

How fMRI Technology Contributes to the Advancement of Research in Mental Imagery: A Review

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1. Introduction

Mental imagery involves the generation of images using information stored in long-term memory, as opposed to the extemporaneous registration of information by our senses, giving rise to introspective experiences, such as 'seeing with the mind's eye', 'hearing with the mind's ear', 'smelling with the mind's nose'. In the past four decades, there has been much debate regarding the extent to which key elements of perception rely upon mental images versus propositional knowledge of sensory principles. Two contrasting approaches were developed i.e. perceptual and propositional theories. According to the perceptual approach, mental imagery is supported by mechanisms and processes involved in the actual perception. It functions as a modal analogue of that which is perceived by the senses (Kosslyn et al., 2006). Thus, mental images resemble perceptual information, e.g., visual images preserve both pictorial and spatial properties. According to the propositional approach, mental imagery is supported by abstract symbols of the sort used in a language-like system. It functions as an a-modal description of the external world (Anderson & Bower, 1973; Pylyshyn, 1981, 2002, 2003). In particular, mental images rely on a code, structured by rules and relationships, rather than on mere verbal descriptions. Therefore, these mental images are epiphenomena of thought: instead of exhibiting the sensory aspects that determine their analogical nature, they are affected by "cognitive permeability," or the tacit knowledge of physical laws in the external world (Pylyshyn, 1981, 2002).

These perspectives have primarily been investigated using visual imagery as a reference modality. After many years of behavioral research, the debate reached an impasse, as empirical evidence could only be explained by considering one of the two competitive approaches at a time (Kosslyn, 1980). The advent of neuroimaging techniques, particularly fMRI, offered the scientific community a new opportunity to solve the imagery debate. Unlike previous neuroimaging techniques, fMRI is capable of isolating many simultaneous and coordinated brain events with high spatial resolution. This facilitates the delineation of

brain anatomy, which increases sensitivity while maintaining selectivity. In comparison to Positron Emission Tomography (PET), fMRI offers increased statistical power for two reasons: first, the activation maps from multiple individuals do not need to be averaged, and the spatial transformation is not necessary, providing an enormous advantage in terms of signal-to-noise ratios (Watson et al., 1993); second, scanning can easily be extended over time.

Because of these advantages, fMRI has been used extensively to identify brain structures uniquely involved in cognitive functions, included mental imagery. This accordingly makes fMRI more suitable than PET and Single Photon Emission Computer Tomography (SPECT) for examining the extent to which imagery and perception share overlapping cortical areas in the functioning of various sensory modalities. In exploring this issue, researchers aimed to clarify whether imagery involves the activation of primary sensory cortices in visual, auditory, tactile, olfactory, gustatory, motor, and proprioceptive modalities. The present review is therefore aimed at investigating the status of fMRI research in all imagery modalities, with separate sections for each imagery modality, followed by collective conclusions.

2. Visual imagery

Visual imagery relies on the “mind’s eye” and has traditionally been associated with the visual buffer (Kosslyn, 1980) or the visuo-spatial sketchpad of working memory (Baddeley & Loogje, 1992). In particular, Kosslyn (1980, 1994) proposed that visual imagery of a known object is generated from a semantic representation that accesses stored visual information about the object. This visual information is then loaded into a short-term “visual buffer”, which functions as a coordinate space that temporarily maintains and manipulates information. Though some constraints are present, research has found that visual mental images can be rotated (Shepard & Metzler, 1971), scaled (Larsen & Bundesen, 1978), scanned (Kosslyn et al., 1978), transformed in shape and color (Dixon & Just, 1978), and inspected (Thompson et al., 2008).

Although these studies appeared to lead to the conclusion that visual imagery and visual perception share common mechanisms and processes, fMRI was used to clarify that the recruitment of the primary visual cortex (calcarine fissure - BA 17) may vary according to different factors. In a previous review Kosslyn & Thompson (2003) suggested that this contradiction in the literature may be accounted for by the fact that the primary visual cortex can be activated when the sensitivity of the neuroimaging technique is high (e.g., using fMRI rather than PET), and when inspecting details of visual mental images with high resolution to visualize shapes rather than spatial patterns. Amedi et al. (2005) later demonstrated that deactivating the auditory cortex, as measured by BOLD functional magnetic resonance imaging, may differentiate between visual imagery and visual perception. During visual imagery, the deactivation of the auditory cortex is negatively correlated with the activation of the visual cortex as well as with scores on the subjective Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973). When using fMRI, however, primary visual cortex activity correlated with the reported vividness of visual images when participants were instructed to visualize themselves or another person either bench pressing or stair climbing (Cui et al., 2007), or imagining concrete objects (e.g., to see a bucket) (Olivetti et al., 2009).

Under specific circumstances visual mental images seem to involve neural mechanisms recruited by visual perception, as evidenced by the fact that the lateral geniculate nucleus is activated during visual imagery (Chen et al., 1998). Ganis et al. (2004) clarified, however, that when participants were instructed to either imagine or see faint drawings of simple objects, and then judge specific aspects of the drawings, such as 'taller than wider', visual imagery and visual perception recruited similar neural machinery, especially in frontal and parietal regions. Though the calcarine cortex was activated in both conditions, this spatial overlap was neither complete nor uniform.

The spatial overlap observed during imagery and perception does not necessarily imply that the corresponding representations are qualitatively similar to each other. Reddy et al. (2010) accordingly explored the extent to which it is possible to establish which item participants were imagining, as well as the comparability between representations evoked during imagery and visual perception. Participants were instructed to both imagine and see stimuli belonging to four object categories: food, tools, faces, buildings. By using pattern classification techniques, which test each classifier (perceptual or imagery) on the other condition, authors were capable to decode category information from ventro-temporal cortex in both imagery and perceptual conditions, but only during actual viewing from visual primary area. Using the same logic, Stokes et al. (2009) found similar results, revealing that imagery of the letter X versus the letter O could be decoded from the lateral occipital complex.

3. Auditory imagery

Intons-Peterson (1992, p. 46) defined auditory imagery as "the introspective persistence of an auditory experience, including one constructed from components drawn from long-term memory, in the absence of direct sensory instigation of that experience". This type of imagery runs auditory traces from prior experiences (e.g., someone's voice, environmental sounds, melodies) through the "mind's ear". In this section, the fMRI studies on auditory verbal imagery will be presented first, followed by auditory imagery of environmental sounds, and musical imagery will be discussed last.

3.1 Auditory verbal imagery

Auditory verbal imagery can occur spontaneously or deliberately when recalling the sound of our own voice or someone else's voice. Within the frame of working memory, auditory verbal imagery has been associated with the operation of the phonological loop sub-system (Baddeley & Loggie, 1992). Two components have been discerned: a short-lived store that represents material in phonological form (inner ear), and an articulatory rehearsal process (inner voice) that is used to recode and refresh decaying representations into the phonological store (Smith et al., 1995).

By using fMRI, Shergill et al. (2001) found that there is a lack of activation in the primary auditory cortex (Heschel gyrus - BA 41/42) during auditory verbal imagery. Relative to the baseline condition (listening to each word carefully), first person imagery (imagining sentences of the form "I like..." in ones' own voice) showed no activation in the auditory cortex, while second and third person imagery (imagining sentences of the form "You like..." and "He likes..." in voices that participants had heard on a tape) showed activation in the secondary auditory cortex (BA 22), namely in the superior temporal gyrus. Jancke &

Shah (2004) also showed that the primary auditory cortex was not activated during auditory verbal imagery. Relative to the resting condition, imagining hearing a syllable (e.g., Ka, Ta, Pa) yielded activation in the bilateral superior temporal gyri, including the planum temporale, and the dorsal bank of the superior temporal sulcus. By exploring the fMRI correlates of auditory verbal imagery associated with the phonological processing of words, Aleman et al. (2005) confirmed the lack of activation of the primary auditory cortex. Participants were presented with bi-syllabic words and were required to indicate the syllable that carried the stress, discriminating between weak-initial words and strong-initial words. In the perceptual condition, words were delivered by headphones, whereas in the imagery condition, words were presented on a screen and participants were instructed to imagine hearing the word being spoken by another person. Results revealed that both perceptual and imagery conditions activated the bilateral supplementary motor area, bilateral post-central gyrus, bilateral insula, the left inferior frontal gyrus (Broca's area), the posterior left superior temporal sulcus/superior temporal gyrus, and the left intra-parietal sulcus/superior parietal lobule. Kim et al. (2008) reported a deactivation in the left superior temporal cortex (BA 22/42) and anterior cingulate cortex during auditory verbal imagery of another's remarks expressed toward self, which were derogatory in content, relative to auditory verbal imagery of another's remarks expressed toward self, which were non-derogatory and neutral in content. In addition, activation was found in both medial frontal cortex, left inferior frontal cortex, both pre-central gyrus, both inferior parietal lobule, right occipital-temporal cortex, left occipital cortex, both posterior insula, and both amygdala.

3.2 Auditory imagery of environmental sounds

This type of auditory imagery can occur spontaneously or deliberately when recalling the sound produced by environmental objects or auditory sources, such as the ringing of the phone, the shot of a gun, or sound produced by animals. In this direction, Olivetti Belardinelli et al. (2004a) investigated the neural correlates of mental imagery in different sensory modalities, including the auditory modality, by contrasting imagery sentences (e.g., hearing a shot) with abstract sentences (e.g., the power of reason). Relative to the abstract condition, there was no activation found in the primary auditory cortex during auditory imagery. There was, however, activity in the left middle temporal gyrus (BA 22/37), left inferior temporal gyrus (BA 37), left inferior-middle frontal gyrus, left inferior parietal lobule, and left insula. Using the same methodology, Olivetti Belardinelli et al. (2009) found a bilateral activation in the Heschl's gyrus comparing high-vivid participants with low-vivid participants in generating auditory images of environmental sounds, and in the right hemisphere of the same gyrus regressing the vividness scores of auditory images onto the bold signal. These activations, however, were not significant at the corrected threshold for multiple comparisons. Significant activations were found in the left middle frontal gyrus, right angular gyrus, right posterior cingulate, and left lingual gyrus. Authors explained the lack of significant modality-specific activation in the Heschl's gyrus in the light of the interference of the scanner noise on the auditory image formation process, which may have led to signal decrease solely in the primary auditory cortex, as showed by Gaab et al. (2007). Nonetheless, Bunzeck et al. (2005) used the fMRI technique and did not find any activation of the primary auditory cortex during imagery of familiar complex environmental sounds, either. Compared to watching a silent scrambled movie of familiar scenes (control condition), watching familiar scenes and listening to the corresponding sounds (perception

condition) yielded activations in the bilateral Heschl's gyrus, superior temporal gyrus, and left fusiform gyrus, and planum temporale. In contrast, the imagery condition consisted of watching the same movies presented in the perception condition but without the appropriate sounds, which had to be imagined by the participants. This condition elicited bilateral hemodynamic responses only in the right superior temporal gyrus, including the bilateral planum temporale.

3.3 Musical imagery

Musical imagery is a type of auditory imagery that relies upon the capacity to mentally conceptualize songs, tunes, and general musical input. Musical imagery processes the tempo, temporal extension (Halpern, 1988), pitch (loudness) (Intons-Peterson Russell & Dressel, 1992), and timbre (sound quality of different instruments or voices) of real music (Pitt & Crowder, 1992). The first event-related fMRI study showed activation in the bilateral primary and secondary auditory areas in the superior temporal gyri when participants imagined a single computer-generated note (Yoo et al., 2001). The results also revealed significant activation in the medial and inferior frontal gyri, precuneus, middle frontal gyri, superior temporal gyri, and anterior cingulate gyri. This suggests that fMRI may be sensitive at least to the activation caused by simple internally generated sounds. This study, however, had no control conditions or task validation, and did not isolate timbre. Halpern et al. (2004) examined musical imagery of timbre relative to the visual imagery control. They found that the former activated the posterior temporal cortex, but not the primary auditory cortex, whereas the perception condition (judgments of the timbres of sounds) activated primary and secondary auditory areas with some right-sided asymmetry.

No activation was found in the primary auditory cortex during musical imagery, even in musicians. Langheim et al. (2002) asked to musicians to imagine musical performances for 30 seconds alternated with resting periods. Relative to the resting condition, musical imagery activated supplementary motor and pre-motor areas, right superior parietal lobule, right inferior frontal gyrus, bilateral mid-frontal gyri, and bilateral lateral cerebellum. Yet, Lotze et al. (2003) did not find any activation of the primary auditory cortex when asking amateurs and professional violinists to mentally perform Mozart's "Violin concerto in G major" (KV216). During the musical imagery condition, professionals recruited the supplementary motor area, the superior premotor cortex, anterior areas (Larsell's lobule HVI) in the left cerebellar hemisphere, and bilateral superior parietal areas. Latter Zatorre et al. (2010) carried out two fMRI experiments with musicians. Participants were presented with the first few notes of a familiar tune (Experiment 1) or its title (Experiment 2), followed by a string of notes that was either an exact or an inexact reversal. The task was to judge whether the second string was correct or not by mentally reversing all its notes, which required both maintenance and manipulation of the represented string. During the reversal process, neither experiment showed activation of the primary auditory cortex, but both showed activation of the superior parietal lobe (intraparietal sulcus). Ventrolateral and dorsolateral frontal cortices were also activated, consistent with the memory load required during the task. Authors interpreted these results in the context of other mental transformation tasks, such as mental rotation in the visual domain, which are known to recruit the intraparietal sulcus region.

Kraemer et al. (2005) conducted the only fMRI study that showed activation in the primary auditory cortex. In this study, participants were asked to listen to excerpts of songs with

lyrics and instrumentals with no lyrics. Each piece of music was pre-rated by subjects as either familiar or unknown. Short sections of music (lasting for 2–5 s) were extracted at different points during the soundtrack and replaced with silent gaps. Participants were instructed to continue imagining the musical selection. Results revealed that imagining the continuation of familiar songs induced greater activation in auditory association areas than imagining the continuation of unknown songs (in both songs with lyrics and without lyrics). Moreover, when familiar songs contained no lyrics, cortical activity extended into the left primary auditory cortex. However, authors revealed that neural activation during lyrics were in the auditory association areas, whereas with instrumental music, neural activity extended to the primary auditory cortex.

4. Tactile imagery

Tactile imagery can be considered part of the haptic system, based on sensors in skin, muscles, tendons, and joints (Klatzky et al., 1991). Similar to other modalities, Craig & Rollman (1999) included the tactile sense as part of the working memory system, characterized by 3 different processing stages: retention up to 500 ms after stimulus offset; vivid recollections of uncategorized stimulus information, with interfering tasks affecting process until approximately 5 s after stimulus offset. The rehearsal mechanisms would last up to 30 seconds after stimulus offset (Burton & Sinclair, 2000).

Few fMRI studies were conducted to clarify the neural correlates of tactile imagery (Falgatter et al., 1997). Querleux et al. (1999) found that during the imagination of tactile stimulation, activation was mostly localized in the ipsilateral somato-sensory cortex (post-parietal gyrus – BA 1/2/3). During a period of tactile perception, there was a strong activation in the contra-lateral cortex. Yoo et al. (2003) demonstrated that the left primary (post-central gyrus - BA 1/2/3) and left secondary somatosensory areas (frontal operculum, area 43) were activated when participants imagined a tactile stimulation on the back of the right hand, relative to resting condition. Although the left primary and secondary somatosensory areas were modulated by the mental imagery of tactile sensation, a significant portion of the activation occurred solely during the actual perception. In Yoo et al. (2003), tactile imagery also selectively activated the inferior parietal lobule. Olivetti Belardinelli et al. (2004a) found activation in the inferior parietal lobule, but not in the primary or secondary somatosensory cortex, during the imagination of tactile properties of objects when verbally cued (e.g., to touch something grainy), as compared to the abstract condition. Yet, Olivetti Belardinelli et al. (2009) demonstrated that the primary somatosensory cortex (right parietal post-central gyrus - BA 2), as well as the right post-central gyrus (BA 5) were more activated in high-vivid participants compared to low-vivid participants. In other words, the level of vividness of tactile imagery can modulate the activation of primary somatosensory cortex. This study also revealed that the inferior occipital cortex (BA 18) was strongly activated in high-vivid participants.

5. Motor imagery

Motor (or kinaesthetic) imagery is the result of first-person kinaesthetic information processing, as people feel themselves executing a given action (Jeannerod, 1995). This experience is called internal imagery or first-person perspective, which is different from the

representation of the external imagery or third person perspective, in which information processing involves the visualization of spatial components of the perceived world (Ruby & Decety, 2001).

Various studies using fMRI have yielded contrasting results regarding the involvement of primary motor cortex during motor imagery. On one hand, the first studies revealed bilateral supplementary motor area and pre-motor activations, without an increase in signal intensity in the primary motor cortex (pre-central gyrus - BA 4) or somatosensory cortex during self-paced complex finger movements (Rao et al., 1993) or sequential finger opposition movements (Tyszka et al., 1994). However, using stance and locomotion (walking and running) imagery condition (Jahn et al., 2004), complex imagery actions (e.g., running) (Olivetti Belardinelli et al., 2004a), mental training-related changes on a finger-tapping task (Nyberg et al., 2006), and fingers or objects movements imagery task (Lorey et al., 2010), there was no reported activity in the primary motor cortex. Even when participants were instructed to imagine using a common tool, such as the brush for an action related to the hair, activity was observed in the pre-motor cortex, posterior part of the parietal cortex, and cerebellum, but not in the primary motor cortex (Higuchi et al., 2007). On the other hand, there was activity in the primary motor cortex more reduced for motor imagery than for actual performance (Fieldman et al., 1993). In particular, the primary motor cortex was activated during the mental execution of movements with either the left or right hand (Dechent et al., 2004; Lotze et al., 1999; Porro et al., 1996; Roth et al., 1996), when participants were instructed to imagine a right-hand self-paced button press sequence before (novel condition) and after (skilled condition) one week of intensive physical practice (Lacourse et al., 2005), when participants imagined dancing Tango after five training days (Sacco et al., 2006), when participants were instructed to imagine complex everyday movements (e.g., eating a meal, swimming) (Szameitat et al., 2007), or situations involving actions cued by appropriate motor phrases (e.g., to cut) (Tomasino et al., 2007). Sharma, Jones, Carpenter, & Baron (2008) likewise revealed that both the anterior and posterior primary motor area can be bilaterally activated when imaging a finger opposition sequence (2, 3, 4, 5; paced at 1 Hz). According to these authors, the role of the primary motor area and its subdivisions may be non-executive, perhaps related to spatial encoding. Recently, Olivetti Belardinelli et al. (2009) demonstrated that primary motor cortex can be activated in high-vivid participants rather than in low-vivid participants, but did not confirm the same activation when motor imagery vividness was regressed onto the BOLD signal, showing activation for only the left pre-central gyrus (BA 6), the right medial frontal gyrus (BA 6), and the inferior parietal lobule. Nevertheless, even considering the studies showing the activation of the primary motor area during motor imagery, it should be noted that the majority of these experiments did not employ electrophysiological monitoring to exclude muscle contractions during scanning. To exclude this possible confounding factor, Takashi et al. (2003) employed electromyographic monitoring within the scanner while participants performed sequential finger-tapping movements in response to visually presented number stimuli in either a movement or an imagery mode of performance. Results revealed that the movement condition activated the primary sensory and motor areas, parietal operculum, anterior cerebellum, caudal pre-motor areas, and area 5 that had mild-to-moderate imagery-related activity, whereas the motor imagery condition yielded the activation of the pre-central sulcus at the level of middle frontal gyrus (BA 6/44), and the posterior superior parietal cortex/pre-cuneus (BA 7), and bilateral cerebellum. Moreover, activity of the

superior pre-central sulcus and intra-parietal sulcus areas, predominantly on the left, was associated with the accuracy of the imagery task performance.

However, the fMRI approach based on “effective connectivity” between network components, defined as the influence of one neural system over another, clarified the issue of the primary motor cortex activation during motor imagery. In particular, Solodikin et al. (2004) demonstrated the connectivity between the supplementary motor area and the primary motor cortex during motor imagery. By using structural equation modelling to estimate the effective connectivity networks underlying motor execution, visual mental imagery, and kinesthetic mental imagery with specified regions of interests, Solodikin et al., (2004) showed that the inputs from the supplementary motor area and lateral-dorsal pre-motor cortex to the primary motor cortex had a suppressing effect during motor imagery. These results suggest a physiological mechanism encompassing the prevention of overt movements. Using Dynamic Causal Modeling, Kasess et al. (2008) confirmed that the activity of the primary motor cortex was heavily suppressed by the supplementary motor area during motor imagery, namely imagine pressing buttons on a small panel, first with the index finger, then the middle finger, and again with the index finger, as rapidly as possible. Then, by using the Granger Causality Mapping method, Chen et al. (2009) found forward and backward connectivity between the supplementary motor area and the contra-lateral primary motor cortex during both the left- and right-hand motor imagery (finger tapping sequences cued by pictures). Gao et al. (2011) extended these results revealing the influence of the brain asymmetry of right-handedness on effective connectivity networks: left dorsal pre-motor cortex, inferior parietal lobule, and superior parietal lobule were identified as causal sources in both motor imagery and motor execution.

6. Olfactory imagery

Olfactory mental images can be defined as short-term memory representations of olfactory events that give rise to the experience of smelling with the “mind’s nose” (Rinck et al., 2009). However, experimental evidence about the existence of olfactory imagery is controversial given that it is not clear whether an olfactory mental image is semantically or perceptually mediated, or whether it reflects the influence of explicit knowledge of olfactory principles rather than a specific mode of operation of odour imagery (Elmes, 1998; Herz, 2000). Using fMRI, Levy et al. (1999), and Henkin & Levy (2002) found a substantial overlap in the areas activated by real and imagined stimuli (ripe banana and peppermint), although all activations were reduced in the imagery condition. However, given the lack of anatomical details, it is not possible to draw reliable conclusions from these two studies. Later, Olivetti Belardinelli et al. (2004a) found activation in the left insula, but not in the primary olfactory area, when the olfactory imagery condition was contrasted with the abstract condition. The lack of activity in the primary olfactory cortex was also observed when high-vivid participants were contrasted with low-vivid participants (Olivetti Belardinelli et al., 2009). In Olivetti et. al.’s studies, the olfactory-specific modality activations likely were not found because of the difficulty in generating vivid images of smells, especially when they are verbally cued (Herz, 2000). This is confirmed by Zelano et al. (2009), who found that remembering nameable odorants was reflected in sustained activity in prefrontal language areas, and remembering unnameable odorants was reflected in sustained activity in primary olfactory cortex. In other words, only smells dissociated from their verbal label were eligible to activate the primary olfactory cortex.

In the past few years, the role of the piriform cortex during olfactory imagery was reconsidered according to two points of view: retrieval-related processes and expertise. First, it was surmised that piriform cortex activation reflects retrieval-related olfactory “imagery” processes (Elmes, 1998; Bensafi et al., 2003). Because odour imagery was shown to elicit sniffing (Bensafi et al., 2003), which in turn can elicit activation in piriform cortex (Sobel et al., 1998), it is possible that the piriform activity indicates odour imagery associated with sniffing. In an fMRI study, Bensafi et al. (2007) evoked hedonic-specific activity in piriform cortex by asking participants to sniff during the perception and imagination of a pleasant odour (strawberry) and an unpleasant odour (rotten eggs). In particular, activity induced by imagining odours mimicked that induced by perceiving real odours, and for both real and imagined odours, unpleasant stimuli induced greater activity than pleasant stimuli in the left frontal portion of piriform cortex and left insula. Regarding the expertise issue, it was also surmised that experience with odours plays a key role for the reorganization of brain regions involved in olfactory imagery. In fact, Plailly et al. (2011) revealed that expertise plays a key role: olfactory imagery activated the primary olfactory (piriform) cortex, as well as the orbitofrontal cortex, and the hippocampus during the creation of mental images of odours by professional perfumers.

7. Gustatory imagery

Gustatory imagery refers to the ability to generate mental images of tastes. Although gustatory imagery is involved in food craving, or the “irresistible urge to consume” (Tiggemann & Kemps, 2005), which in turn may have implications for clinical and non-clinical population, relatively little experimental research has been devoted to this imagery system. It is also uncertain whether proper gustatory mental imagery can be evoked, and to what extent images of tastes activate the primary gustatory cortex. In an fMRI study, Kobayashi et al. (2004) instructed their participants to perceive (water stimuli) and imagine several tastes (grapefruit, candy, pudding, coffee, lemon, banana, beer, sugar). Images were verbally cued by written words, by spoken language, and by using pictures. In general, results revealed that gustatory imagery can activate the primary gustatory cortex (anterior insula/frontal operculum), especially the left side, sharing common parts of neural substrates with gustatory perception. Authors also clarified that the middle and superior frontal gyri were not activated by gustatory perception, but they participated in the generation of gustatory images, plausibly mediating the top-down control of retrieving gustatory information from the storage of long-term memories. The activation of the anterior insula and the middle frontal gyri during gustatory imagery (the spicy taste, the tart taste, etc) were confirmed also by Olivetti Belardinelli et al. (2004a) relative to an abstract condition, and by Olivetti Belardinelli et al. (2009) according to the level of vividness of participants. Finally, Kikuki et al. (2005) revealed that when participants concentrated on pickled plums (umeboshi), a traditional Japanese food with a strong and sour taste, activations were observed weakly in the right insula, but more strongly in the bilateral opercula, the bilateral orbitofrontal cortices, and the left Broca’s area.

8. Proprioceptive imagery

Proprioceptive processing is part of the haptic system. In particular, proprioceptive imagery involves the ability to generate organic images based on body sensations, such as the

sensations of hungry, thirsty, cold, drunkenness, etc. Very few fMRI studies were devoted to proprioceptive imagery. Olivetti Belardinelli et al. (2004a) did not show any activation of the primary somatosensory cortex during proprioceptive imagery, whereas Olivetti Belardinelli et al. (2009) revealed that high vivid participants activated the right post-central gyrus (BA 2/3) during proprioceptive imagery in comparison with low-vivid participants.

9. Conclusions

Compared to previous neuroimaging techniques, fMRI technology has generally improved our understanding of neural networks involved in mental imagery in all sensory modalities. The higher sensitivity of fMRI allowed researchers to better differentiate between primary and secondary sensory cortices, whereas the extreme flexibility of scanning procedures allowed the implementation of different imagery paradigms, which likewise has implications for the imagery debate issue.

Several, several conclusions can be made from the fMRI literature reviewed above. First, the involvement of the primary sensory cortices varies according to the imagery modality investigated, and may be modulated by different factors, such as the individual differences in generating mental images or expertise, tasks, types of paradigms, or analyses employed. Second, the activation of the secondary sensory cortices in all imagery modalities is more consistent, as well as the recruitment of pre-frontal areas or associative cortices, the former plausibly participating in the top-down processes which are executed for retrieving information from long-term memory, the latter facilitating supra-modal processing of sensory information. This picture is partially in contrast with the perceptual approach, which assumes that mental images correspond with percepts and events also in terms of both mechanisms and processes used. It also supports the propositional approach, which assumes an amodal format for all types of mental images. Indeed, when generating mental images, the human brain seems to rely mostly on secondary sensory cortices rather than primary ones, clearly indicating that imagery and perception rely on overlapping but dissociable neural networks.

Looking separately at the relevant fMRI literature on imagery modalities, more detailed information can be obtained. First, fMRI showed that under specific conditions, visual imagery corresponds to the isolated activation of visual cortical areas, including the primary one, with concurrent deactivation of irrelevant sensory processing (Amedi et al., 2005). However, the overlap between visual imagery and visual perception is more consistent in the frontal and temporal cortices (Ganis et al., 2004) or ventro-temporal cortex (Reddy et al., 2010), rather than in the occipital cortex. The insights for visual imagery cannot be simply generalized, given the different sensory characteristics of percepts, as well as the roles that each imagery system can play in the cognitive system.

Indeed, fMRI literature showed that auditory verbal imagery relies mostly on the secondary auditory cortex, left inferior frontal cortex, supplementary motor area, and inferior parietal areas, rather than the primary auditory cortex. The former regions were found to be involved in the verbal perception domain: particularly, left pre-frontal areas mediate phonological recoding (Thierry et al., 1999), whereas the supplementary motor area is important for silent articulation or inner speech, and posterior superior temporal gyrus or temporo-parietal junction are involved in the acoustic-phonetic feature-based processing (Scott & Johnsrude, 2003).

Moreover, auditory imagery of environmental sounds never yielded activation in the primary auditory cortex. Even when the sparse temporal sampling technique was used to

ensure that the acoustic scanner noise did not lead to interferences with the auditory perception and imagery conditions, the primary auditory cortex was not activated (Bunzeck et al., 2005). This pattern of results shows that when imaging environmental sounds the top-down process is initiated mostly by the inferior frontal gyrus and insular regions, and manages to activate only secondary auditory areas.

Still, the fMRI literature on musical imagery, with the exception of Kraemer et al. (2005), showed no activation of the primary auditory cortex, even when enrolling musicians. Given the pattern of activation yielded by musical imagery, an associative network independent of primary sensory-motor and auditory activity is likely representing the cortical elements most intimately linked to music production. In addition, considering that both amateurs and professional musicians did not report any activation in the primary auditory cortex, and that motor areas were not recruited, either, during musical imagery involving mental performances, it is highly probable that these areas become tightly coupled with executed activities during musical training. Finally, given that musical imagery in professional musicians revealed more anterior cerebellar activations, it is possible to conclude that musical imagery involves the recruitment of stored movement programs of sequential finger movements (Lotze et al., 2003).

The extent to which the primary motor cortex is involved in motor imagery remains unclear. However, recent fMRI studies have highlighted the importance of the supplementary motor area, which seems to be involved in suppressing the activity of the primary motor cortex, and consequently, movements that are not intended to be performed. This would mean that motor imagery and motor execution do not rely on the same neural network.

Regarding olfactory imagery, fMRI results are in line with behavioral findings: if images of smells are cued by verbal labels it is hard to detect the activation of the primary olfactory cortex. On the contrary, if odors are perceptually encoded, it is possible to find activation in the piriform cortex when generating images of smells. However, the activity in the olfactory primary cortex was found to be modulated by the hedonic pattern of stimuli to be imagined, and by expertise in generating or using olfactory images. This means that olfactory imagery may activate olfactory areas under specific conditions, basically when people really evoke images of smells.

The literature on gustatory, tactile, and proprioceptive imagery is more consistent. All three of these modalities seem to rely on the primary sensory cortices. Nevertheless, given the scarcity of studies carried out on these imagery systems, especially on the proprioceptive imagery, any conclusion would be premature.

In conclusion, fMRI technique has helped to clarify the neural circuits of mental imagery, but a lot of work needs to be still done. For example, the role of certain cortical areas remains unclear, as does the connectivity among cortices in mental imagery. Research is trying to clarify this issue in respect to the motor imagery modality, but it should also be addressed in respect to the others. It is also important to explore the common cortical networks involved in all imagery modalities to clarify the extent to which mental imagery relies on non-sensory cortices. Indirectly, this information would contribute to improve our understanding of the imagery debate, as having access to the common areas shared by all imagery modalities provides an understanding of the extent to which imagery involves propositional encoding. Currently, only Olivetti Belardinelli et al. (2001, 2004b) have attempted to investigate this issue. Though there has been some difference in terms of anatomical extension, results revealed that the generation of images in all sensory modalities activated the left inferior temporal cortex (including the left fusiform gyrus) and the bilateral inferior parietal lobule.

The left inferior temporal area has been associated with semantic processing (Thompson-Schill et al., 1999), and visual mental imagery (D'Esposito et al., 1997), whereas the inferior parietal lobule was linked to supra-modal transformation of information (Jordan et al., 2001). In light of the imagery debate, these results showed that the generation of mental imagery in different sensory modalities may involve visual appearance and to some extent semantic processing. Afterwards, Palmiero et al. (2009) found that, relative to the resting condition, all imagery modalities showed activity in the pre-central gyri (BA 6), likely involving pre-motor feed-forward control during imagery generation. However, it is important to develop techniques that allow researchers to be sure that images are really generated by participants in the scan. Indeed, in most studies, it is assumed that participants generated mental images, resulting in cortical activations that may reflect the lack of generation of images. It is also essential to better differentiate between pure imagery-based representations and memory-based representations, which may engage different neural networks. Finally, the inter-modal issue should also be addressed. Thus, given the above literature, it seems that mental images are mapped on the human brain according to the request of the psychological system, with implications for both thinking and performance.

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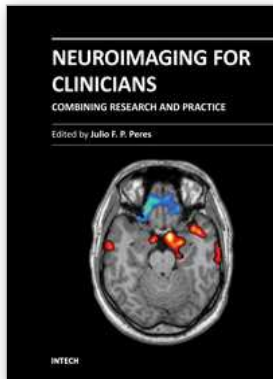
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Neuroimaging for clinicians sourced 19 chapters from some of the world's top brain-imaging researchers and clinicians to provide a timely review of the state of the art in neuroimaging, covering radiology, neurology, psychiatry, psychology, and geriatrics. Contributors from China, Brazil, France, Germany, Italy, Japan, Macedonia, Poland, Spain, South Africa, and the United States of America have collaborated enthusiastically and efficiently to create this reader-friendly but comprehensive work covering the diagnosis, pathophysiology, and effective treatment of several common health conditions, with many explanatory figures, tables and boxes to enhance legibility and make the book clinically useful. Countless hours have gone into writing these chapters, and our profound appreciation is in order for their consistent advice on the use of neuroimaging in diagnostic work-ups for conditions such as acute stroke, cell biology, ciliopathies, cognitive integration, dementia and other amnesic disorders, Post-Traumatic Stress Disorder, and many more

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