Review

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Shared Neural Mechanisms of Visual Perception and Imagery

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For decades, the extent to which visual imagery relies on the same neural mechanisms as visual perception has been a topic of debate. Here, we review recent neuroimaging studies comparing these two forms of visual experience. Their results suggest that there is a large overlap in neural processing during perception and imagery: neural representations of imagined and perceived stimuli are similar in the visual, parietal, and frontal cortex. Furthermore, perception and imagery seem to rely on similar top-down connectivity. The most prominent difference is the absence of bottom-up processing during imagery. These findings fit well with the idea that imagery and perception rely on similar emulation or prediction processes.

Externally and Internally Generated Visual Experience

A large part of our sensory experience is visual. When walking down the street, we are bombarded with different colors, shapes, and textures. Also, when thinking about future or past events, most people tend to experience a rapid stream of detailed images [1]. Visual experience can be triggered externally, by events in the outside world that change the light that falls unto our retinas, such as during **perception** (see Glossary), or internally, by information from memory via a process known as **mental imagery** (see Box 1 on the relationship between imagery and working memory). Generally, these are seen as two distinct phenomena. However, they are phenomenologically similar, which can sometimes lead us to question whether we really saw something or whether it was just our imagination.

The question of to what extent visual imagery relies on the same neural mechanisms as perception has been a topic of debate for decades. Originally, the debate was centered around the question of whether imagery, like perception, relies on depictive, picture-like representations or on symbolic, language-like representations [2–5]. Due to imagery's inherently private nature, for a long time it was impossible to address this question. Neuroimaging studies on the involvement of the primary visual cortex during imagery have now largely resolved this debate in favor of the depictive view [6]. However, a broader perspective, addressing the involvement and interaction of brain regions beyond the primary visual cortex, has been missing.

The current review explores to what extent externally and internally generated visual experiences rely on similar neural mechanisms. We discuss the findings with respect to visual areas, which are important in the depictivism-versus-symbolism debate, but we also focus on the involvement of parietal and frontal areas. Next, we focus on the temporal dynamics of neural processing during both forms of visual experience. After that, we discuss the overlap in directional connectivity between perception and imagery. We finish by concluding that perception and imagery are in fact highly similar and we discuss the issues and questions raised by this conclusion.

Highlights

Imagery and perception generate similar neural representations for the same content in occipital, parietal, and frontal brain areas. There is more overlap in more high-level visual areas. During both perception and imagery, the parietal cortex is involved in spatial and feature-based attention, while the frontal cortex represents task-relevant stimulus structure.

There is similar top-down connectivity between frontoparietal and visual areas during perception and imagery. Furthermore, imagery overlaps with specific time points during perception, corresponding with high-level processing. By contrast, the early bottom-up processing characterizing perception is absent during imagery.

These findings are in line with emulation and predictive coding theories. Together, they suggest that imagery and perception rely on partly the same top-down emulation/prediction processes.

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Trends in Cognitive Sciences, Month Year, Vol. xx, No. yy https://doi.org/1

https://doi.org/10.1016/j.tics.2019.02.004 1 © 2019 Elsevier Ltd. All rights reserved.

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Neural Representations

Most processing during perception occurs in the occipital and temporal lobes. In this part of the cortex, also referred to as the visual cortex, basic visual features are detected and merged into coherent percepts. The subjective overlap between perception and imagery is caused by the fact that they lead to the experience of similar visual features: perceiving and imagining a cat both give rise to an experience of pointy ears, whiskers, and almond-shaped eyes. In accordance with this intuition, early neuroimaging studies showed that imagery and perception are associated with similar category-specific responses in the high-level occipitotemporal cortex [7,8].

Studies using more sensitive **multivariate pattern analysis (MVPA)** showed that perception and imagery rely on similar neural representations throughout the ventral visual stream [8–13]. There also appears to be a gradient in this overlap, with more similar representations in more high-level visual areas [14] (Figure 1A). The overlap in low-level visual areas depends on the required visual detail of the task [15] and imagery vividness [10,14,16], such that people who experience more vivid mental imagery show more overlap with perception in retinotopic visual areas (Figure 1B and Box 2).

To convincingly make the point that mental imagery, like perception, uses depictive representations [4], it is not enough to show that imagery activates low-level visual areas in a similar way to perception since the variation in activation between the stimuli that is picked up could be caused by other factors such as attention, reward expectation, coherent shape perception, auditory stimulation, or overlap in semantic representations [13]. To exclude these alternative explanations, the activation in the early visual cortex during imagery should represent low-level features. It was shown that activity is retinotopically organized during imagery [17,18] and that encoding models based on low-level features derived from perception can successfully identify imagined stimuli [13]. Furthermore, behavioral priming effects of imagery on perception (discussed in more detail in the section 'Function of the Overlap') are location and orientation specific [19,20], further suggesting that imagery activates low-level perceptual features.

Neuropsychological evidence regarding the effects of specific cortical damage on imagery and perception has been more mixed. For example, one patient experienced both perceptual and imagery deficits after extensive bilateral damage to the temporal poles. However, after the

Box 1. Visual Imagery and Working Memory

It has been suggested that imagery and working memory are one and the same [93]. There is overlap in neural representations between imagined stimuli and stimuli held in working memory [10,28]. Furthermore, imagery strength correlates positively with visual working memory performance [94,95]. By contrast, a recent study showed that an individual with aphantasia – the inability to generate mental images – was still able to perform a number of working memory tasks [96]. Working memory seems to encompass other cognitive processes besides the generation of mental images, such as the recoding of visual information into appropriate task responses. Furthermore, imagery is not restricted to working memory, but plays a role in other cognitive processes such as thinking about the future. The exact overlap between mental imagery and working memory remains unclear. In this review we discuss working memory studies as evidence converging to imagery research if they included a clear visual imagery aspect.

Because of the strong relationship between the two, the large neural overlap between perception and imagery reported in this review is in line with the sensory recruitment model of working memory. This theory proposes that the same cortical regions that support perceptual processing of a stimulus are recruited to maintain that information in working memory [97–99]. One argument that has been used against this theory is that working memory content is often represented in the frontoparietal cortex [100]. However, these observations would be in accordance with the sensory recruitment model if those areas are also involved in perceptual processing. The overlap between imagery and perception in frontoparietal areas reported here supports this idea. Future studies should further investigate the differences and similarities between working memory and imagery to fully understand the implications of the overlap between imagery and perception for theories of working memory.

Glossary

Dynamic causal modeling (DCM): effective connectivity estimation technique. Per brain region, the expected signal is predicted based on the hypothesized connectivity profile. The model is then inverted to find the parameters that give the best tradeoff between model fit and complexity. Parameters are interpreted as being significant if the

parameter exceeds zero with 95% confidence. Mental imagery: visual experience where the content does not directly

where the content does not directly relate to any afferent stimulus but is derived from (working) memory. **Multivariate pattern analysis**

(MVPA): a form of decoding

whereby a classifier is trained to dissociate stimuli based on the pattern of activation across multiple voxels (fMRI) or sensors (EEG/MEG). If the classifier can classify a test set above chance, it can be concluded that the pattern of activation represented the stimulus. If it is possible to use a classifier trained in one condition to classify neural activity in another condition, this suggests that similar neural representations are activated in the two conditions.

Perception: visual experience where the content reflects and is caused by an afferent physical stimulus.

Temporal generalization: by training a classifier on the brain activity at one time point, and then testing this classifier on other time points, the temporal stability of neural processing can be inferred. This is usually shown in a testing-time-bytraining-time generalization matrix (e. g., Figure 3).

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Figure 1. Overlap in Neural Representations Between Perception and Imagery Estimated Using fMRI. (A) The overlap in neural representations of imagined and perceived stimuli was assessed using cross-decoding in four different regions of interest along the ventral visual stream. The results indicate that there is more overlap between imagery and perception in high-level, object-selective areas than in low-level, retinotopic areas. Adapted from [14]. (B) The overlap in retinotopic areas was correlated with participants' imagery vividness scores. The positive correlation shows that people reporting more vivid imagery have higher overlap with perception in these areas. Adapted from [14]. (C) The neural overlap between imagined and perceived stimuli was assessed across the whole brain. Red/yellow indicates significant overlap and blue/green indicates modulation of the overlap by imagery vividness. There was significant overlap in visual, parietal, and frontal areas but only the overlap in visual areas is modulated by imagery vividness. Adapted from [25].

perceptual deficits disappeared, the imagery impairment remained [21]. Furthermore, whereas most patients with unilateral visual field deficits are worse at imagining stimuli on the side of their visual field loss, some patients do not show this associated imagery defect [22]. These findings suggest a dissociation between imagery and perception in the ventral visual stream. However, it is difficult to draw firm conclusions from these studies because the damage is heterogeneous between patients and rarely concerns only one specific brain area. In the case of impaired imagery with intact perception, it is possible that brain areas involved in the generation of mental images were also damaged. Moreover, in the case of intact imagery with impaired perception, the damage might have been specific to the input layer of the visual cortex, disrupting bottom-up signals while keeping top-down signals intact [23,24].

Most of the studies mentioned above focused on the ventral visual stream. However, a recent study showed that imagery and perception also activate similar neural representations in frontoparietal areas [25] (Figure 1C). Other studies have shown stimulus information in the

Box 2. Vividness of Visual Imagery and the Visual Cortex

In 1880, Francis Galton observed that people vary in the degree to which they can generate vivid mental images [101]. In the past few years, a lot of attention has been given to the case of aphantasia, a term that describes people who completely lack the ability to form mental images [88]. The neural mechanisms of aphantasia remain largely unknown. However, many studies have investigated the neural correlates of imagery vividness.

The activation in visual areas during imagery and especially the overlap of this activation with perception correlate positively with self-reported measures of imagery vividness [10,14,16,25,102] (for more details, see main text). Furthermore, imagery vividness modulates top-down connectivity to early visual areas [74] (see Figure 4 in main text). Finally, a recent study [20] reported that the size of V1 was negatively correlated with imagery strength and positively with imagery precision. Taking these findings together, the visual cortex seems to be essential in determining the vividness of internally generated visual experience. This fits well with the idea that this part of the brain is involved in retinotopically representing visual information in a detailed manner during both forms of visual experience.

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frontoparietal cortex during perception [26,27] and working memory [28,29], indicating that these areas contain content representations during both forms of visual experience. As these areas are not likely to represent exactly the same information, the question arises of what the functions of these different neural representations are for visual experience.

The parietal cortex has been known to play an important role in spatial and feature-based attention in perception [30]. One study showed that also during imagery, focusing on different features of an imagined stimulus increased the activity in the intraparietal sulcus (IPS) [31]. Furthermore, a recent meta-analysis showed that the parietal cortex is most consistently activated in imagery tasks requiring spatial comparisons [32]. Moreover, TMS above the intraparietal sulcus leads to decreased performance during spatial comparisons between mental images [33]. Together, these results suggest that the parietal cortex is specifically involved in spatial and feature-based attention during both perception and imagery. However, decoding studies have revealed stimulus representations in the parietal cortex during perception, imagery, and working memory [25,34]. An explanation for these findings is that the parietal cortex encodes which parts of imagined and perceived stimuli are salient [35,36], which can then be used for top-down attention (Figure 2, Key Figure).

The frontal cortex has also been implied in selective attention during perception as well as imagery [37,38]. At the same time, stimulus identity can be decoded from frontal areas during working memory [34] as well as perception [27,39,40]. Furthermore, there is some evidence that the neural representations of imagined and perceived stimuli in frontal areas are similar [9,25]. Representations in the frontal cortex seem to be strongly influenced by task demands [27,41,42]. There is little overlap in stimulus representations between tasks [41] and decoding of the task identity leads to much higher accuracies than decoding of the stimulus [27,41,42]. Therefore, the frontal cortex might be involved in representing the task-relevant structure of the

Key Figure

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Figure 2. Neural representations of imagined and perceived stimuli show overlap in ventral visual areas as well as parietal and frontal areas. During both perception and imagery, visual areas represent the visual features of the sensory experience. Parietal areas encode the saliency, which is used for top-down spatial and featured-based attention during perception as well as during imagery. Representations in frontal areas are more task than content dependent, indicating that frontal areas represent task-relevant structure during both imagery and perception. There seems to be a large overlap in top-down mechanisms between imagery and perception whereas the bottom-up processing characteristic of perception is absent during imagery.

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stimuli during both perception and imagery (Figure 2). Future research should further explore neural representations of imagined and perceived stimuli during different tasks to disentangle their function in generating visual experience.

Temporal Dynamics

How activation progresses through the brain during perception has been studied extensively for many years [43–45]. After light hits the retina, activation reaches the cortex after approximately 50 ms [46]. Then, signals travel towards more anterior visual areas over time, where high-level category representations are activated at around 150 ms [47–50]. Recurrent processing is assumed to then further sharpen the visual representation [51–53]. Finally, depending on the exact task, after about 300 ms activation reaches frontoparietal areas [54–56]. In contrast to perception, imagery is caused by internal signals from (working) memory. To what extent do imagery and perception rely on similar temporal dynamics?

The dynamics of neural processing can be investigated by looking at the **temporal generalization** of neural representations, which is inferred by training a classifier on one time point and testing it on other time points, usually using whole-brain EEG or MEG signals [57]. An example of such a temporal generalization matrix during perception is shown in Figure 3A. A diagonal pattern indicates that the classifier can generalize only to neighboring time points, which means that the neural representation changes rapidly over time. By contrast, off-diagonal above-chance accuracy indicates that the representation is stable over time or becomes reactivated at different times [57]. Temporal generalization during perception generally shows a combination of diagonal and off-diagonal decoding, indicating sequential as well as sustained processing [47,48,58,59] (Figure 3A).

Recently, the temporal generalization during imagery was investigated [60] (Figure 3B). The onset of imagery is defined as the onset of a cue that instructs the generation of a mental image. In contrast to perception, during imagery there was broad off-diagonal generalization from the onset. This is in line with findings on representational stability during working memory [61,62]. This could indicate that during imagery there are no clear distinct processing stages, but instead the entire visual representation becomes activated at once [57]. However, it is also



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Figure 3. Temporal Dynamics During Perception and Imagery. Temporal generalization matrices: a classifier is trained on a specific time point and then tested on all other time points, providing a measure of how well neural representations at certain time points generalize. The y-axis represents the training time and the x-axis represents the testing time. The colors show decoding accuracy. (A) Temporal generalization of MEG signals during object perception. The ellipse shows diagonal generalization, indicating rapidly changing representations. The rectangle indicates off-diagonal generalization, indicating a stable representation around that training time. Adapted from [52]. (B) Temporal generalization of MEG signals during imagery of faces and houses. The square pattern indicates broad off-diagonal generalization. Adapted from [54]. (C) Temporal generalization of MEG signals between perception and imagery. A classifier was trained at different time points during imagery and tested at different time points during perception. Perceptual processing around 130 ms and after 300 ms generalized to imagery. Adapted from [54].



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possible that this strong off-diagonal generalization is caused by jitter in the onset between different trials [63]. Since these analyses require averaging over trials per time point, any time-locked process will be obscured by large timing differences between trials. At this point, it is impossible to confidently rule out this explanation and more research is needed to fully uncover the temporal dynamics during imagery.

Temporal overlap between perception and imagery was also investigated (Figure 3C). The results indicate that imagery specifically overlaps with perceptual processing around 150 ms and after 300 ms. This overlap around 150 ms found with MEG is in line with the robust fMRI findings on overlap in category representations during perception and imagery [7,8,50]. Furthermore, the overlap after 300 ms fits well with the reported overlap in frontoparietal areas [25,54–56]. The absence of early overlap shows that the earliest processing steps of perception do not generalize to imagery. This could be because low-level representations first have to be sharpened by feedback before they are in a format that can be accessed by top-down imagery. Another possibility is that the activation of early perceptual representations during imagery is more transient and variable over time than the activation of late perceptual representations [60].

Furthermore, it should be noted that temporal generalization methods generally rely on scalp EEG and MEG. These methods are well known for their spatial ambiguity: the same scalp distribution could be caused by different underlying neural sources. This makes it hard to draw firm conclusions about overlap in neural representations over time and between conditions. However, recently it has been shown that within-participant decoding, the method underlying temporal generalization, is potentially more sensitive to subtle differences in underlying spatial patterns [64,65]. Furthermore, the temporal generalization results reported here are largely in line with electrophysiological and fMRI studies. To conclude, more research is needed to fully understand the temporal dynamics underlying perception and imagery, but the studies presented here provide interesting first ideas.

Directional Connectivity

The development of a detailed understanding of the overlap in neural mechanisms during perception and imagery requires going beyond neural representations to interactions between different neural populations. In one study, **dynamic causal modeling (DCM)** [66] on fMRI data revealed that the category-specific activation in the occipitotemporal cortex could best be explained by bottom-up connections from the inferior occipital cortex during perception and by top-down connections from the frontal cortex during imagery [67]. A more recent high-density EEG study found stronger bottom-up coupling between the inferior occipital cortex and the superior parietal lobe during perception compared with imagery [68].

These studies are in line with the traditional notion of perception as a purely bottom-up process and imagery as a top-down process [4]. However, bottom-up processing could theoretically also be involved in imagery. For example, early visual areas might first be activated in a topdown manner, followed by bottom-up propagation of activity. Furthermore, there exists a large body of research showing that top-down processes also play an important role in perception [69–71]. Using DCM on fMRI data [72,73], a recent study showed that during both imagery and perception there is a strong increase in top-down coupling between the inferior frontal gyrus (IFG) and visual cortex compared with baseline [74] (Figure 4). This increase was much stronger during imagery than during perception. Furthermore, there is an increase in top-down coupling between the parietal cortex and visual cortex during perception. This connection is also

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Figure 4. Effective Connectivity During Perception and Imagery. The results were obtained using dynamic causal modelling (DCM) of fMRI data during perception and imagery on four regions of interest (ROIs): early visual cortex (EV), high-level visual cortex/fusiform gyrus (FG), intraparietal sulcus (IPS), and inferior frontal gyrus (IFG). The arrows reflect connections that were significantly modulated on the group level by the different factors. The widths of the arrows indicate the strength of the influence and light arrows reflect inhibitory connections while dark arrows reflect excitatory connections. Both imagery and perception rely on top-down recruitment of visual areas. The vividness of visual imagery correlates with the strength of top-down recruitment of early visual areas. Furthermore, whereas perception is accompanied by bottom-up connectivity, this is absent during imagery. Adapted from [74].

modulated by imagery vividness. In line with previous studies, the increase in bottom-up connectivity characteristic for perception was absent during imagery [74].

Top-down coupling between the IFG and visual cortex has been proposed to be important for selective attention in the presence of a visual stimulus [75,76] as well as for the maintenance of visual information in the absence of a stimulus [37,77]. One hypothesis is that this coupling reflects the transformation from more abstract stimulus information into more sensory stimulus representations. During perception, this would result in an attentional template in the visual cortex that enhances the response to task-relevant information. During imagery, this coupling is stronger, which might lead to increased activation of these sensory representations and therefore give rise to internally generated visual experience in the absence of bottom-up input. Future studies should investigate which factors modulate the strength of this coupling. Furthermore, in line with the idea that the IPS is involved in spatial and feature-based attention during both forms of visual experience, top-down coupling between the IPS and visual cortex was found during perception [67,74] and imagery [67,68] and was modulated by imagery vividness [74]. It should be noted that the results of these directional connectivity studies rely to some extent on the assumptions made by the specific models. More studies with different methodologies are needed to ensure the robustness of the results.

Function of the Overlap

The large overlap in neural mechanisms between perception and imagery reported here raises the question of to what extent this overlap has functional relevance. One hypothesis is that the overlap does not have a function, but that it is just more efficient to use the same neural



mechanisms for similar processes. Alternatively, the large overlap between imagery and perception might reflect an underlying cognitive function.

This is proposed in the emulation theory of mental imagery [78,79]. This theory posits that mental imagery is a way to simulate what the world would look like in different situations. The emulation part of the theory indicates that it concerns a form of simulation whereby the processes involved in the simulated event, and not only the event itself, are also mimicked [79]. In the case of imagery, this means that not only is the content/stimulus simulated but also the processes involved in the perception of that content are mimicked. This is in line with the large overlap in sensory representations during imagery and perception. In other words, emulation theory states that mental imagery provides a way to generate explicit predictions about sensory input given different situations [78,79]. In the context of artificial intelligence, it has been shown that the emulation of sensory events can be used to inform future actions [80].

This idea could also explain behavioral results on the influence of imagery on conscious perception during binocular rivalry. Binocular rivalry is the phenomenon that when a different image is presented to each eye, only one of them is consciously perceived while the other one is suppressed [81]. A series of studies have shown that when one of the two images is imagined prior to the rivalry display, this image has a higher probability of becoming dominant [19,82,83]. In other words, imagery can prime conscious perception. These results can be explained by the idea that imagery simulates perception. In this setup, prior imagery would then preactivate the perceptual representation of one image, leading to an enhanced response for that image on congruent sensory input [84]. In line with this idea, it has been shown that imagining a face prior to perceiving a face leads to an enhanced face-specific ERP response [85].

The emulation theory of imagery also states that perception is in part emulation: 'The role played by sensation (bottom-up sensory input) is to constrain the configuration and evolution of this (emulated) representation. In motto form, perception is a controlled hallucination process' ([78], see p. 393). This idea fits well with predictive coding accounts of perception, stating that perception arises by comparing top-down predictions with bottom-up sensory input [51,86]. The high overlap between imagery and perception for top-down mechanisms reported in this review (high-level representations, top-down connectivity) would then suggest that imagery and perception processes.

However, the case of aphantasia, a condition describing people who are unable to form mental images (Box 2), argues against such a strong interpretation. People with aphantasia do not report any perceptual deficits, suggesting no issues with simulation *per se*. By contrast, they do lack the imagery priming reported above [87]. The majority of people with aphantasia report involuntary imagery; for example, during dreams [88]. This suggests a dissociation between the involuntary, automatic simulation underlying perception and dreaming and the deliberate, conscious simulation that underlies imagery [89,90]. However, the large overlap in the top-down mechanisms of perception and imagery presented here suggests that they rely at least on partly similar processes. Future research should focus on further characterization of the overlap and dissociation between these two forms of simulation by utilizing individual differences in imagery ability.

Concluding Remarks and Future Perspectives

Taking these findings together, there is convincing evidence that perception and imagery share a variety of neural mechanisms. Neural representations of perceived and imagined stimuli are similar in the visual, parietal, and frontal cortex. Visual features are represented in the ventral visual stream during both forms of visual experience. The overlap between perception and

Outstanding Questions

Imagery and perception activate similar low-level representations in low-level visual cortex. However, phenomenologically, imagery has less visual detail than perception. How are representations of perceived and imagined stimuli in low-level visual areas different?

Activation in the visual cortex during imagery correlates with imagery vividness (Box 1). However, this activation is the result of deliberate top-down imagery generation processes. How can the neural mechanisms underlying this generative process explain the large individual differences in imagery ability?

Perception and imagery activate similar neural representations in visual, parietal, and frontal areas. What is the exact function of these different representations and do they serve different functions during imagery and perception?

Temporal jitter in the onset of imagery could obscure fine-grained temporal dynamics in the neural processing during imagery. Resolution of this issue could reveal whether the direction of activation within visual areas is reversed during imagery compared with perception.

The large overlap between visual perception and imagery begs the question of how the brain knows what is real and what is imagined. One possibility is that the neural populations activated by bottom-up input are different from those activated by top-down processes. Another possibility is that there is a separate mechanism that infers whether a neural representation is caused by external or internal signals.

To what extent do imagery from longterm memory and imagery from shortterm memory rely on similar neural mechanisms? Can differences be fully explained by differences in imagery vividness?

What is the functional relationship between imagery and perception? Do they rely on similar emulation/prediction processes? If so, how do these functionally interact in daily life when imagery and perception are not so clearly separated?

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imagery is higher in more high-level visual areas, but there is significant overlap even in V1. Moreover, the overlap in early visual areas is modulated by imagery vividness. Together with behavioral evidence, this suggests that imagery simulates perceptual events, thereby explicitly predicting the sensory effects of different situations.

Furthermore, the parietal cortex seems to be involved in spatial and feature-based attention during both forms of visual experience. By contrast, frontal areas represent task-relevant stimulus structure in a similar way during perception and imagery. The temporal dynamics during imagery and perception seem to be different, but it is hard to draw firm conclusions due to the temporal uncertainty during imagery. Finally, in contrast to perception, there is no clear bottom-up connectivity during imagery. However, top-down coupling from the frontal cortex to visual areas is present during both perception and imagery. These findings are in line with the idea that imagery and perception rely on similar top-down simulation/prediction processes. The fact that it is possible to have imagery deficits without associated perceptual issues indicates that the simulation processes underlying perception and imagery are not exactly the same.

These findings converge to the idea that our visual experience, regardless of whether it is triggered by external events or internally generated, relies for a large part on a simulation process. This process is initiated automatically during perception and can be utilized voluntarily during imagery. This idea fits well with predictive processing accounts of perception [51,91]. The findings mentioned here also indicate an anterior-to-posterior hierarchy of abstraction, with more abstract task rules represented frontally and concrete sensory details represented in posterior visual areas. Future research should explore the function of each of these representations within this simulation process. It should be investigated what kind of information is communicated between these areas and to what extent this is similar during imagery and perception.

One question that arises with respect to the large overlap between imagery and perception is how the brain knows what is really out there and what is imagined. If only the top-down mechanisms overlap between perception and imagery, this problem might easily be solved by checking for corresponding bottom-up input [24]. However, if top-down signals activate the same neuronal populations as bottom-up signals do, dissociation between real and imaginary sensory content becomes more difficult. To explore this issue further, future research could investigate how neural representations change when people are aware that what they see is not there, such as during voluntary imagery, versus when they are not aware, such as during hallucinations. Uncovering the mechanism responsible for dissociating real and imagined sensory experience will also have important clinical implications [92].

In conclusion, there is a large body of research showing that perception and imagery rely on similar neural mechanisms. Still, a number of major questions remain unsolved (see Outstanding Questions). Future research should explore to what extent these conclusions extend to other modalities (Box 3). Furthermore, a relatively unexplored issue is which neural mechanism dissociates sensory activity during imagery and perception and ensures that we generally do

Box 3. Overlap in Other Sensory Modalities

A question that arises is to what extent the overlap between imagery and perception reported here for visual experience generalizes to other modalities. There is evidence for recruitment of the corresponding sensory cortex during auditory imagery [103,104], odor imagery [105,106], tactile imagery [107], and motor imagery [108,109]. Future research is necessary to fully explore whether all of the results in the visual domain generalize to other domains. For example, is there also a low-level to high-level gradient in the overlap, does vividness correlate with the overlap, and is there overlap in top-down connectivity?



not confuse the two in daily life. Finally, there is relatively little research on the interaction between imagery and perception. Such studies would provide insight into the functional relevance of the neural overlap between imagery and perception.

Acknowledgments

S.E.B. and M.A.J.v.G. were supported by VIDI grant number 639.072.513 of The Netherlands Organization for Scientific Research (NOW). N.D. was supported by institutional funding.

References

- 1. Delamillieure, P. et al. (2010) The resting state questionnaire: an introspective questionnaire for evaluation of inner experience during the conscious resting state. Brain Res. Bull. 81, 565-573
- 2. Pylyshyn, Z.W. (1973) What the mind's eye tells the mind's brain: a critique of mental imagery. Psychol. Bull. 80, 1-24
- Pylyshyn, Z.W. (1981) The imagery debate: analogue media З. versus tacit knowledge. Psychol. Rev. 88, 16-45
- 4. Kosslyn, S.M. (1980) Image and Mind, Harvard University Press
- 5. Kosslvn, S.M. (1973) Scanning visual images; some structural implications. Percept. Psychophys. 14, 90-94
- 6. Pearson, J. and Kosslyn, S.M. (2015) The heterogeneity of mental representation: ending the imagery debate. Proc. Natl. Acad. Sci. U. S. A. 112, 10089-10092
- 7. Ishai, A. et al. (2000) Distributed neural systems for the generation of visual images, Neuron, 28, 979-990
- 8. O'Craven, K.M. and Kanwisher, N. (2000) Mental imagery of faces and places activates corresponding stimulus-specific brain regions. J. Cogn. Neurosci. 12, 1013-1023
- Stokes, M. et al. (2010) Codes in visual cortex during mental imagery. J. Neurosci. 29, 1565-1572
- 10. Albers, A.M. et al. (2013) Shared representations for working memory and mental imagery in early visual cortex. Curr. Biol. 23, 1427-1431
- 11. Reddy, L. et al. (2010) Reading the mind's eye: decoding category information during mental imagery. Neuroimage, 50, 818-825
- 12. Johnson, M.R. and Johnson, M.K. (2014) Decoding individual natural scene representations during perception and imagery. Front. Hum. Neurosci. 8, 59
- 13. Naselaris, T. et al. (2015) A voxel-wise encoding model for early visual areas decodes mental images of remembered scenes. Neuroimage, 105, 215-228
- 14. Lee, S.-H. et al. (2012) Disentangling visual imagery and perception of real-world objects. Neuroimage, 59, 4064-4073
- 15 Kosslyn, S.M. and Thompson, W.L. (2003) When is early visual cortex activated during visual mental imagery? Psychol. Bull. 129, 723-746
- 16. Cui, X. et al. (2007) Vividness of mental imagery: individual variability can be measured objectively. Vision Res. 47, 474-478
- 17. Klein, I. et al. (2004) Retinotopic organization of visual mental images as revealed by functional magnetic resonance imaging. Brain Res. Cogn. Brain Res. 22, 26-31
- 18. Slotnick, S.D. et al. (2005) Visual mental imagery induces retinotopically organized activation of early visual areas. Cereb. Cortex, 15, 1570-1583
- 19. Pearson, J. et al. (2008) The functional impact of mental imagery on conscious perception. Curr. Biol. 18, 982-986
- 20. Bergmann, J. et al. (2015) Smaller primary visual cortex is associated with stronger, but less precise mental imagery. Cereb. Cortex, 26, 3838-3850
- 21. Sirigu, A. and Duhamel, J.R. (2001) Motor and visual imagery as 43. Van Essen, D.C. et al. (1992) Information processing in the two complementary but neurally dissociable mental processes. J. Cogn. Neurosci. 13, 910–919
- 22. Butter, C.M. et al. (1997) Field-specific deficits in visual imagery following hemianopia due to unilateral occipital infarcts. Brain, 120, 217-228

- 23. Roelfsema, P.R. and De Lange, F.P. (2016) Early visual cortex as a multiscale cognitive blackboard. Annu. Rev. Vis. Sci. 2, 131-151
- Kok, P. et al. (2016) Selective activation of the deep layers of the human primary visual cortex by top-down feedback. Curr. Biol. 26, 371-376
- Dijkstra, N. et al. (2017) Vividness of visual imagery depends on 25. the neural overlap with perception in visual areas. J. Neurosci. 37, 1367-1373
- González-García, C. et al. (2018) Content-specific activity in 26. frontoparietal and default-mode networks during prior-guided visual perception. eLife, 7, e36068
- 27. Hebart, M.N. et al. (2018) The representational dynamics of task and object processing in humans. eLife, 7, e32816
- Christophel. T.B. et al. (2015) Parietal and early visual cortices 28 encode working memory content across mental transformations. Neuroimage, 106, 198-206
- Christophel, T.B. et al. (2017) The distributed nature of working 29. memory. Trends Cogn. Sci. 21, 111-124
- 30. Malhotra, P. et al. (2009) Role of right posterior parietal cortex in maintaining attention to spatial locations over time. Brain, 132, 645-660
- 31. Ishai, A. et al. (2002) Visual imagery of famous faces: effects of memory and attention revealed by fMRI. Neuroimage, 17, 1729-1741
- 32. Winlove, C. et al. (2018) The neural correlates of visual imagery: a co-ordinate-based meta-analysis, Cortex, 105, 4-25
- Sack, A.T. et al. (2005) The dynamics of interhemispheric com-33. pensatory processes in mental imagery. Science, 308, 702-704
- Christophel, T.B. et al. (2017) The distributed nature of working memory. Trends Cogn. Sci. 21, 111-124
- 35. Bogler, C. et al. (2011) Decoding successive computational stages of saliency processing. Curr. Biol. 21, 1667-1671
- 36 Yun, K. et al. (2013) Exploring the role of gaze behavior and object detection in scene understanding. Front. Psychol. 4, 917
- 37. Nobre, A.C. et al. (2004) Orienting attention to locations in perceptual versus mental representations. J. Cogn. Neurosci. 16, 363-373
- Ishai, A. et al. (2002) Visual imagery of famous faces: effects of 38. memory and attention revealed by fMRI. Neuroimage, 17. 1729-1741
- 39. Jiang, X. et al. (2007) Categorization training results in shape- and category-selective human neural plasticity. Neuron, 53, 891-903
- 40. Chan, A.W.-Y. (2013) Functional organization and visual representations of human ventral lateral prefrontal cortex. Front. Psychol. 4, 371
- 41. Bugatus, L. et al. (2017) Task alters category representations in prefrontal but not high-level visual cortex. Neuroimage, 155, 437-449
- 42. Lee, S.-H. et al. (2013) Goal-dependent dissociation of visual and prefrontal cortices during working memory. Nat. Neurosci. 16, 997-999
- primate visual system: an integrated systems perspective. Science, 255, 419-423
- 44. Hubel, D.H. and Wiesel, T.N. (1968) Receptive fields and functional architecture of monkey striate cortex. J. Physiol. 195, 215-243



- monkey extrastriate cortex. Annu. Rev. Neurosci. 10, 363-401
- 46. Thorpe, S.J. and Fabre-Thorpe, M. (2001) Seeking categories in the brain. Science, 291, 260-263
- 47. Carlson, T.A. (2011) High temporal resolution decoding of object position and category. J. Vis. 11, 9
- Isik, L. et al. (2014) The dynamics of invariant object recognition 48. in the human visual system. J. Neurophysiol. 111, 91-102
- 49. Seeliger, K. et al. (2017) Convolutional neural network-based encoding and decoding of visual object recognition in space and time. Neuroimage, 180, 253-266
- 50. Thorpe, S. et al. (1996) Speed of processing in the human visual system. Nature, 381, 520-522
- 51. Bastos, A.M. et al. (2012) Canonical microcircuits for predictive coding. Neuron, 76, 695-711
- 52. Bastos, A.M. et al. (2015) Visual areas exert feedforward and feedback influences through distinct frequency channels. Neuron. 85. 390-401
- 53. Cauchoix, M. et al. (2014) The neural dynamics of face detection in the wild revealed by MVPA, J. Neurosci, 34, 846-854
- 54. Anderer, P. et al. (1997) Electrical sources of P300 event-related brain potentials revealed by low resolution electromagnetic tomography. Neuropsychobiology, 37, 20-27
- 55. Soltani, M. and Knight, R.T. (2000) Neural origins of the P300. Crit. Rev. Neurobiol. 14, 26
- 56. Mulert, C. et al. (2004) The neural basis of the P300 potential. Eur. Arch. Psychiatry Clin. Neurosci. 254, 190-198
- 57. King, J.R. and Dehaene, S. (2014) Characterizing the dynamics of mental representations: the temporal generalization method. Trends Cogn. Sci. 18, 203-210
- 58. Cichy, R.M. et al. (2014) Resolving human object recognition in space and time. Nat. Neurosci. 17, 455-462
- 59. Carlson, T. et al. (2013) Representational dynamics of object vision: the first 1000 ms. J. Vis. 13, 1
- 60. Diikstra, N. et al. (2018) Differential temporal dynamics during visual imagery and perception. eLife, 7, e33904
- 61. Spaak, E. et al. (2017) Stable and dynamic coding for working memory in primate prefrontal cortex, J. Neurosci, 37, 6503-6516
- 62. King, J.-R. et al. (2016) Brain mechanisms underlying the brief maintenance of seen and unseen sensory information. Neuron, 92 1122-1134
- Vidaurre, D. et al. (2019) Temporally unconstrained decoding 63. reveals consistent but time-varying stages of stimulus processing. Cereb. Cortex, 29, 863-874
- 64. Cichy, R.M. et al. (2015) Can visual information encoded in cortical columns be decoded from magnetoencephalography data in humans? Neuroimage, 121, 193-204
- 65. Stokes, M.G. et al. (2015) Decoding rich spatial information with high temporal resolution. Trends Cogn. Sci. 19, 636-
- 66. Friston, K.J. et al. (2003) Dynamic causal modelling. Neuroimage, 19, 1273-1302
- 67. Mechelli, A. et al. (2004) Where bottom-up meets top-down: neuronal interactions during perception and imagery. Cereb. Cortex, 14, 1256-1265
- 68. Dentico, D. et al. (2014) Reversal of cortical information flow during visual imagery as compared to visual perception. Neuroimage, 100, 237-243
- 69. Buschman, T.J. and Miller, E.K. (2007) Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. Science, 315, 1860-1862
- 70. Muckli, L. and Petro, L.S. (2013) Network interactions: nongeniculate input to V1. Curr. Opin. Neurobiol. 23, 195-201
- 71. Muckli, J. (2010) What are we missing here? Brain imaging evidence for higher cognitive functions in primary visual cortex V1. Int. J. Imaging Syst. Technol. 20, 131-139
- 72. Friston, K. et al. (2015) Empirical Bayes for DCM: a group inversion scheme, Front, Svst, Neurosci, 9, 164

- 45. Maunsell, J.H.R. and Newsome, W.T. (1987) Visual processing in 73. Friston, K.J. et al. (2016) Bayesian model reduction and empirical Bayes for group (DCM) studies. Neuroimage, 128, 413-431
 - Dijkstra, N. et al. (2017) Distinct top-down and bottom-up 74. brain connectivity during visual perception and imagery. Sci. Rep. 7, 5677
 - 75. Mayer, J.S. et al. (2007) Common neural substrates for visual working memory and attention. Neuroimage, 36, 441-453
 - Zanto, T.P. et al. (2011) Causal role of the prefrontal cortex in 76. top-down modulation of visual processing and working memory. Nat. Neurosci. 14, 656-661
 - 77. Higo, T. et al. (2011) Distributed and causal influence of frontal operculum in task control. Proc. Natl. Acad. Sci. U. S. A. 108, 4230-4235
 - Grush, R. (2004) The emulation theory of representation: motor 78. control, imagery, and perception. Behav. Brain Sci. 27, 377–442
 - 79 Moulton, S.T. and Kosslyn, S.M. (2009) Imagining predictions: mental imagery as mental emulation. Philos. Trans. R. Soc. Lond. B Biol. Sci. 364, 1273–1280
 - Eslami, S.M.A. et al. (2018) Neural scene representation and 80. rendering. Science, 360, 1204-1210
 - Levelt, W.J.M. (1966) The alternation process in binocular rivalry. 81. Br. J. Psychol. 57, 225-238
 - Sherwood, R. and Pearson, J. (2010) Closing the mind's eye: 82. incoming luminance signals disrupt visual imagery. PLoS One. 5. e15217
 - 83. Keogh, R. and Pearson, J. (2014) The sensory strength of voluntary visual imagery predicts visual working memory capacity. J. Vis. 14, 1427-1431
 - 84. Kok, P. et al. (2017) Prior expectations induce prestimulus sensory templates. Proc. Natl. Acad. Sci. U. S. A. 114, 10473-10478
 - 85. Ganis, G. and Schendan, H.E. (2008) Visual mental imagery and perception produce opposite adaptation effects on early brain potentials. Neuroimage, 42, 1714-1727
 - 86. Mumford, D. (1992) On the computational architecture of the neocortex - II: The role of cortico-cortical loops. Biol. Cybern. 66, 241-251
 - 87. Keogh, R. and Pearson, J. (2017) The blind mind: no sensory visual imagery in aphantasia. Cortex, 105, 53-60
 - Zeman, A. et al. (2015) Lives without imagery congenital 88 aphantasia. Cortex, 73, 378-380
 - Barsalou, L.W. (2008) Grounded cognition. Annu. Rev. Psychol. 89 59, 617-645
 - 90. Kent, C, and Lamberts, K, (2008) The encoding-retrieval relationship: retrieval as mental simulation. Trends Cogn. Sci. 12, 92-98
 - 91. Friston, K. (2005) A theory of cortical responses. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360, 815-836
 - Pearson, J. et al. (2015) Mental imagery: functional mechanisms 92. and clinical applications, Trends Coan, Sci. 19, 590-602
 - Tong, F. (2013) Imagery and visual working memory: one and 93. the same? Trends Cogn. Sci. 17, 489-490
 - Keogh, R. and Pearson, J. (2011) Mental imagery and visual 94. working memory. PLoS One, 6, e29221
 - Baddeley, A.D. and Andrade, J. (2000) Working memory and the vividness of imagery. J. Exp. Psychol. Gen. 129, 126-145
 - 96. Jacobs, C. et al. (2017) Visual working memory performance in aphantasia. Cortex, 105, 61-73
 - Scimeca, J.M. et al. (2018) Reaffirming the sensory recruitment 97 account of working memory. Trends Cogn. Sci. 22, 190-192
 - D'Esposito M and Postle B B (2015) The cognitive neurosci-98 ence of working memory. Annu. Rev. Psychol. 66, 115-142
 - 99. D'Esposito, M. (2007) From cognitive to neural models of working memory. Philos. Trans. R. Soc. Lond. B Biol. Sci. 362, 761-772
 - 100. Xu, Y. (2017) Reevaluating the sensory account of visual working memory storage. Trends Cogn. Sci. 21, 794-815
 - 101. Galton, F. (1880) Statistics of mental imagery. Mind, 5, 301-318

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- vividness an fMRI study and literature review. Cortex, 105, 26-40
- 103. Zatorre, R.J. et al. (2007) When the brain plays music: auditorymotor interactions in music perception and production. Nat. Rev. Neurosci. 8, 547-558
- 104. Zatorre, R.J. and Halpern, A.R. (2005) Mental concerts: musical imagery and auditory cortex. Neuron, 47, 9-12
- 105. Djordjevic, J. et al. (2005) Functional neuroimaging of odor imagery. Neuroimage, 24, 791-801
- 106. Djordjevic, J. et al. (2004) The mind's nose. Psychol. Sci. 15, 143–148
- 102. Fulford, J. et al. (2017) The neural correlates of visual imagery 107. Yoo, S.-S. et al. (1990) Neural substrates of tactile imagery: a functional MRI study. Neuroreport, 14, 581-585
 - 108. Porro, C.A. et al. (1996) Primary motor and sensory cortex activation during motor performance and motor imagery: a functional magnetic resonance imaging study. J. Neurosci. 16, 7688–7698
 - 109. Dechent, P. et al. (2004) Is the human primary motor cortex involved in motor imagery? Cogn. Brain Res. 19, 138-144