to underlying basic neural differences between individuals. Therefore, a limitation of decoding is the need for individual classifiers for each participant. Also, limited states can be decoded, as the classifiers need to be trained on each state that has to be detected (Haynes & Rees, 2006). Some generalization between stimuli and session has been obtained (Reddy, et al., 2010; Stokes, et al., 2009), however, flexible classifiers that are able to easily generalize between sessions and participants would add immensely to the applicability of the technique. Yet, this technique of decoding has shown some remarkable insights into brain functions, since decoding is much more sensitive than conventional fMRI analysis. For example, in a study on visual working memory, Harrison and Tong (2009) had participants maintain the orientation of a grating over several seconds. Participants subsequently had to decide whether a test grating was rotated by

3 or 6 degrees compared to the original stimulus. Lower overall activity (or even baseline activity) was found in V1 during maintenance compared to encoding of the stimulus. However, decoding information about the stimulus currently held in working memory could reliably be done for this region, regardless of the levels of activity. This shows that lower amplitude signals still can contain relevant information. Decoding might thus be of great use in investigating the involvement of V1 and other early visual areas during visual mental imagery.

### *Studies applying decoding to mental imagery*

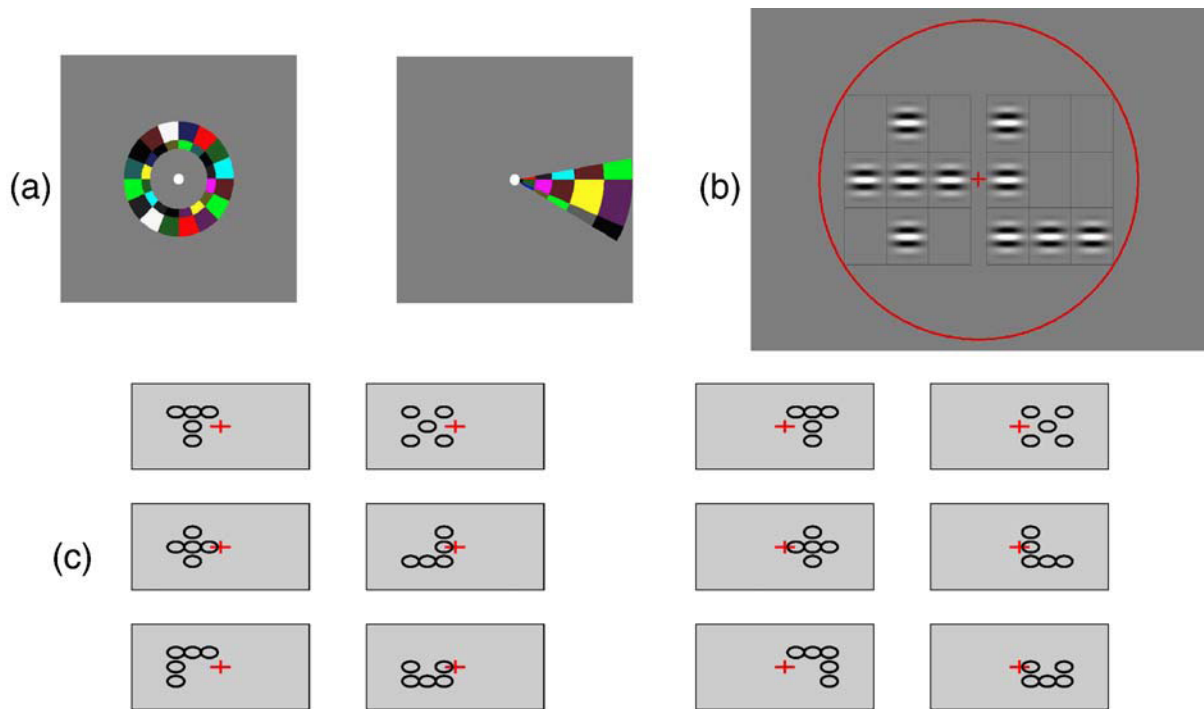
Decoding has been used to investigate the representations of perceived stimuli such as the previously discussed study on orientation columns in V1 and V2 (Kamitani & Tong, 2005), as well as mental states and ongoing perception (Haynes & Rees, 2005; van Gerven, Kok, de Lange, & Heskes, 2011).

Decoding has recently also been used to infer the content of mental images, separate from perception. If imagery is indeed similar to perception, specific activation patterns from perception and imagery should also be alike (Stokes, et al., 2009). However, “the extent to which internally generated activity in visual cortex resembles the fine-scale population coding responsible for stimulus-driven perception is unknown” (Stokes, et al., 2009). Several researchers trained a classifier with perception data and applied it to classify mental imagery too (Cichy, et al., 2011; Reddy, et al., 2010; Stokes, et al., 2009; Thirion et al., 2006). This cross-validation is extremely relevant for investigating the overlap of imagery and perception: if classifiers trained on perception can decode imagery, or vice versa, this indicates that relevant neural codes must be alike to a great extent.

Thirion and colleagues (2006) were able to decode from the primary and secondary visual cortex reliably with a linear SVM classifier. The stimuli were simple and abstract, and



consisted of black-colored Gabor filters in a 3x3 grid (Figure 7). The classifier was trained on perception data and applied to imagery data. Classification was mainly based on voxels from V1. The authors conclude that this is a strong indication that mental imagery involves activation in V1 and that mental images maintain a retinotopic structure.



**Figure 7.** Visual stimuli used in the experiment by Thirion and colleagues. (a) The experiment started with a classical retinotopic mapping experiment during which the participant viewed flickering rotating wedges and expanding and contracting rings. (b) Subsequently, subjects viewed or imagined groups of quickly rotating Gabor filters in an event-related design. These disks appeared simultaneously on the left and right side of the visual field, superimposed on a low-contrast grid and a fixation cross. (c) There were 6 different patterns in each hemifield (*Adapted from Thirion, et al., 2006*).

Stokes and colleagues (2009) investigated whether specific population codes could be observed during imagery. During perception they could decode from temporal occipital area LOC (Lateral Occipital Complex) whether subjects observed the letter, X or O. With a separately trained classifier they could also decode which of the letters they were imagining. Subsequently, they could cross-validate their classification by reliably decoding imagery

related activity with the classifier trained on perceptual data, thus suggesting that imagery indeed activates visual areas with stimulus specific population codes.

Using a similar logic, Reddy and colleagues (2010) investigated whether decoding could be done with a larger set of stimuli. They used four categories (fruits and vegetables, famous faces, tools and famous buildings), and decoded from both object-responsive areas in ventral temporal cortex as well as from retinotopic areas V1 and V2. For the ventral temporal areas, decoding could be done well above chance for both perception and imagery. Classifiers trained during perception also reliably decoded imagined objects and this worked the other way around too: imagery-trained classifiers decoded perceived stimuli equally well. Thus, the finding that cross-validated classifiers performed as well as the imagery classifier on imagery data provides strong evidence that in ventral temporal cortex imagery activates the same neural populations as during perception. Statistical testing showed that the weight maps for each category of the two classifiers were significantly more correlated within stimulus category than across stimulus categories. Decoding these objects from V1 and V2 was only possible for observed stimuli with the perception-trained classifier. Thus, the authors conclude that in ventral temporal cortex, fine-grained representations at the level of individual voxels are shared among perception and imagery, while in V1 this is different.

A largely similar study by Cichy and colleagues (2011) goes one step further. They tried to decode both location and content during imagery and perception. Their stimuli were three exemplars for each of four categories (objects, scenes, body parts and faces), presented and imagined left or right of fixation. The classifier was trained during imagery of these objects. Subsequent decoding of object content during perception was possible in ventral temporal areas in stimulus specific regions. Decoding location was possible in early visual areas V1, V2 and V3, as well as in certain higher ventral visual areas. This study accounts for the different information encoded in different regions: lower level areas allow decoding of spatial

information, while higher levels allow decoding of object categorization as well as some spatial information. The above described studies (Cichy, et al., 2011; Reddy, et al., 2010; Stokes, et al., 2009; Thirion, et al., 2006) are in line with earlier studies (Klein, et al., 2004; Slotnick, et al., 2005; Williams, et al., 2008) where early visual cortex activity was observed when retinotopic or spatial knowledge was required and a lack of activity in those areas whenever this type of information was less relevant.

A specific involvement of areas depending on task requirements could be observed in the reviewed studies, which has also been suggested in the literature (Kaas, et al., 2010; Kosslyn & Thompson, 2003; Kosslyn, et al., 2006; Slotnick, et al., 2005). Depending on the specific mental image required, visual areas might be differently taxed. When stimulus-detail such as orientation and shape are required V1 is activated (Kosslyn & Thompson, 2003). When the concept of a dog needs to be imagined, higher visual areas might provide sufficient information (Kosslyn, et al., 2006). During general imagery of objects, participants might not activate their primary visual cortex as higher areas are adequate, while during imagery of specific gratings, they should do this to comply with task demands. Neural populations activated during mental imagery thus reflect features required for the imagery task, while during perception all these features are constantly present. This might also have to do with short-term memory (Kaas, et al., 2010), which might make detailed imagery more easy, as details are still available. When specifically investigating the role of details, Klein and colleagues (2000) found that primary visual cortex was more involved when participants had to evaluate the mental image instead of simply observing it. Sung & Ogawa (2008) also suggest that the more detail required, the more specific visual areas are involved. This is also in accord with the above findings that retinotopy is observed, whenever the spatial features are relevant for the imagery task. The meta-analysis by Kosslyn and Thompson (2003)

identified stimulus-detail as one of the most important factors determining whether early visual cortex was involved.

Interestingly, in this last study (Cichy, et al., 2011) the classifier trained on perceptual data could not classify the imagery data equally well as the other way around. This is the opposite of earlier findings that perceptually trained classifiers performed best (Stokes, et al., 2009), or at least equally well (Reddy, et al., 2010). Cichy and colleagues maintain that this is due to imagery having certain, but not all, characteristics present during perception, yet, these characteristics are always present during perception and therefore allow classification. On the other hand, not all characteristics during perception are equally present during imagery, leading to more difficulty classifying imagery data. Why these results differ from the previous studies is not clear though. Since specific details of the stimulus set-up seem to be important (Kosslyn & Thompson, 2003), it might be small differences in specific stimulus-characteristics.

### **Involvement of visual cortex during mental visual imagery**

Several lines of evidence indeed show that imagery and perception share neural networks and principles in visual cortex. Together these studies sketch a picture of the extent of overlap between imagery and perception and what this implies for perceptual processing.

Not all visual areas are activated to the same extent. Higher perceptual areas, that show category specific responses to stimuli, generally show involvement during mental imagery too. The fusiform face area, for example, is activated as a whole during imagery of familiar or famous faces (O'Craven & Kanwisher, 2000; Reddy, et al., 2010) and face-category related activity can reliably be decoded from this area (Cichy, et al., 2011; Reddy, et al., 2010). However, earlier visual areas, which are retinotopically organized, do not always show activity during imagery (Kaas, et al., 2010), nor provide reliable decoding information in

every study (Reddy, et al., 2010). Brain damage in this region not always resulted in imagery difficulties either (Bartolomeo, 2008; Moro, et al., 2008).

The distinction between early and late(r) visual areas occurs in all lines of research. Late visual areas seem to be most commonly activated during imagery, whereas activity in early visual areas is rarer. Imagery is a top-down process and it could be envisioned that signals might not always reach the early areas, just as not all bottom-up input to visual areas will eventually reach higher cognitive areas in parietal and prefrontal regions. Three aspects of the imagery process seem to relate to activity in early visual areas, two of which have been already discussed. Imagery of stimuli maintained in short-term memory usually involved V1 activity. This might be due to the early areas having just been activated by the stimulus itself, but the evidence remains limited. In their meta-analysis, Kosslyn and Thompson (Kosslyn & Thompson, 2003) reported a study in which stimuli retrieved from long-term memory still activated early visual cortex. Secondly, imagery requiring detail or spatial information as processed in early visual areas seems to also activate V1 (Kaas, et al., 2010; Klein, et al., 2004; Kosslyn & Thompson, 2003), while this area is not always active when higher areas are sufficient.

The third aspect is related to the brightness (d'Angiulli, 2002) and overall level of detail of the stimulus: the vividness of the image. A positive correlation between vividness, as assessed with a vividness questionnaire, and V1 activity has been found for visual imagery (Amedi, et al., 2005; Cui, et al., 2007) as well as for other sensory modalities (Olivetti Belardinelli et al., 2009). This is in line with the idea that V1 is required for detailed imagery (Klein, et al., 2000). When more detailed imagery is required, participants might try to compose a more vivid image, resulting in stronger V1 activity. The other way around, more V1 activity might render participants better able to provide details of the image. Finke and Kosslyn actually found vivid imagers to perform more similarly for imagery and perception in a visual acuity

task than did non-vivid imagers (Finke & Kosslyn, 1980). Olivetti Belardinelli and colleagues (2009) suggested that vivid imagers form a more analogue representation during imagery. Notwithstanding, it can be questioned whether vividness can consciously be induced. Several studies explicitly asked participants to imagine as vividly as possible (e.g. Reddy, et al., 2010; Slotnick, et al., 2005), yet not all do find significant involvement of primary visual cortex (Reddy, et al., 2010). Imagery abilities seem to differ strongly per individual, as does imagery related activity in V1 (*Figure 1*) (Amedi, et al., 2005; Cui, et al., 2007; Klein, et al., 2000; Kosslyn & Thompson, 2003; Mazard, et al., 2005). Finally, vividness seems related to the level of luminance present (d'Angiulli, 2002) and this again points to the possible difference between open and closed eyes during imagery.

The effect of vividness and level of details on the activation of certain areas also points to a problem with the decoding studies. The decoding studies investigating higher visual areas tried to assign specific objects to specific categories (Cichy, et al., 2011; Reddy, et al., 2010), whereas the decoding studies investigating early visual areas tried to discern specific objects (Stokes, et al., 2009; Thirion, et al., 2006). This approach is totally different. Stimuli used for decoding in V1 were simple and discernable by just lines and orientations, like the stimuli used in the study by Thirion (2006). Since the stimuli used for the first group of experiments were usually quite detailed and naturalistic, same-category stimuli might have been much too complex and therefore too different regarding shapes, orientation and gratings, for them to be considered the same in V1. A banana and an apple are sufficiently different that lower level visual features might not generalize. Thus, assigning an apple and a banana to the same category based on V1 activity would not have been a logical step for the classifier. The classifier for higher areas, on the other hand, had been trained to find the commonalities between apples and banana's, which should be more abstract concepts. Had individual stimuli been assessed, and the classifier been trained accordingly, it might have been possible to

actually distract some information on stimulus identity from the early visual areas too. Notably, the most reliable category decoding in retinotopic areas in the study by Reddy and colleagues (2010) was observed for perceived faces, which all should more or less have the same overall shape. Thus, decoding can be very valuable in assessing which areas carry what kind of information, but care is required when interpreting the results.

One of the remarkable findings of decoding is that, even though overall activity is lower, areas might still carry information. Harrison and Tong (2009) found lower activity in V1, but were still able to decode information which was maintained in working memory. Moreover, they claimed that the absolute level of activity was not relevant for the decoding accuracy (Harrison & Tong, 2009). This suggests that for other studies, such as the one by Kaas et al (2010), who actually find deactivation in V1-V3, this information might also be present. Although deactivation is quite different from reduced - but still above baseline – activity, these areas might also in those cases still carry information. Importantly, decoding should be relatively insensitive to this overall level of activity. It might therefore prove valuable where conventional fMRI analysis methods fall short.

The same holds for the findings of Amedi and colleagues (2005) who found that auditory cortex is deactivated during ‘pure’ visual imagery, while it is active during visual perception. This finding has been interpreted as cross-modal inhibition (Kaas, et al., 2010) to prevent irrelevant stimulus input. That this could be functionally relevant is clear from the study by Wais and colleagues (Wais, et al., 2010), who find indeed interference effects. On the other hand, a recent study showed that when subjects viewed sound implying, but silent, visual stimuli, object category and individual object identity could reliably be decoded from auditory cortex (Meyer, et al., 2010). This again indicates that early sensory cortices are involved in perceptual experiences rather than sensory stimulation alone (Meyer, et al., 2010). It also

suggests that, as in visual cortex, the specific stimulus and task might influence exactly which areas become activated.

### **Conclusion, implications, future research**

Overall, a picture arises of highly similar processes for imagery and perception, but with imagery resulting in more selective and weaker activations. Task requirements and context such as level of detail, vividness, and short-term memory of the stimulus seem to play a role in whether early areas are activated, or higher visual areas are sufficient. Often, activation patterns are highly similar, as evident from the decoding studies. Can this also resolve the original debate by Kosslyn (Kosslyn, et al., 2003) and Pylyshyn (Pylyshyn, 2003a, 2003b) about the format of the mental images?

Overlapping brain activity has generally been taken to indicate that mental images are depictive; at least to the extent that perception is depictive. It is highly unlikely that imagery and perception share brain areas and activate these in similar manners, yet do not share representations. Especially the decoding studies suggest that similar activity cannot be just an epiphenomenon of imagery. However, it has been suggested that the ventral visual pathway is not only used for visual representations, but also for more abstract representations (Pietrini, 2004), due to it being activated by haptic perception in both healthy and blind (Amedi, Razb, Azulay, Malach, & Zoharyb, 2010; Klein, et al., 2004). These areas might contain conceptual knowledge which might be represented propositionally and yet, could provide support for the hypothesis by Pylyshyn (Pylyshyn, 1981, 2003a, 2003b) that imagery involves propositional representations. On the other hand, some researchers suggest that even (some) conceptual knowledge is grounded in the perceptual system, rather than it being represented by linguistic-like codes (Barsalou, 2005). Currently, the format of the images cannot be directly determined



and therefore remains elusive. This issue hence becomes a semantic and philosophical debate of theoretical interest but of practical irrelevance.

Highly relevant for daily life is the finding that imagery and perception are so closely related and can mutually affect each other (Johnson, et al., 2007; Pearson, Clifford, & Tong, 2008; Wais, et al., 2010; Yi, et al., 2008). Certain mental disorders involve psychosis and hallucinations due to blurring of imagery and perception blur (Amedi, et al., 2005). Anorexia entails erroneous perception of the own body as being fat, resulting in self-starvation (Johnson, et al., 2007; Mohr, et al., 2011).

However, outside the domain of mental disorders, imagery can also influence daily life perceptions. Gonsalves and colleagues (2004) had participants either view photographs of objects or imagine it after an auditory presented word. When participants were later tested on these objects presented with or without picture and additional words that had not occurred before, participants often (27% of the cases) reported having actually seen the picture even though only the word had been presented. This indicates that participants created a false memory of having actually seen the picture. Diekhof and colleagues (2011) found that anticipatory mental imagery of fearful faces influenced the subsequent rating of fearfulness in perceived faces. When participants had imagined a mildly fearful face, they perceived subsequent fearful faces as less fearful than did controls. Thus, these influences also can occur when V1 is possibly not even activated as with face imagery.

All these findings regard the visual system. Even if vision is a dominant sense, there is no reason to expect a largely different system for the other sensory modalities, nor for the motor system. Imagery, being a top-down process, probably activates feature relevant areas depending on specific task demands. Future studies should investigate these other sensory systems as has been done for vision. Decoding might prove very valuable in this respect. Moreover, decoding possibly allows the investigation of the interactions between the different

senses, which have been reported even for imagery (Amedi, et al., 2005; Amedi, et al., 2010; Klein, et al., 2004; Meyer, et al., 2010; Pietrini, 2004). It has been suggested that space is represented supramodally (Struiksma, 2011), thus, spatial imagery might depend on modality interactions.

Finally, as mental imagery seems to play a role in certain cognitive processes as learning, decoding of mental imagery might provide a means to online follow such processes. Having access to representational patterns, at various levels of abstractness, might elucidate how information is retrieved, manipulated and finally (re)stored.

## References

- Amedi, A., Malach, R., & Pascual-Leone, A. (2005). Negative BOLD Differentiates Visual Imagery and Perception. *Neuron*, 48(5), 859-872. doi: 10.1016/j.neuron.2005.10.032
- Amedi, A., Razb, N., Azulay, H., Malach, R., & Zoharyb, E. (2010). Cortical activity during tactile exploration of objects in blind and sighted humans. *Restorative Neurology and Neuroscience*, 28, 143-156. doi: 10.3233/rnn-2010-0497
- Annett, J. (1995). Motor imagery: perception or action? *Neuropsychologia*, 33(11), 1395-1417.
- Barsalou, L. (2005). Continuity of the conceptual system across species. *Trends in Cognitive Sciences*, 9(7), 309-311. doi: 10.1016/j.tics.2005.05.003
- Bartolomeo, P. (2008). The neural correlates of visual mental imagery: an ongoing debate. *Cortex*, 44(2), 107-108.
- Bensafi, M., Sobel, N., & Khan, R. M. (2007). Hedonic-Specific Activity in Piriform Cortex During Odor Imagery Mimics That During Odor Perception. *Journal of Neurophysiology*, 98(6), 3254-3262. doi: 10.1152/jn.00349.2007
- Bisiach, E., & Luzzatti, C. (1978). Unilateral neglect of representational space. *Cortex*, 14(1), 129-133.
- Cichy, R. M., Heinzle, J., & Haynes, J. D. (2011). Imagery and Perception Share Cortical Representations of Content and Location. *Cerebral Cortex*. doi: 10.1093/cercor/bhr106
- Cui, X., Jeter, C. B., Yang, D., Montague, P. R., & Eagleman, D. M. (2007). Vividness of mental imagery: Individual variability can be measured objectively. *Vision Research*, 47(4), 474-478. doi: 10.1016/j.visres.2006.11.013
- d'Angiulli, A. (2002). Mental image generation and the contrast sensitivity function. *Cognition*, 85, B11-B19.
- de Araujo, I. E., Rolls, E. T., Velazco, M. I., Margot, C., & Cayeux, I. (2005). Cognitive modulation of olfactory processing. *Neuron*, 46(4), 671-679. doi: S0896-6273(05)00357-0 [pii]10.1016/j.neuron.2005.04.021
- De Baene, W., Kühn, S., & Brass, M. (2011). Challenging a decade of brain research on task switching: Brain activation in the task-switching paradigm reflects adaptation rather than reconfiguration of task sets. *Human Brain Mapping*, n/a-n/a. doi: 10.1002/hbm.21234
- de Lange, F. P., Roelofs, K., & Toni, I. (2008). Motor imagery: A window into the mechanisms and alterations of the motor system. *Cortex*, 44(5), 494-506. doi: 10.1016/j.cortex.2007.09.002

- Diekhof, E. K., Kipshagen, H. E., Falkai, P., Dechent, P., Baudewig, J., & Gruber, O. (2011). The power of imagination — How anticipatory mental imagery alters perceptual processing of fearful facial expressions. *NeuroImage*, *54*(2), 1703-1714. doi: 10.1016/j.neuroimage.2010.08.034
- Engel, S. A., Glover, G. H., & Wandell, B. A. (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex*, *7*(2), 181-192.
- Farah, M. J. (1988). Is visual imagery really visual? overlooked evidence from neuropsychology. *Psychological Review*, *95*(3), 307-317.
- Finke, R. A. (1980). Levels of equivalence in imagery and perception. *Psychological Review*, *87*(2), 113-132. doi: 10.1037/0033-295x.87.2.113
- Finke, R. A. (1985). Theories relating mental imagery to perception. *Psychol Bull*, *98*(2), 236-259.
- Finke, R. A., & Kosslyn, S. M. (1980). Mental imagery acuity in the peripheral visual field. *J Exp Psychol Hum Percept Perform*, *6*(1), 126-139.
- Ganis, G. (2004). Brain areas underlying visual mental imagery and visual perception: an fMRI study. *Cognitive Brain Research*, *20*(2), 226-241. doi: 10.1016/j.cogbrainres.2004.02.012
- Gonsalves, B., Reber, P. J., Gitelman, D. R., Parrish, T. B., Mesulam, M.-M., & Paller, K. A. (2004). Neural Evidence that Vivid Imagining can lead to false remembering. *Psychological Science*, *15*(10), 655-660.
- Grill-Spector, K., Henson, R., & Martin, A. (2006). Repetition and the brain: neural models of stimulus-specific effects. *Trends in Cognitive Sciences*, *10*(1), 14-23. doi: 10.1016/j.tics.2005.11.006
- Grill-Spector, K., & Malach, R. (2001). fMRI-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293-321.
- Harrison, S. A., & Tong, F. (2009). Decoding reveals the contents of visual working memory in early visual areas. *Nature*, *458*(7238), 632-635. doi: 10.1038/nature07832
- Haynes, J.-D., & Rees, G. (2005). Predicting the Stream of Consciousness from Activity in Human Visual Cortex. *Current Biology*, *15*(14), 1301-1307. doi: 10.1016/j.cub.2005.06.026
- Haynes, J.-D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, *7*(7), 523-534. doi: 10.1038/nrn1931

- Hermes, D., Vansteensel, M. J., Albers, A. M., Bleichner, M. G., Benedictus, M. R., Mendez Orellana, C., . . . Ramsey, N. F. (2011). Functional MRI-based identification of brain areas involved in motor imagery for implantable brain-computer interfaces. *Journal of Neural Engineering*, 8, 6.
- Ishai, A. (2010). Seeing with the mind's eye: top-down, bottom-up, and conscious awareness. *F1000 Biology Reports*. doi: 10.3410/b2-34
- Johnson, M. R., Mitchell, K. J., Raye, C. L., D'Esposito, M., & Johnson, M. K. (2007). A brief thought can modulate activity in extrastriate visual areas: Top-down effects of refreshing just-seen visual stimuli. *NeuroImage*, 37(1), 290-299. doi: 10.1016/j.neuroimage.2007.05.017
- Kaas, A., Weigelt, S., Roebroek, A., Kohler, A., & Muckli, L. (2010). Imagery of a moving object: The role of occipital cortex and human MT/V5+. *NeuroImage*, 49(1), 794-804. doi: 10.1016/j.neuroimage.2009.07.055
- Kamitani, Y., & Tong, F. (2005). Decoding the visual and subjective contents of the human brain. *Nature Neuroscience*, 8(5), 679-685.
- Klein, I., Dubois, J., Mangin, J.-F., Kherif, F., Flandin, G., Poline, J.-B., . . . Le Bihan, D. (2004). Retinotopic organization of visual mental images as revealed by functional magnetic resonance imaging. *Brain Res Cognitive Brain Research*, 22(1), 26-31. doi: 10.1016/j.cogbrainres.2004.07.006
- Klein, I., Paradis, A.-L., Poline, J.-B., Kosslyn, S. M., & Le Bihan, D. (2000). Transient activity in the human calcarine cortex during visual-mental imagery: an event-related fMRI study. *Journal of Cognitive Neuroscience*, 12(Supplement 2), 15-23.
- Knauff, M., Kassubek, C. A. J., Mulack, T., & Greenlee, M. W. (2000). Cortical activation evoked by visual mental imagery as measured by fMRI. *Cognitive Neuroscience and Neuropsychology Neuroreport*, 11(18), 3957-3962.
- Kosslyn, S. M. (1981). Research on mental imagery: some goals and directions. *Cognition*, 10(1-3), 173-179.
- Kosslyn, S. M., Ganis, G., & thompson, W. L. (2001). Neural Foundations of imagery. *Nature Reviews Neuroscience*, 2, 635-642.
- Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2003). Mental imagery: against the nihilistic hypothesis. *Trends Cogn Sci*, 7(3), 109-111. doi: S1364661303000251 [pii]

- Kosslyn, S. M., & Thompson, W. L. (2003). When is early visual cortex activated during visual mental imagery? *Psychological Bulletin*, *129*(5), 723-746. doi: 10.1037/0033-2909.129.5.723
- Kosslyn, S. M., Thompson, W. L., & Ganis, G. (2006). *The case for mental imagery* (Vol. 39). Oxford: Oxford University Press.
- Kraemer, D. J. M., Macrae, C. N., Green, A. E., & Kelley, W. M. (2005). Sound of silence activates auditory cortex. *Nature*, *434*, 158.
- Lee, J.-H., Marzelli, M., Jolesz, F. A., & Yoo, S.-S. (2009). Automated classification of fMRI data employing trial-based imagery tasks. *Medical Image Analysis*, *13*(3), 392-404. doi: 10.1016/j.media.2009.01.001
- Marzi, C. A., Mancini, F., Metitieri, T., & Savazzi, S. (2006). Retinal eccentricity effects on reaction time to imagined stimuli. *Neuropsychologia*, *44*(8), 1489-1495. doi: S0028-3932(05)00364-7 [pii]10.1016/j.neuropsychologia.2005.11.012
- Mazard, A., Laou, L., Joliot, M., & Mellet, E. (2005). Neural impact of the semantic content of visual mental images and visual percepts. *Cognitive Brain Research*, *24*(3), 423-435. doi: 10.1016/j.cogbrainres.2005.02.018
- Meyer, K., Kaplan, J. T., Essex, R., Webber, C., Damasio, H., & Damasio, A. (2010). Predicting visual stimuli on the basis of activity in auditory cortices. *Nature Neuroscience*, *13*(6), 667-668. doi: 10.1038/nn.2533
- Mohr, H. M., Linder, N. S., Dennis, H., & Sireteanu, R. (2011). Orientation-specific aftereffects to mentally generated lines. *Perception*, *40*, 272-290.
- Mohr, H. M., Linder, N. S., Linden, D. E. J., Kaiser, J., & Sireteanu, R. (2009). Orientation-specific adaptation to mentally generated lines in human visual cortex. *NeuroImage*, *47*(1), 384-391. doi: 10.1016/j.neuroimage.2009.03.045
- Moro, V., Berlucchi, G., Lerch, J., Tomaiuolo, F., & Aglioti, S. M. (2008). Selective deficit of mental visual imagery with intact primary visual cortex and visual perception. *Cortex*, *44*(2), 109-118. doi: 10.1016/j.cortex.2006.06.004
- Mur, M., Bandettini, P. A., & Kriegeskorte, N. (2008). Revealing representational content with pattern-information fMRI--an introductory guide. *Social Cognitive and Affective Neuroscience*, *4*(1), 101-109. doi: 10.1093/scan/nsn044
- O'Craven, K. M., & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *J Cogn Neurosci*, *12*(6), 1013-1023.

- Olivetti Belardinelli, M., Palmiero, M., Sestieri, C., Nardo, D., Di Matteo, R., Londei, A., . . . Romani, G. L. (2009). An fMRI investigation on image generation in different sensory modalities: The influence of vividness. *Acta Psychologica*, *132*(2), 190-200. doi: 10.1016/j.actpsy.2009.06.009
- Pearson, J., Clifford, C. W., & Tong, F. (2008). The functional impact of mental imagery on conscious perception. *Curr Biol*, *18*(13), 982-986. doi: S0960-9822(08)00723-9 [pii]10.1016/j.cub.2008.05.048
- Pietrini, P. (2004). Beyond sensory images: Object-based representation in the human ventral pathway. *Proceedings of the National Academy of Sciences*, *101*(15), 5658-5663. doi: 10.1073/pnas.0400707101
- Podgorny, P., & Shepard, R. N. (1978). Functional representations common to visual perception and imagination. *Journal of Experimental Psychology: Human Perception and Performance*, *4*(1), 21-35. doi: 10.1037/0096-1523.4.1.21
- Pylyshyn, Z. W. (1981). The imagery debate: Analogue media versus tacit knowledge. *Psychological Review*, *88*(1), 16-45. doi: 10.1037/0033-295x.88.1.16
- Pylyshyn, Z. W. (2002). Mental imagery: in search of a theory. *Behav Brain Sci*, *25*(2), 157-182; discussion 182-237.
- Pylyshyn, Z. W. (2003a). Explaining mental imagery: now you see it, now you don't. Reply to Kosslyn et al. *Trends Cogn Sci*, *7*(3), 111-112. doi: S1364661303000044 [pii]
- Pylyshyn, Z. W. (2003b). Return of the mental image: are there really pictures in the brain? *Trends Cogn Sci*, *7*(3), 113-118. doi: S1364661303000032 [pii]
- Reddy, L., Tsuchiya, N., & Serre, T. (2010). Reading the mind's eye: Decoding category information during mental imagery. *NeuroImage*, *50*(2), 818-825. doi: 10.1016/j.neuroimage.2009.11.084
- Rich, A. N., Williams, M. A., Puce, A., Syngeniotis, A., Howard, M. A., McGlone, F., & Mattingley, J. B. (2006). Neural correlates of imagined and synaesthetic colours. *Neuropsychologia*, *44*(14), 2918-2925. doi: 10.1016/j.neuropsychologia.2006.06.024
- Seurinck, R., de Lange, F. P., Achten, E., & Vingerhoets, G. (2011). Mental rotation meets the motion aftereffect: the role of hV5/MT+ in visual mental imagery. *J Cogn Neurosci*, *23*(6), 1395-1404. doi: 10.1162/jocn.2010.21525
- Slotnick, S. D., Thompson, W. L., & Kosslyn, S. M. (2005). Visual Mental Imagery Induces Retinotopically Organized Activation of Early Visual Areas. *Cerebral Cortex*, *15*(10), 1570-1583. doi: 10.1093/cercor/bhi035

- Stokes, M., Thompson, R., Cusack, R., & Duncan, J. (2009). Top-Down Activation of Shape-Specific Population Codes in Visual Cortex during Mental Imagery. *Journal of Neuroscience*, *29*(5), 1565-1572. doi: 10.1523/jneurosci.4657-08.2009
- Struiksma, M. E. (2011). *On the language of space: neurocognitive studies in blind and sighted individuals*. PhD, Utrecht University, Utrecht. (978-90-8891-246-7)
- Sung, Y. W., & Ogawa, S. (2008). A property of face representation at the categorical level. *Neurosci Lett*, *448*(1), 1-5. doi: S0304-3940(08)01294-9 [pii]10.1016/j.neulet.2008.09.053
- Thirion, B., Duchesnay, E., Hubbard, E., Dubois, J., Poline, J.-B., Lebihan, D., & Dehaene, S. (2006). Inverse retinotopy: Inferring the visual content of images from brain activation patterns. *NeuroImage*, *33*(4), 1104-1116. doi: 10.1016/j.neuroimage.2006.06.062
- Tootell, R. B. H., Hadjikhani, N. K., Mendola, J. D., Marrett, S., & Dale, A. M. (1998). From retinotopy to recognition: fMRI in human visual cortex. *Trends in Cognitive Sciences*, *2*(5), 174-183.
- van Gerven, M. A., Kok, P., de Lange, F. P., & Heskes, T. (2011). Dynamic decoding of ongoing perception. *NeuroImage*, *57*(3), 950-957. doi: S1053-8119(11)00508-8 [pii]10.1016/j.neuroimage.2011.05.020
- Wais, P. E., Rubens, M. T., Boccanfuso, J., & Gazzaley, A. (2010). Neural Mechanisms Underlying the Impact of Visual Distraction on Retrieval of Long-Term Memory. *Journal of Neuroscience*, *30*(25), 8541-8550. doi: 10.1523/jneurosci.1478-10.2010
- Williams, M. A., Baker, C. I., Op de Beeck, H. P., Mok Shim, W., Dang, S., Triantafyllou, C., & Kanwisher, N. (2008). Feedback of visual object information to foveal retinotopic cortex. *Nature Neuroscience*, *11*(12), 1439-1445. doi: 10.1038/nn.2218
- Yi, D.-J., Turk-Browne, N. B., Chun, M. M., & Johnson, M. K. (2008). When a thought equals a look: refreshing enhances perceptual memory. *Journal of Cognitive Neuroscience*, *20*(8), 1371-1380.
- Young, M. P., Hilgetag, C. C., & Scannell, J. W. (2000). On imputing function to structure from the behavioural effects of brain lesions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *355*(1393), 147-161. doi: 10.1098/rstb.2000.0555
- Zago, S., Corti, S., Bersano, A., Baron, P., Conti, G., Ballabio, E., . . . Bresolin, N. (2010). A cortically blind patient with preserved visual imagery. *Cogn Behav Neurol*, *23*(1), 44-48.