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Visual imagery and touch: Mental image creation at the interface of external and internal realities

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Abstract

Visual mental imagery is of essential importance for human cognition, serving a wide variety of functions. For instance, mental images are critical for remembering, planning the future, or navigating. Further, the creation of mental representations of the external world by means of visual images is particularly relevant. Such visual representations are not created as an objective mirror of the external world, but their formation is strongly influenced by prior experiences, knowledge, and cognitive frameworks. The human sense of touch is a direct mediator between these internal realities and the external, allegedly objective reality. When grasping something tactilely, a corresponding internal image can be created at the direct interface of external and internal realities, through a combination of bottom-up sensory input and top-down processes. Besides prior beliefs and expectations, the interplay of the different senses in our multimodal world influences imagery creation. Despite the ubiquitous functions of visual imagery in human cognition, mechanisms of how, on the one hand, familiarity affects mental image creation remain unknown. Similarly, on the other hand, knowledge about the role of multisensory input on image creation is scarce, although there is preliminary evidence for an inhibitory role of other sensory modalities on visual image generation. In this dissertation, I therefore investigated how familiarity affects visual imagery creation and whether tactile input inhibits visual imagery creation. To do this, I used an experimental paradigm that employed haptic objects in combination with visual imagery and manipulated different degrees of familiarity and tactile input. Behavioural measures and functional magnetic resonance imaging (fMRI) data were collected from 30 participants with high imaginative abilities. I thereby aimed to determine processing preferences and neurofunctional correlates of the creation of visual imagery at the interface between external and internal realities. The results suggest a fundamental effect of familiarity on imagery creation, supported by an increased vividness of imagery and greater involvement of sensory and associative brain areas. The inhibitory influence of tactile input on visual imagery was confirmed by a dominance of somatosensory brain activity over visual cortical activity. A lack of perceived differences at the behavioural level points towards metamodal sensory processing and the importance of unconscious imagery in human cognition. Our results contribute to the understanding of mental image creation in light of existing internal biases and multisensory processing. Moreover, our findings point out directions for further research, such as the development of novel imagery techniques within psychotherapy, aiming to influence existing visual memories and pathologic patterns in imagery creation.

Zusammenfassung

Visuelle mentale Bilder sind für die menschliche Kognition von wesentlicher Bedeutung. Sie erfüllen eine Vielzahl kognitiver Funktionen und sind unter anderem essenziell, um sich bildhaft zu erinnern, die Zukunft zu planen oder zu navigieren. Darüber hinaus ist die Kreation mentaler Repräsentationen der Außenwelt durch mentale Bilder von besonderer Bedeutung. Dabei wird die Realität nicht objektiv abgebildet, sondern durch vorbestehende Erfahrungen, Wissen und kognitive Rahmenbedingungen beeinflusst. Der menschliche Tastsinn ist ein direkter Vermittler zwischen diesen inneren Realitäten und der äußeren, vermeintlich objektiven Realität. Wenn wir Dinge mit den Händen begreifen, kann durch die Kombination sensorischer ‚bottom-up' Prozesse und kortikaler ‚top-down' Prozesse ein entsprechendes inneres Bild entstehen. Neben den erwähnten Erfahrungen und Erwartungen beeinflusst auch das Zusammenspiel verschiedener Sinnesmodalitäten die Kreation visueller Vorstellungen. Trotz der ubiquitären Funktionen mentaler Bilder in der menschlichen Kognition ist weitgehend unbekannt, wie sich die Vertrautheit von Objekten auf die mentale Bilderzeugung auswirkt. Ebenso ist das Wissen über die Rolle multisensorische Eindrücke bei der Bilderzeugung begrenzt, obwohl es erste Hinweise auf eine hemmende Rolle anderer sensorischer Modalitäten gibt. In dieser Dissertation untersuchte ich daher, wie Vertrautheit und taktiler Input die mentale Bilderzeugung beeinflussen. Dazu verwendete ich ein experimentelles Paradigma, in dem anhand haptischer Objekte mentale Bilder kreiert werden sollten, während der Einfluss von Vertrautheit sowie taktilem Input manipuliert wurde. In einer Gruppe von 30 Probanden mit sehr guter visueller Vorstellungskraft wurden mittels Fragebögen und funktioneller Magnetresonanztomographie Daten erhoben, um Verarbeitungspräferenzen sowie neurofunktionale Korrelate der Erzeugung visueller Bilder an der Schnittstelle zwischen äußerer und innerer Realität zu ermitteln. Die Ergebnisse deuten auf einen dominierenden Effekt von Vertrautheit auf die Bilderzeugung hin, der auf erhöhter Lebendigkeit der kreierten Bilder, sowie einer stärkeren Beteiligung sensorischer und assoziativer Hirnareale beruht. Der hemmende Einfluss taktiler Information auf die Bildkreation wurde durch die Dominanz somatosensorischer Gehirnaktivität gegenüber visueller kortikaler Aktivität bestätigt. Das Fehlen wahrgenommener Unterschiede auf Verhaltensebene weist dabei auf eine metamodale sensorische Verarbeitung hin und hebt die Rolle unbewusster bildlicher Vorstellungen in der menschlichen Kognition hervor. Die Ergebnisse dieser Arbeit tragen zum Verständnis der Entstehung mentaler Bilder vor dem Hintergrund bestehender Erfahrungen, Erwartungen und multisensorischer Eindrücke bei. Darüber hinaus weisen sie auf zukünftige Forschungsziele hin, insbesondere die Entwicklung neuer Techniken für den Einsatz mentaler Bilder in der Psychotherapie.

1 Introduction

1.1 Visual imagery

1.1.1 Definition

Imagery is the cognitive ability to experience sensory processing in the absence of sensory stimuli. While humans are also capable of auditory, motor, tactile, olfactory, and gustatory imagery, visual imagery has largely dominated mental imagery research to date (Pearson, 2019). Specifically, visual imagery is defined as the ability to (re)create visual representations of objects or scenes without that object or scene being physically present (e.g. Kosslyn, 2005; Pearson et al., 2015). It is also referred to as 'seeing with the mind's eye' (e.g. Ishai, 2010; Kosslyn et al., 2001), emphasising the visual experience elicited in spite of the lacking involvement of actual external perceptual vision. Historically, visual imagery has been used to describe conscious experiences of such mental images, e.g. during mind-wandering and episodic memory retrieval. However, recently, the important role of unconscious visual imagery in enabling cognitive tasks has been indicated (Brogaard & Gatzia, 2017; Nanay, 2021; Phillips, 2014). Besides the distinction in conscious and unconscious imagery, mental images can arise voluntarily and involuntarily, explaining their central importance for psychopathologic conditions, such as post-traumatic stress disorder (PTSD), depression, or phobias (Ji et al., 2019). While visual imagery is experienced to be akin to visual perception, mental images are usually not as clear and vivid as actual sensory vision but appear to be comparably vague (Koenig-Robert & Pearson, 2021). However, visual imagery abilities vary on a spectrum reaching from aphantasia, i.e. the complete lack of the ability to imagine something, to hyperphantasia, characterised by mental images as clear and realistic as in actual vision (Phillips, 2014; Zeman et al., 2020).

1.1.2 Functions of visual imagery in human cognition

Visual imagery is omnipresent in human cognition, serving a wide variety of functions that range from mind-wandering (Delamillieure et al., 2010; Smallwood & Schooler, 2015) to decision making (Gaesser & Schacter, 2014). By providing mental representations of the world, visual imagery is embedded strongly in numerous cognitive processes that enable us for instance to remember (D'Argembeau & Van der Linden, 2006), navigate (Bocchi et al., 2017; Moulton & Kosslyn, 2009; Piccardi et al., 2017), be creative (Benson & Park, 2013) or plan the future (Schacter et al., 2012). Visual imagery's relevance in cognitive processing is mirrored in a rich history of research, being rooted in ancient Greek philosophers' works such as Aristotle, and subject to discussion for Descartes, Kant, and many more (for a review see MacKisack et al., 2016). Continuing the tradition of investigating imagery as a means of thinking and therefore a central process influencing human thought and action, Francis Galton was the first to scientifically measure imagery ability in the late 19th century (Galton, 1880). Within psychology, imagery was investigated already by founding father Wilhelm Wundt (Wundt, 1912/2014). Despite a rich history of imagery research in behavioural, conceptual, and later neuroimaging studies, a comprehensive classification of visual imagery's functions within cognition is still lacking to this day. To examine visual imagery's extensive relevance for human cognition in a structured way, time can offer a framework as visual imagery is crucial in facilitating cognitive processes in the past, present, and future (*Figure 1*).

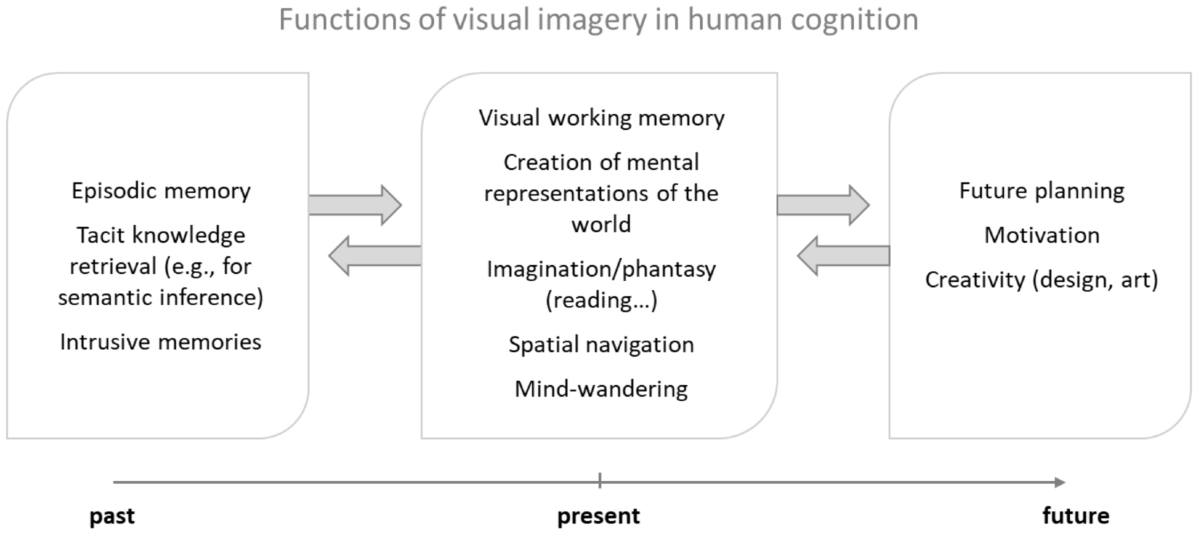

Figure 1. Functions of visual imagery in human cognition. Visual imagery facilitates numerous cognitive processes and is essential to make visual representations of future, past, or present content available for cognitive operations independent of time and place.

Firstly, imagery is of critical importance to envision the future. Moulton & Kosslyn (2009) describe imagery as "mental emulation", serving the function to simulate the future based on previous experiences. Often, imaginative scenes of the future are constructed based on visual imagery of past events (D'Argembeau & Van der Linden, 2006; Schacter & Addis, 2007; Szpunar & McDermott, 2008). Because we can picture ourselves in the near and distant future, visual imagery helps us to generate, believe in, and strive for specific goals. Similarly, imagining the outcome of an action or a task can help to find motivation for both direct actions and long-term projects (McMahon, 1973; Szpunar & Schacter, 2013). The power of imagery to influence future behaviour has been shown extensively (see Baumeister et al., 2011 for a review), proving that imagery increases the likelihood of an action or plan becoming reality. For instance, picturing themselves voting in an upcoming election significantly increased the likelihood of participants to vote (Libby et al., 2007). Besides its relevance for planning and shaping the future, visual imagery is a prerequisite of creativity by facilitating the mental creation of novel and innovative solutions for problems and projects, which can then be implemented in real life (Benson & Park, 2013; Dahl et al., 1999; Miller, 2002). Benson & Park (2013) point towards Albert

Einstein as a famous example of a genius creative mind based largely on visual imagery, as he is said to have rigorously preferred images as his means of thinking, rather than words and language. Research has shown that visuospatial imagery abilities in fact enable creative and logical thinking and can predict school achievements as well as successful careers in science, technology, and engineering (Kell et al., 2013; Li & Geary, 2017; Webb et al., 2007). Working memory is another cognitive mechanism closely connected to visual imagery, that allows us to store specific information over a short period of time in order to solve complex cognitive tasks (Baddeley, 1992). Such information can be stored in form of visual images (Albers et al., 2013; Borst et al., 2012; Keogh & Pearson, 2011; Pearson & Keogh, 2019; Tong, 2013). Better imagers perform better in visual working memory tasks (Keogh & Pearson, 2014), for example when completing visual search or matching tasks to detect changes in the environment. Until today, it is subject to debate if and how visual imagery and visual working memory can be separated both functionally and neurobiologically (Christophel et al., 2017; Pearson et al., 2015; Tong, 2013). Generally, the demarcation of conscious as well as unconscious visual imagery processes from other cognitive mechanisms is still very much subject to debate within the field (for discussions see e.g. Nanay, 2021; Pearson & Kosslyn, 2015).

Turning the idea of mental time travel around, imagery is important to human cognition by making content of the past available for the present. The most prominent example for the provision of visual information from the past is episodic memory, also referred to as “mnemonic pictorial knowledge” (Pöppel & Bao, 2011), indicating the representation of visual scenes or ‘episodes’ of one’s past in the mind (Tulving, 1972, 1993, 2002). Mediated by visual imagery, information stored in episodic memory can be retrieved and visually recreated years and decades after a scene has originally occurred. Thus, past episodes can be scanned in the present and the pictorial character of such episodic memories allows the retrieval of implicit information entrained within the imagery’s detail (Pearson & Kosslyn, 2015). In consequence, this information can be made available for conscious report as well as for solving cognitive tasks related to the past (e.g. Fletcher et al., 1995). Importantly, episodic memory’s imagery further provides and vivifies access to autobiographic memory, thereby contributing decisively to the creation of a stable sense of identity (S. B. Klein & Nichols, 2012; Lin, 2018; Zhou et al., 2014).

When exploring imagery and its functions in the present in the precise sense of consecutive perceptual ‘moments of now’ (Bao et al., 2015; Wittmann, 2016), the transformation of externally perceived stimuli into an inner mental representation is of central importance. Visual stimuli and their representations as visual imagery have historically been the center of sensory research, with good cause, following the words of Zeki (1999, p. 8) “the pre-eminent function of the visual brain is the acquisition of knowledge about the world around us”, and Pöppel & Bao (2011) “seeing is knowing”.

When viewing and attending to scenes, persons, or objects, humans can always create a visual mental image corresponding to the stimulus. The term 'offline perception' (Fazekas et al., 2021) provides another apt description of this core function of visual imagery, which is to make perceptual 'online' experiences re-experienceable even if the stimulus is not physically present. Thereby, mental imagery ensures durability and availability of visual information as a basis for future thoughts and tasks. When creating such inner visual representations of the outside world, humans necessarily attribute meaning to what is seen in a top-down approach, embedding the newly acquired pictorial knowledge within existing conceptual frames (Pöppel & Bao, 2011; Silveira et al., 2015; Yang et al., 2019). Consequently, the process of mental image creation is subject to a complex interplay of external stimuli with internal expectations, knowledge, and emotional states. Upon creating inner visual representations, it is therefore essential to match internal priors with the incoming stimuli (Clark, 2013; Teufel & Nanay, 2017; von Helmholtz, 1866). Bayesian inference offers a model to describe how the human brain constantly forms and refines predictions about its sensory environment by synthesising top-down cognition with bottom-up sensory input (Ballard et al., 1983; K. Friston & Kiebel, 2009; Mumford, 1992; Rao & Ballard, 1999; *Figure 2*). Hence, the way humans experience the external world is unique on an individual level, based on prior knowledge, cultural frames, and not least on prior experiences stored in form of mental visual representations of the past (Nanay, 2018; Winkler & Czigler, 2012). It is the balance of these internal representations on the one hand and the incoming external stimuli on the other hand, that is crucially important to the way humans perceive and act in the world (de Lange et al., 2018; Kok et al., 2012). The creation of mental representations of external stimuli signifies the interface between internal and external realities. Yet, to date, knowledge on the exact interplay of internal and external factors in mental image creation remains scarce.

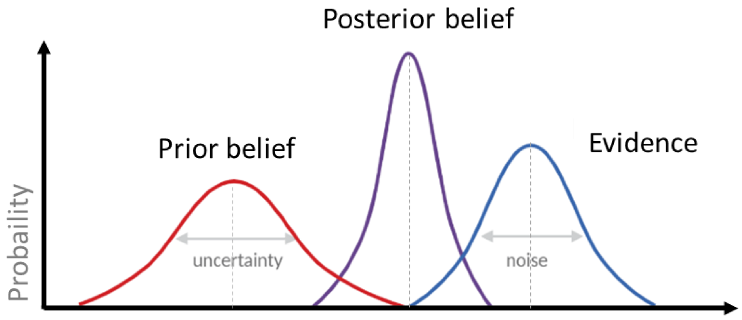

Figure 2. Example of Bayesian inference modelling in perception. Probability distributions explain perception in light of prior beliefs (red curve), which are created based on existing mental frames, memories, and imagery (containing some uncertainty). The evidence or likelihood function (blue) represents the sensory input (the variance is explained by noise). Applying Bayesian inference, priors and likelihood are matched to form a posterior belief (purple), that corresponds to the actual conscious percept (modified from Yanagisawa et al., 2019).

The relevance of visual imagery in human cognition is fortified by its central importance in psychopathology (for a recent review see Ji et al., 2021). When the balance of the interplay between internal and external realities cannot be maintained, psychological functions suffer. One of the most prominent examples of imagery-related pathologies is depression, where restricted, fundamentally negative imagery permeates and dominates cognition, resulting in negative views about oneself, the world, and the future (Beck et al., 1979; Holmes et al., 2016; Moritz et al., 2014; Weßlau et al., 2015). Further, in PTSD, visual imagery pathologically intrudes patients' minds in form of distressing involuntary flash-back memories (American Psychiatric Association, 2013; Ehlers et al., 2004). Other examples for imagery-related pathologies include schizophrenia, which is accompanied by hyper-realistic and manipulation-prone imagery (Benson & Park, 2013; Oertel et al., 2009) or catastrophising imagery in phobias (Hackmann et al., 2000; Holmes & Mathews, 2010). Yet, the role of imagery techniques in psychotherapy has only recently gained some momentum. Successful and promising examples include imagery modification in depression, where positive imagery is supported and trained (Blackwell et al., 2015; Burnett Heyes et al., 2017), imagery exposure and rescripting in PTSD treatment (Arntz et al., 2007; Ehlers et al., 2004), as well as imaginal exposure to treat phobias (Agren et al., 2017; Hoppe et al., 2021a). However, evidence is still scarce and partly conflicting (e.g. De Voogd et al., 2017; Holmes et al., 2016; Hoppe et al., 2021; Weßlau & Steil, 2014), calling for the extension of knowledge on imagery in psychopathology. Of particular importance is the development of treatment strategies to serve the vast societal and individual need for targeted, efficient, easily accessible treatment strategies with low side effects (e.g. Patel et al., 2018). Yet, the potential and development of therapeutic imagery techniques depend critically on our fundamental understanding of visual imagery formation, maintenance, and retrieval. Despite its major relevance for cognition in mental health and disease, visual imagery research has remained a niche area of research, with many, partly fundamental, questions unresolved to this day (Fazekas et al., 2021).

Due to the central importance of the interface of external and internal realities in imagery generation, it was the aim of this dissertation to investigate how mental visual representations of external stimuli are created. Neurofunctional correlates of imagery creation were investigated using functional magnetic resonance imaging (fMRI). In the remainder of this introduction, I will give an overview of the neurobiological foundations of visual imagery before I will introduce touch as the external sensory modality that served as the perceptual basis for mental image creation in this study. Eventually, I will define objectives and hypotheses for this thesis.

1.1.3 Neurofunctional correlates of visual imagery

As an entirely subjective process, visual imagery was historically prominent in the philosophical discourse (for a review see MacKisack et al., 2016), yet difficult to investigate scientifically. The first seminal experimental work was provided by Mary Perky (1910), who suggested a similarity in visual imagery and visual perception, fuelled by her findings of a functional symbiosis rather than disturbance when combining imagery and faded perceptual images. In consequence, successive research in the field was largely centred around the 'imagery debate', i.e. the discussion as to whether imagery is actually pictorial in nature (Farah, 1988; Finke & Pinker, 1983; Kosslyn et al., 1993) or, on the contrary, propositional with semantic rather than visual content (Pylyshyn, 1973, 2002). The advent of neuroimaging brought about by fMRI in the 1990s (Ogawa et al., 1990) finally provided a means to delve deeper into the neurobiological foundations and internal processes constituting human mental imagery (*Figure 3).*

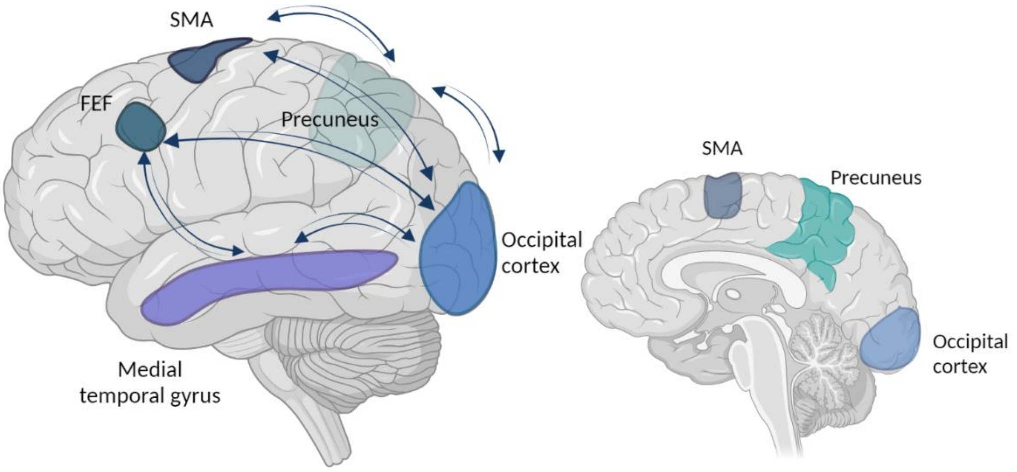

Figure 3. Cortical regions involved in visual imagery processing. The lateral brain view (left) is complemented by a medial brain view (right) to visualize mid-cortical structures involved in visual imagery: the supplementary motor area (SMA), the precuneus, and the occipital cortex. The precuneus in the lateral view is a projection from the cortical midline for a better overview. Arrows symbolise feed-forward and feed-back loops during imagery processing on network-level (compare Winlove et al., 2018; figure created with BioRender.com).

Owing to the imagery debate, cortical areas known to be associated with visual perception were awarded great attention and soon provided proof of imagery's considerable comparability to visual perception, both phenomenologically and in terms of neurofunctional correlates (Dijkstra et al., 2019; Fulford et al., 2018; Ganis et al., 2004; Kosslyn et al., 1993; Mellet et al., 2000). Of particular interest was the contribution of primary visual cortex (V1) activity during visual imagery, which seems to follow a retinotopic-like pattern, similar to visual perception (I. Klein et al., 2004; Slotnick et al., 2005). In line with this, researchers managed to deduce details of imagery based on cortical activity patterns with fair accuracy (Boccia et al., 2015; Cichy et al., 2012; Reddy et al., 2010; Senden et al., 2019; Thirion et al., 2006). However, visual cortex and particularly primary visual cortex involvement in imagery has been subject to debate, as several studies did not identify V1 activation during imagery (Ishai, Ungerleider, & Haxby, 2000; Roland & Gulyás, 1994; Yomogida et al., 2004). Possible reasons for these discrepant findings include prominent evidence for the necessity of V1-involvement only for very detailed or particularly vivid imagery (Cui et al., 2007; Dijkstra et al., 2017; Kosslyn & Thompson, 2003). Another possible explanation for the apparent inconsistencies is V1's versatile function in cognition and its potential involvement during rest and other experimental comparison conditions (for a review and discussion see Winlove et al., 2018). Besides V1, several higher cortical structures within the visual system were found to be related to visual imagery, namely the middle and lateral occipital gyri and the fusiform gyrus (Spagna et al., 2021; Stokes et al., 2009; Winlove et al., 2018). Just like during perception, content-specific visual areas such as the fusiform face or place area are involved in content-specific imagery (Ishai, Ungerleider, & Haxby, 2000; O'Craven & Kanwisher, 2000). Notably, visual imagery abilities have been reported and experimentally confirmed in blind subjects (Bridge et al., 2012a; Chatterjee & Southwood, 1995; von Trott zu Solz et al., 2017). This points towards the plasticity of the visual cortex and the cognitive machinery in general and underlines the diversity of cortical visual (imagery) processing (Ffytche & Zeki, 2011; Zhou et al., 2016). In sum, evidence speaks for regular, yet not necessary visual cortex involvement in visual imagery, while early visual cortex involvement can be considered a particular surrogate of detailed visual imagery.

In contrast to visual perception, which is largely characterised by bottom-up sensory processing, visual imagery is decisively governed by cognitive top-down processing. While visual perception is also influenced by top-down processes to a relevant degree (Bar et al., 2006; Kanwisher & Wojciulik, 2000; Rolls, 2008), their role in visual imagery is critical for the initiation, configuration, and maintenance of mental images (Dijkstra, Zeidman, et al., 2017; Ishai, 2010; Mechelli et al., 2004). Cortical regions exerting this executive top-down control comprise areas in the parietal and frontal cortices. Precisely, frontoparietal areas are suggested to be involved in the facilitation of the attentional component of visual imagery (Mechelli et al., 2004), in line with their top-down role across many other cognitive processes (Hopfinger et al., 2000; Kanwisher & Wojciulik, 2000; Lindsay, 2020). Both parietal and frontal regions are crucial in the orchestration of image creation from both short- and long-term memory (Ishai et al., 2002). Notably, on the network level, frontoparietal and visual areas do not only interact in one top-down direction, but in a complex interplay of feed-forward and feed-back loops (Koivisto & Silvanto, 2012; Macuga & Frey, 2014). Generally in visual imagery, left hemispheric activity seems to outweigh right hemispheric activity (Farah et al., 1985; Winlove et al., 2018).

Parietal cortex activity during imagery was specifically observed in the posterior parietal cortex (McNorgan, 2012; Winlove et al., 2018), comprising the precuneus, a mid-cortical structure known to be related to episodic memory retrieval. Crucially, the precuneus serves as a structural and functional hub between frontal- and parietal brain networks (Bullmore & Sporns, 2009; Cavanna & Trimble, 2006). Further, left superior parietal lobule activation was suggested to enable the retrieval of sensory representations from the occipitotemporal cortex for imagery generation (Mechelli et al., 2004). Frontal lobe activation related to visual imagery was observed in the prefrontal cortex. Most prominently, the supplementary motor area (SMA) and specifically the supplementary and cingulate eye fields (SCEF)[1] are involved in imagery. SMA involvement seems to be of particular importance for imagery generation because of its early activation during the imagery process (De Borst et al., 2012; Formisano et al., 2002; Sack et al., 2002; Sheets et al., 2021). Additionally stressing the SCEFs importance in imagery, local activity was shown to predict imagery performance and has been suggested as a possible neuronal surrogate for information retrieval and integration during imagery (De Borst et al., 2012), matching its general role in cognition for attention and executive control (Carter et al., 1999; Rossi et al., 2009). Moreover, additional superior motor areas such as the frontal eye fields (FEF) are related to visual imagery activation in the frontal lobe (McNorgan, 2012; Winlove et al., 2018). The FEFs provide top-down input to both early visual areas and temporal lobes and are hence suggested to mediate visual cortex activation related to imagery (Ganis et al., 2004; Mechelli et al., 2004).

In addition to visual, frontal, and parietal cortices, specific areas within the temporal cortex were shown to be activated during imagery tasks. Neuronal activation within the ventral temporal cortex has been interpreted in relation to the 'ventral visual stream', a network enabling the identification of objects (Grill-Spector & Weiner, 2014; Ishai, Ungerleider, Martin, et al., 2000). In addition to the involvement of the precuneus in episodic memory retrieval, medial temporal lobe regions related to memory processing are regularly activated during imagery processing, predominantly the parahippocampal gyri (McNorgan, 2012; Schmidt et al., 2014; Winlove et al., 2018). Moreover, classical memory-related areas such as the hippocampus, the entorhinal cortex, and the amygdala were shown to be active during imagery in single-neuron-recording during intracranial electroencephalography (EEG) experiments (Kreiman et al., 2000). Yet during fMRI experiments, these areas are often underrepresented as they frequently cancel out due to the high at-rest-activation level of the hippocampal network (Stark & Squire, 2001). While the neurofunctional correlates in relation to visual imagery described here are in line with recent meta-analyses (Fulford et al., 2018; McNorgan, 2012;

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[1] Previous research has often labelled activation in this area less specifically as anterior cingulate cortex (ACC), or medial prefrontal cortex (MPFC) activation (compare Winlove et al., 2018).

Spagna et al., 2021; Winlove et al., 2018), throughout, research on the neurofunctional correlates of imagery has provided only partial and rather diverse results, leaving precise mechanisms of imagery and particularly imagery generation unresolved.

To reduce the complexity of human visual imagery for feasible experimental research, a majority of neuroimaging studies on visual imagery has used simple object imagery as an experimental model for complex real-life imagery (for reviews see Pearson et al., 2015a; Winlove et al., 2018). To ensure comparability of our results, and to model the interaction of external sensory stimuli and internal visual imagery experimentally within a feasible paradigm, haptic objects were chosen as the sensory input for this study. Visual imagery had to be created based on the information derived by tactile exploration of these objects.

1.2 Touch and multisensory imagery

Touch is one of the core sensory modalities of human perception. Due to the necessarily immediate interaction of humans with tactilely explored objects (and humans), touch is crucial in our engagement with the world around us. The term 'to grasp' something (German '*begreifen'*) emphasises the importance of touch in our aim to make sense of the world by interacting with it on a sensory level. Quite literally, touch is the interface of humans and the world, and in particular, but not only during the first months of life, while vision is still developing, the ability to grasp is vital (Bremner & Spence, 2017; De Haan & Dijkerman, 2020; Gallace & Spence, 2014; Hutmacher, 2019). Anatomically, the sense of touch is facilitated by different skin organelles, which translate tactile input into neuronal signals. The obtained information is then transmitted to the thalamus via the spinal cord and medulla oblongata, where afferent axons cross to the contralateral side. Subcortically, the thalamus distributes incoming sensory signals to the somatosensory cortex in the postcentral gyrus, which contains a functional spatial organisation, where each part of the body is represented by a specific cortical area (Gallace & Spence, 2014; E. R. . Kandel et al., 2000). Within this somatotopic organisation, the hand is represented in a relatively large area in the upper medial part of the gyrus, mirroring its high tactile resolution abilities (Blatow et al., 2011; Huang et al., 2012). Once tactile information reaches the primary somatosensory cortex, it is further distributed to higher hierarchical areas, that are responsible for the detection of more complex features, such as shape or surface structure. Eventually, higher association areas like the superior parietal cortex, the insula, or frontal structures are addressed, where different features related to the percept are combined using feed-forward and feed-back connections (De Haan & Dijkerman, 2020). The complex neural circuits employed for tactile perception depend on the type of somatosensory processing, such as object recognition, action planning, or affective body perception, and spread widely across the cortex. Interestingly, parallel to visual imagery, tactile imagery also employs cortical structures largely corresponding to tactile perception (McNorgan, 2012; Schmidt et al., 2014; Yoo et al., 2003). Studying tactile perception networks, several studies demonstrated the activation of visual cortex areas in relation to tactile perception (Lacey & Sathian, 2014; Sathian & Zangaladze, 2002; Snow et al., 2014; M. Zhang et al., 2004), pointing towards the relevance of multisensory processing and, likely, the addition of visual imagery to tactile perception as a means to construe the multisensory world. One particularly prominent area with this regard is the lateral occipitotemporal complex (LOC), which has an important role in processing object forms across modalities, as it is not only visually shape-selective, but also haptically shape-selective (Amedi et al., 2007; M. Zhang et al., 2004), and particularly responds to crossmodal processing (Kassuba et al., 2013). Other cortical areas related to multimodal processing include the fusiform gyrus or the intraparietal sulcus (Kassuba et al., 2011). However, understanding the precise distribution of activation (let alone deactivation) patterns in relation to imagery and perception in multimodal processing remains an unresolved challenge in the field.

Generally, albeit being subject to debate for decades (e.g. Lacey et al., 2009; Lacey & Sathian, 2014; Pascual-Leone & Hamilton, 2001), the question as to whether multisensory cognitive processing is based on converging modality-specific sensory representations, or modality-inspecific "metamodal" processing (Pascual-Leone & Hamilton, 2001) remains unanswered. Traditionally, much of cognitive science has focussed on unisensory research, attempting to study the senses independently from one another (Bertelson & de Gelder, 2004). This contrasts the omnipresence of multimodal processing requirements throughout cognition in the multisensory world we live in. Like perception, imagery is typically employed in multi- rather than unisensory contexts. While visual imagery can aid cognitive processing in other modalities, it is also susceptible to changes based on sensory input from other modalities (Nanay, 2018). Previous research has predominantly discussed the integration of multisensory signals (Berger & Ehrsson, 2013; Ernst & Bülthoff, 2004; Kassuba et al., 2013), but there is also first evidence for the importance of inhibition in crossmodal sensory processing (Boorman et al., 2010; Daselaar et al., 2010; von Trott zu Solz et al., 2017). While this is in line with the role of inhibition as a fundamental principle of cognition, ranging from cellular to large-scale cortical processing (Gibson et al., 1999; Haider et al., 2013; Isaacson & Scanziani, 2011), a comprehensive model of multisensory imagery is lacking to this day. Consequently, further research on multisensory imagery processing and the effect of sensory, tactile input on visual imagery is required.

1.3 Objective

Visual imagery is crucial in numerous cognitive processes ranging from future planning to memory retrieval. Moreover, visual imagery is impaired in a variety of psychiatric disorders and is considered a promising tool for psychotherapy. However, the exact mechanisms of imagery creation remain unresolved to this day. It was thus the aim of this dissertation to advance knowledge on how mental images are created at the interface of internal priors and external sensory input. Using tactile object exploration as the basis for a visual imagery task closely models imagery generation at this interface of internal and external realities, while reflecting the multisensory world we live in. Therefore, we investigated the role of stimulus familiarity as well as the influence of tactile input on mental image creation in a visuotactile imagery paradigm. To examine the neurofunctional correlates of visual imagery creation, we used functional magnetic resonance imaging (fMRI) and asked the following two questions:

(1) How does stimulus familiarity influence visual imagery creation?

(2) Does tactile input inhibit visual imagery creation?

We hypothesised that (1), familiar object imagery would elicit more vivid imagery compared to imagery of unfamiliar objects, and that this processing benefit would be accompanied by corresponding higher visual cortical activity. We further hypothesised that top-down structures are more involved in familiar object imagery, while we anticipate that unfamiliar object imagery employs bottom-up somatosensory structures to a higher extent. Secondly, we hypothesised that (2) tactile input would inhibit visual imagery, reflected by lacking primary visual cortex involvement.

2 Material and Methods

2.1 Participants

Participants for the experiment were recruited via an official mailing list of Ludwig-Maximilians-University (LMU) Munich. The e-mail was distributed among all faculties except the faculty of psychology, to obtain participants with no prior knowledge of the applied questionnaires and concepts. The age span of the participants was limited to 18 - 29 years. Further, participants were required to have German as their mother tongue. Left-handers and participants that are not suited for an experimental MRI scan due to metal parts in the body, claustrophobia, or a current pregnancy, were excluded from the experiment. Further, participants with a pre-existing neurological or psychiatric disorder were excluded. In total, 116 people registered their interest to take part in the study. To ensure sufficient visual imagery ability, i.e. increased likelihood of successful task completion, participants were screened for a high imagery ability with the short version of Bett's Questionnaire upon Mental Imagery (QMI; Sheehan, 1967; see attachment 9.1). The QMI is a 35-item questionnaire, asking participants to rate the vividness of their imagery on a 7-point Likert scale ranging from 1 = 'perfectly clear and as vivid as the actual experience' to 7 = 'I am thinking about it, but I cannot imagine it'. The QMI-score is generated by the sum of Likert-ratings, with low scores indicating good imagery ability. Sample screening resulted in a low average QMI score of 67.8 (SD 13.3). Specifically, the sample showed good imagery ability in the visual domain, reflected by a mean score of 9.7 (SD 2.4) in the five visual imagery items of the QMI. In addition, participants were asked to take the Edinburgh handedness questionnaire (EHI) to ensure true right-handedness (Oldfield, 1971). The EHI is a 10-item questionnaire, asking participants to decide which hand they would use for day-to-day activities such as writing, toothbrushing, or cutting (see attachment 9.2). As a result of the questionnaire, a laterality quotient (LQ) is calculated. All participants that were invited to take part in the study were truly right-handed as assessed by the inventory (mean LQ = + 82.7 (SD = 12.6)). To ensure comprehensibility, both questionnaires were translated to German.

After the screening, 30 participants were invited to take part in the study. For an overview of their demographic and screening data, see *Table 1*. The sample consisted of 17 male and 13 female participants. All participants had normal or corrected-to-normal vision. All participants gave written consent to participate in the study and were financially reimbursed. The study was approved by the Ethics committee of the medical faculty of the LMU Munich.

Table 1: Overview of participant demographics and screening results. Provided are mean values (M), standard deviations (SD), and ranges.

	M (SD)	Range
Age	24.1 years (2.7)	19 - 29 years
QMI	67.8 (13.3)	49 - 110
QMI-visual	9.7 (2.4)	5 - 15
EHI	82.7 (12.4)	55.5 - 100

Note: QMI = Bett's shortened Questionnaire upon Mental Imagery; EHI = Edinburgh handedness inventory.

2.2 Procedure

All experiments took place during the daytime between 9 am and 5 pm to limit the influence of circadian rhythms on cognitive processes and experimental performance. The experiment's total duration was 1.5 h, including approximately 30 minutes of questionnaire participation, 40 minutes of fMRI scanning, and rest. The experiment commenced with the opportunity for participants to ask questions regarding the study and the consent form. After the consent form was signed by the participant and the experimenter, participants were asked to fill in the German Version of the Vividness of Visual Imagery Questionnaire (VVIQ; Marks, 1973; see attachment 9.3). The VVIQ is a 16-item questionnaire asking participants to rate the experienced vividness of their visual imagery of objects and scenes on a scale from 1 = 'perfectly clear and as vivid as normal vision' to 5 = 'no image at all, only 'knowing' that you are thinking about the object'. Such objects and scenes include for instance "a close friend" or "the rising sun". Before commencing with the fMRI procedure, participants were given an information sheet explaining the tasks of the study in detail (see attachment 9.4). Here, a financial incentivisation for focussed task completion was introduced. Participants were given the prospect of additional payments if they would a) manage to lie still, and b) succeed to recognise at least four of five images of the tactilely explored abstract objects after the experiment.

Participants then entered the fMRI scanner and had earplugs and headphones fitted to protect them from scanner noise. Instructions were shown via a monitor that projected onto a mirror attached to the head coil. After obtaining overview scans to check and improve scanner settings, at first, a 7 min resting-state scan was conducted, during which participants were asked to lie awake and still with their eyes closed. Next, participants performed two experiments with a duration of 18 and 14 minutes, respectively. The two experiments were always presented in the same order. This fixed order was installed to prevent verbal cues related to objects used in experiment 2 to interfere with bottom-up tactile exploration and imagination as required in experiment 1. To prevent effects of order within the experiments, two different versions of pseudorandomisation were applied. Visual instructions prompting the respective task in each trial were programmed using Presentation software (Neurobehavioral Systems, Inc., Berkeley, CA, USA, www.neurobs.com). Where required by the task, the respective objects were placed in the participants' hand by the experimenter standing on the left side next to the participant in the scanning room. The experimenter was always positioned at the same place and did not change between participants. She aimed to hand the objects to the participants without touching their hands and apart from that behaved as motionless and quietly as possible.

After the fMRI scan, participants were given the opportunity to rest. Then, they were asked to complete a questionnaire on the perceived difficulty of imagery creation and the vividness of the imagery they created during the different conditions of both experiments (see attachment 9.5). Difficulty was rated on a 4-point Likert scale ranging from '1 = very difficult' to '4 = very easy', while imagery vividness was rated on a 5-point Likert scale in accordance with the VVIQ, ranging from '1 = very clear and as vivid as normal vision' to '5 = no image at all, only being aware of thinking about an object'. In addition, participants completed a quiz trying to identify as many images of the five abstract objects explored during the experiment as possible (see attachment 9.6). The actual images were presented amidst two other very similar abstract object forms. Those were derived from different evolutionary steps of the actual object's design development, ensuring this task to be difficult enough to give proof of concentrated and successful task completion and imagery creation.

2.3 Stimuli

Stimuli for the first experiment consisted of ten objects for tactile exploration. These comprised five geometric, familiar objects: a cube, a pyramid, a rectangular cuboid, a cylinder, and a cone. Further, five highly abstract objects served as stimuli, unfamiliar to the participants and without predefined verbal notations (*Figure 4*). For the second experiment, only the five familiar figures were used as stimuli (*Figure 4a).* To exclude confounding effects of differences in surface texture or weight, all objects were specifically produced for the experiment using a 3D printer. Thermoplastic polymers were used for fused deposition modelling, and each printed layer was only 0.16 mm thick, ensuring a smooth surface. All figures were scaled to a maximal extension of 3,5 cm so they would fit a standard-sized palm. This is to ensure tactile exploration is ergonomic, feasible for the experimental paradigm, and as realistic as possible. To avoid confounding influence of shape-related differences between the familiar and unfamiliar objects, both categories comprised 3 angular structures and 2 structures including roundings.

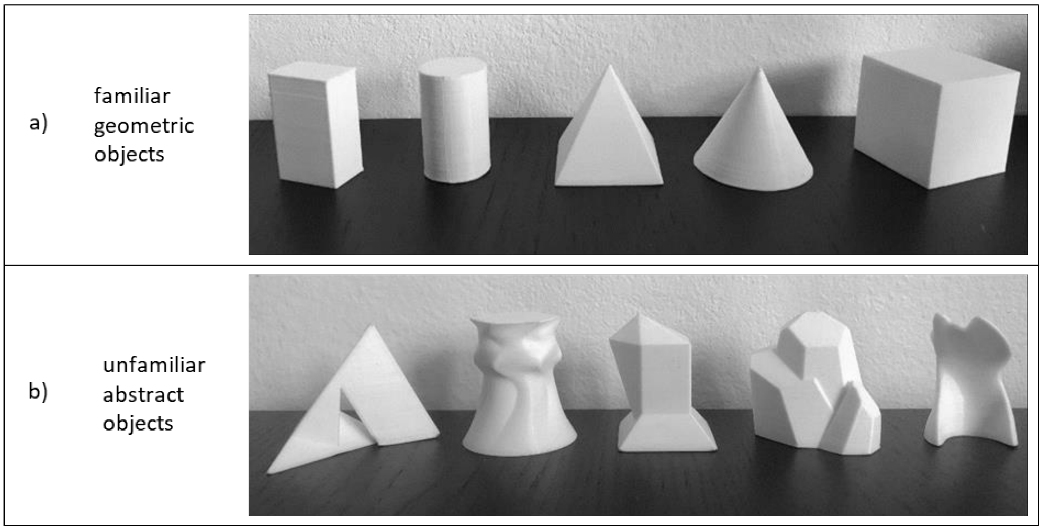

Figure 4. 3D printed (a) familiar geometric and (b) unfamiliar abstract objects used to create visual imagery based on tactile exploration. All figures are scaled to a maximum height of 3.5 cm.

2.4 Experimental Paradigms

2.4.1 Experiment 1 - How does familiarity influence visual imagery creation?

The experiment was designed to contain ten blocks per experimental condition. To investigate both the influence of familiarity and laterality, four conditions were derived in a 2x2 factorial design, with the factors laterality (left hand, right hand) and familiarity (familiar geometric vs. unfamiliar abstract objects), see *Figure 5.* Participants completed 40 trials over a duration of 18 minutes. The order of stimuli and blocks was pseudorandomised. At the beginning of the experiment, initial instructions were displayed for 10s. Trial-based instructions were displayed for 6s prior to each imagination period, and the respective object was handed to participants by the experimenter during this time. Participants were instructed to keep their eyes closed during the entire imagination period, which lasted 15s. They were informed that a green dot indicated that imagination was meant to continue, should they accidentally open their eyes before the end of the trial. Then, the object was taken away from the participants, signalising the end of the task. Each imagination period was followed by a 6s inter-trial rest, allowing the participants to relax and the haemodynamic response function to return to baseline. Visual instructions contained a colour-coded bar at the top to signalise the upcoming condition to the experimenter. Participants were instructed that they do not need to pay attention to these colour changes.

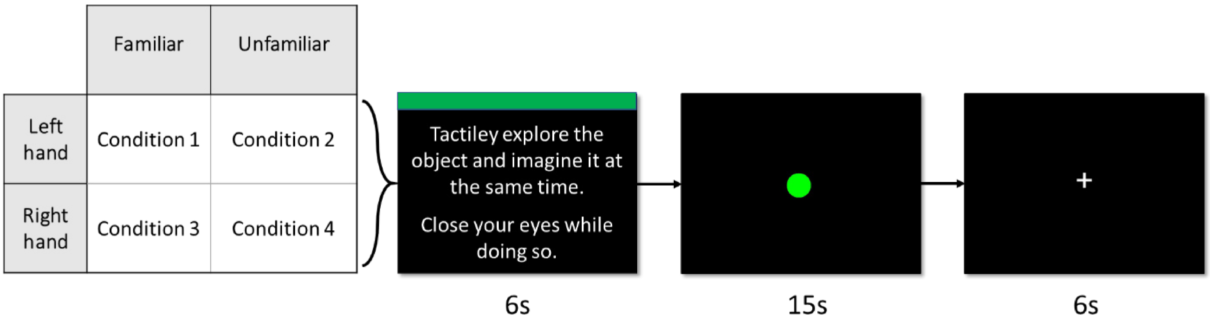

Figure 5. Experimental paradigm 1. Left: The table shows the four experimental conditions in a 2x2 factorial design with factors object familiarity, as well as laterality, i.e. the hand used for tactile exploration as the basis for visual imagery creation. Right: Exemplary display of instruction screens as viewed by participants including temporal sequence and duration of display (s = seconds).

2.4.2 Experiment 2 – Does tactile input inhibit visual imagery creation?

The second experiment also followed a block design, with three conditions of imagery creation involving varying degrees of tactile exploration of the objects to imagine. For each condition, there were eight blocks, resulting in a total of 24 trials. The order of stimuli and blocks was pseudorandomised. Initial instructions for the experiment were viewed for 10s once. During each trial, trial-based instructions were viewed for 6s prior to the imagination period which lasted 15s (see *Figure 6*). Participants were instructed to keep their eyes closed during the imagination period. Each imagination period was followed by a 6s inter-trial rest.

In the first condition (I), participants had to imagine a geometric object after getting a verbal, written instruction to do so. Therefore, participants had to create a visual image from memory without external, sensory stimulation. In the second condition (I&T), participants were instructed to tactilely explore a geometric object with their right hand, while creating a visual image of that object at the same time. The object was given directly into their right hand by the experimenter while participants were viewing the task instruction. In the third condition (I/T), the process of tactile exploration and visual imagination was temporally separated. Here, participants were handed the object as in the second condition but were instructed to tactilely explore it with their eyes open while looking at a fixation cross on a bright screen. The bright light and open eyes were employed to interfere with and avoid visual imagery creation during the phase of tactile exploration (Keogh & Pearson, 2011; Sherwood & Pearson, 2010). After 15s of tactile exploration, the object was taken away from the participants and they were instructed to imagine the object they had just explored with their eyes closed.

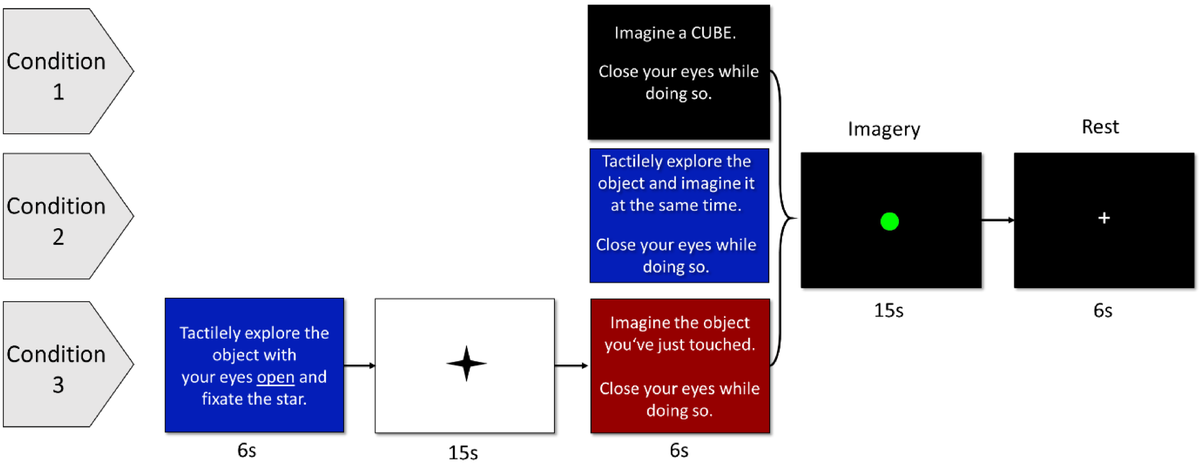

Figure 6. Experimental paradigm 2. Instruction screens as viewed by the participants including sequence of display and duration (s = seconds). Condition 1 = imagery without tactile input, condition 2 = imagery based on simultaneous tactile input of a familiar object handed to the participants by an experimenter, condition 3 = imagery period shortly after tactile exploration of a familiar object. Note that screen colours were relevant for the experimenter but not the participant, which was clarified prior to the experiment.

2.5 Methodology

2.5.1 Functional magnetic resonance imaging

To investigate the neurofunctional correlates of mental imagery creation, fMRI data was collected. Since the discovery of blood oxygen level-dependent (BOLD) signalling in the early 1990ies (Ogawa et al., 1990, 1992), neuroimaging research has experienced a dramatic increase in productivity, promoting a vast and growing body of knowledge on brain function. Today, the use of BOLD contrast based fMRI remains a highly popular technique in psychology and cognitive neuroscience, owing to its relatively good temporospatial resolution, non-invasiveness, cost-efficiency, and availability (Logothetis, 2008; Rosen & Savoy, 2012).

Magnetic resonance imaging makes use of the magnetic properties of hydrogen nuclei in the human body, which consist of a single proton. Normally, the magnetic moment of these protons is randomly aligned, but the strong magnetic field in the MRI scanner forces them to align parallel to this magnetic field, reaching an equilibrium state. The application of radio frequency (RF) pulses leads to the alignment of the protons' magnetic moment in a particular flip angle (FA) relative to the magnetic field. After the RF pulse ends, the magnetic moment of the protons returns to its equilibrium orientation by performing a rotation motion (Larmor precession). The frequency of this process and the emitted energy depend on the magnetic characteristics of the tissue surrounding the protons and lead to changes in the magnetic field, which induce an electrical current in the coils of the MRI scanner. This electrical signal is then Fourier-transformed to obtain a detailed image of the tissue (Liang & Lauterbur, 2000; Weishaupt et al., 2006).

BOLD imaging of differentially activated brain areas is facilitated by exploiting the difference in magnetic susceptibility of oxygenated and deoxygenated haemoglobin. Deoxygenated haemoglobin is paramagnetic and hence causes magnetic field distortions, resulting in a weakened BOLD signal (Ogawa et al., 1990; Pauling & Coryell, 1936; Thulborn et al., 1982). Functional imaging of brain activity therefore relies on the synchronisation of cerebral blood flow (CBF) to neuronal activity *(see Figure 7)*. As the brain itself has no relevant energy storage capacities, glucose and oxygen need to be delivered to active brain areas via the bloodstream in real-time. Therefore, tight neurovascular coupling mechanisms are applied (Kaplan et al., 2020; Roy & Sherrington, 1890), ensuring energy supply in particular for, but not limited to synaptic signalling, which was found to be the main component of the brain’s energy consumption (Attwell & Iadecola, 2002; Attwell & Laughlin, 2001; Harris et al., 2012). Initially, neuronal activity and hence energy consumption in active brain areas leads to an increase of deoxygenated haemoglobin, represented by a BOLD signal dip. Shortly thereafter, blood supply (CBF) and cerebral blood volume (CBV) increase in reaction to the energy demand, peaking about five seconds after stimulus onset (Buxton, 2012). This increase leads to an overshoot of oxygen supply, as the actual metabolic rate of oxygen consumption ($CMRO_2$) in response to neuronal activity does not match the increase of CBF (Fox & Raichle, 1986). Consequently, oxygen concentration in the veins of active brain regions increases, leading to over-oxygenation and a higher BOLD signal (Buxton, 2012; Hillman, 2014). After approximately ten seconds, the haemodynamic response function returns to baseline, preceded by a temporal undershoot which is debated to be caused by delays in vascular compliance as well as maintained increases in $CMRO_2$ (Kim & Ogawa, 2012). Despite the BOLD signal change being relatively small at 1-3%, it is very sensitive to changes in deoxygenation (Logothetis, 2008). The BOLD signal is thus an indirect, yet robust measure of brain activity, that is widely applied and accepted in spite of the ongoing debate on the detailed neurophysiologic basis of the measurement (Rosen & Savoy, 2012; Sutterer & Tranel, 2017, but see also 4.4).

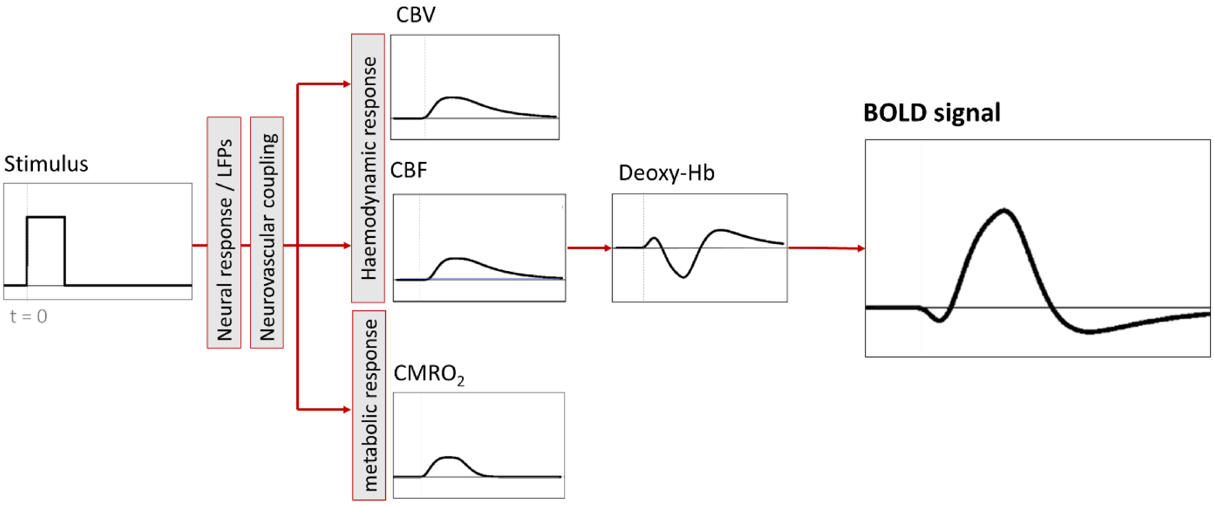

Figure 7. Constituents of the BOLD signal in response to a stimulus (t=0). The neural response is dominated by local field potentials and causes the coupled haemodynamic response. The latter is characterised by an increase in cerebral blood flow (CBF) and volume (CBV). The metabolic rate of oxygen consumption ($CMRO_2$) lags the increase of CBF and CBV, leading to a local decrease in deoxygenated haemoglobin (Deoxy-Hb). The BOLD signal is collected based upon the magnetic properties of deoxygenated haemoglobin and is characterised by an initial undershoot, followed by the oxygen overshoot, and a subsequent post-stimulus undershoot (modified from Buxton, 2012).

2.5.2 FMRI data collection

The fMRI experiment was conducted using a 3T scanner (PHILIPS Ingenia, Best, the Netherlands) at the University hospital of LMU Munich. To minimize movement artefacts, foam cushions surrounded the participant’s heads. Participants viewed instructions via a special monitor which projected onto a mirror system mounted onto the head coil of the scanner. For anatomical reference and to exclude morphological anomalies, a structural T1-weighted 3D turbo field gradient echo sequence was performed using parallel sensitivity encoding (SENSE)-imaging, which allows for detailed yet fast data collection. T1 images were acquired axially (parallel to the anterior-posterior commissure line) and in ascending sequence with the following parameters: RF pulse sequence repetition time (TR) = 8.194 ms, echo time (TE) from first RF pulse to spin-echo = 3.746 ms, FA = 8°, field of view (FOV) = 240 x 240 mm, number of slices = 240, spatial resolution = 0.94 x 0.94 x 1mm. A trained radiologist checked the structural images of all participants for pathologies. For functional BOLD imaging, T2-weighted axial gradient echo planar imaging (EPI)-scans were acquired in sequential ascending order, using parallel SENSE-imaging and the following parameters: TR = 2500 ms, TE = 30.001 ms, FA = 90°, FOV = 237.18 x 237.18 mm, number of slices = 43, spatial resolution = 1.65 x 1.65 x 3 mm, interslice gap = 3 mm. Regularly, 452 functional images were obtained for each participant during experiment 1, and for experiment 2, 345 functional images were collected.

2.6 Data analysis

2.6.1 Behavioural data analysis

Likert-type scale ratings of vividness and difficulty for each condition were plotted as histograms, and non-parametric statistical testing was applied. For experiment 1, Wilcoxon signed-rank tests were performed to test the influence of familiarity and laterality on imagery creation. To analyse differences in vividness and difficulty ratings between the three conditions of experiment 2, Friedman's tests were performed. Significance levels were set at $\alpha = .05$. Behavioural data analysis and graph creation were executed using GraphPad Prism (Version 9.2.0 for Windows, GraphPad Software, San Diego, California USA, ww.graphpad.com).

2.6.2 FMRI data analysis

Preprocessing

FMRI data analysis was conducted using statistical parametric mapping software (SPM 12; The Wellcome Center for Neuroimaging, University College London, UK; http//www.fil.ion.ucl.ac.uk/spm) in MATLAB (Version 9.4.0; Natick, Massachusetts: The MathWorks Inc.). To allow net magnetisation to reach a steady state, the first five images of each run were discarded from further analyses. The last image of each acquisition was also excluded to avoid artefacts by partial coverage of brain tissue in the final slice of some participants. Images acquired from each subject were realigned to one single image of the same subject to account for movement between scans. Deviations from the reference image in transformation and rotation (six parameter, rigid-body spatial transformation) were stored in each image's file headers and included as covariates in later statistical analyses of the data. Here, we chose scan number 50 as the reference scan to account for our motion-sensitive task. This assumes that participants become experienced in tactile exploration and movement patterns after completing the first trials. As a result, scans contain fewer movement artefacts than in the very first trials, while participants are still highly concentrated. In a two-pass procedure, images were subsequently registered to the mean of the realigned data and resliced accordingly to match the reference image. Next, to correct differences in the acquisition time of the 43 slices scanned in ascending order, slice time correction was conducted. Timing differences between single slices of one image are corrected by introducing a phase shift into the signal which aligns signals of all slices temporally with slice 1 as the reference slice. Next, each subject's realigned mean functional images were coregistered to the structural T1 image for alignment of functional and anatomical data. Functional images were then segmented into grey and white matter by combining probabilities of each subject's image intensity distribution with probability maps of the likelihood of a tissue belonging to grey or white matter (or areas outside the brain) derived from the ICBM space template of European brains (SPM). Spatial normalisation to the ICBM template was administered in the same step, aligning brain images of all subjects to the common European ICBM space for comparability and scaling voxel sizes to 3 x 3 x3 mm. To reduce noise and remaining differences in functional and gyral anatomy between subjects, images were smoothed with a Gaussian kernel (full width at half maximum: 8 mm).

First-level analysis

To analyse within-subject data, first-level analyses were conducted for each subject separately. After all voxels had been aligned and made consistent in location over time during preprocessing, a general linear model was built using SPM12, incorporating the BOLD signal as the dependent variable. The design matrix was specified based on the experimental paradigm and individual logfiles recorded during scanning. The resulting stimulus boxcar function was convolved with a canonical haemodynamic response function. Further, realignment parameters were included as a regressor to account for movement artefacts, as was an error matrix. Data were orthogonalised and eventually, parameter estimates (β-values) were calculated that account for task-related differences of the BOLD signal. After model estimation, contrasts were specified for each subject using SPM's contrast manager. For experiment 1, F-contrasts were created using a 2 x 2 factorial design, as were t-contrasts of each condition vs. baseline. For experiment 2, F-contrasts and t-contrasts for the three conditions versus (vs.) baseline were calculated.

Second-level analysis

For *whole-brain analyses (WBA)* on the group level, a mixed-effects model with a one-sample t-test was applied for experiment 1, contrasting familiar and unfamiliar object conditions, as well as left- and right-hand-based tactile exploration. Results of experiment 2 were computed using linear t-contrasts comparing each condition to the two remaining conditions. Results for the WBA were adjusted for multiple testing by using family-wise error (FWE) Bonferroni correction at a significance level of $p < .05$. For exploratory purposes, results were also examined on the uncorrected significance level of $p < .001$. Throughout, a cluster-level false discovery rate (qFDR) < .05 was used as an inclusion criterion for significantly activated clusters, to further limit the probability of false positive findings. Cortical regions were labelled using SPM's anatomy toolbox (Eickhoff et al., 2005) and figures were created using bspmview toolbox (Spunt, 2016).

To additionally analyse task-related differences in specific cortical regions, region of interest (ROI) analyses were conducted using the MarsBar toolbox (Brett et al., 2002). On the one hand, *structural ROI* analyses were planned based on anatomical data of regions that are known to be relevant for visual imagery and tactile exploration. These include the calcarine sulci, the middle occipital gyri, the postcentral gyri, the precentral gyri, the supplementary motor areas, the superior parietal cortices, as well as regions related to memory retrieval in the context of imagery, i.e. the parahippocampal gyri and the precunei (for a recent meta-analysis see Winlove et al., 2018, and compare 1.1.3). Anatomical masks for the ROI analyses were created using Wake Forest University (WFU) PickAtlas (Version 3.0.5, Maldjian et al., 2003, 2004), with coordinates derived from the Automatic Anatomical Labelling Atlas (AAL; Tzourio-Mazoyer et al., 2002). On the other hand, to further explore the data, *functional ROI analyses* were intended to be computed based on potential novel findings of the WBA. While these are naturally biased towards the region of observed additional activation that serves as the mask for ROI creation, they still allow comparisons (yet not inferences) between the different conditions of the experiment (Poldrack, 2007). These functional ROIs have been created by overlaying spheres with 5mm radii around peak voxels of significant clusters identified by the WBA contrasts. For experiment 1, both left and right middle temporal gyri have been analysed as ROIs. For experiment 2, no additional functional ROIs were defined. All ROI analyses were calculated using β-parameter estimates as specified by SPM. Statistical analyses were computed, and figures were created using GraphPad Prism (Version 9.2.0, GraphPad Software, San Diego, California, USA). For experiment 1, paired t-tests have been performed to test for significant differences between familiar and unfamiliar, as well left- and right-handed tactile exploration-based imagery. For experiment 2, repeated measures one-way analyses of variance (ANOVA) were computed to test for significant β-value differences between the three conditions. Post-hoc testing was performed using Tukey's correction for multiple comparisons. Significance levels were set at $\alpha = .05$.

3 Results

3.1 Behavioural Results

3.1.1 VVIQ and Quiz

Collected data of the VVIQ (n = 30) revealed a mean score of 31.07 (SD = 6.34), with scores ranging from 18 to 43, indicating very good imagery ability of the participants. The quiz testing recognition of unfamiliar objects after the experiment revealed high performance with a median of 5 out of 5 correct answers (see *Figure 8*). Two participants scored below the cut-off set at three out of five correct answers. Those two participants have been excluded from fMRI analyses of experiment 1, as their specific imagery ability in this visuohaptic, particularly demanding imagery task has not met our imagery proficiency demand.

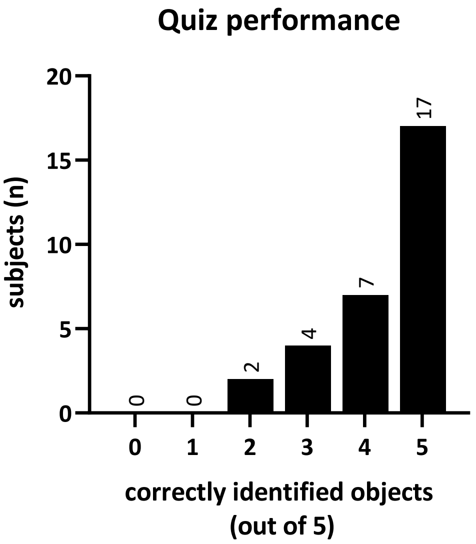

Figure 8. Frequency distribution of scores for the recognition quiz (n = 30) that took place after the fMRI experiment to check imagery ability especially for the more complex unfamiliar objects.

3.1.2 Vividness and difficulty ratings

Experiment 1

Frequency distributions for participants' perceived vividness and difficulty of visual imagery during the four conditions (familiar/unfamiliar object imagery; left-/right-handed exploration) were plotted (*see Figures 9 and 10*). A Wilcoxon signed-rank test of ratings of perceived difficulty revealed a highly significant difference between visual image creation from tactilely explored familiar objects (F) compared to unfamiliar, abstract objects (U; W = 361, p < .001). Participants rated imagery creation of abstract, unfamiliar objects to be significantly more difficult than imagery of familiar objects (F: median= 1; U: median = 3). The Wilcoxon signed-rank test for vividness-ratings of imagery creation when exploring familiar vs. unfamiliar objects also revealed a highly significant difference with higher vividness for imagery of familiar objects (W = 435, p < .001; F: median = 1; U: median = 3).

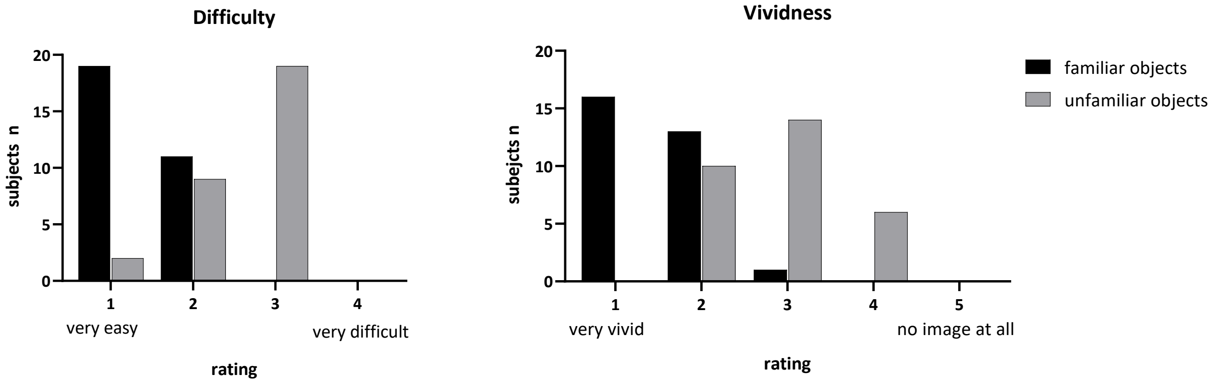

Figure 9. Frequency distributions of Likert-type scale ratings of difficulty and vividness for familiar vs. unfamiliar object imagery.

Wilcoxon signed-rank tests were also performed for difficulty and vividness ratings comparing left- and right-handed tactile exploration-based imagery. They revealed a significant difference between the difficulty of mental images created from right-handed (RH) vs. left-handed (LH) exploration (W = -35, p = .039), with imagery supported by RH exploration rated to be less difficult than imagery created by LH tactile exploration (RH: median = 2; LH: median = 2). Ratings of perceived vividness of imagery created during tactile exploration with the right hand were not significantly different from those of left-handed object exploration (RH: median = 2; LH: median = 2; W = -27, p = .070).

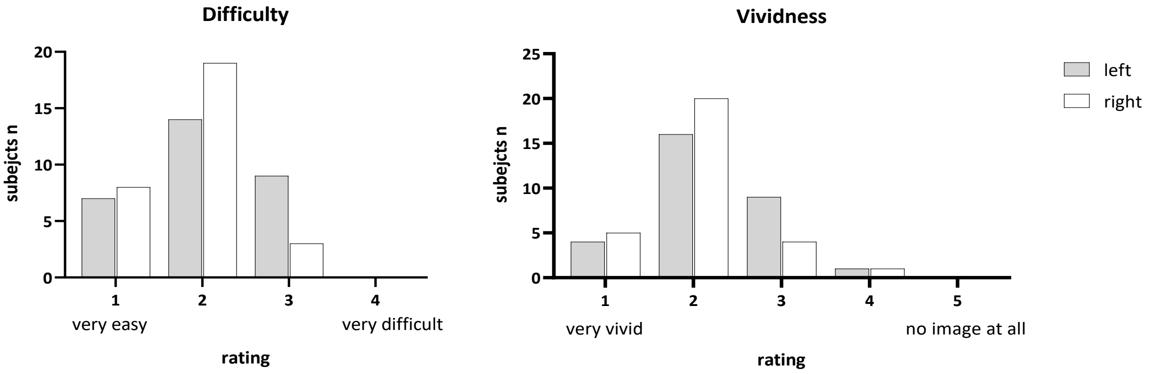

Figure 10. Frequency distributions of Likert-type scale ratings of vividness and difficulty of imagery based on left- and right-handed tactile exploration.

Experiment 2

Data obtained from Likert-type scale ratings for difficulty and vividness during the three different conditions of experiment 2 are shown in *Figure 11*. A non-parametric Friedman's test revealed no significant difference in difficulty ratings between the three conditions (χ^2 (2) = 1.20, p = .549). For vividness ratings, Friedman's test also revealed no significant difference between conditions (χ^2 (2) = 1.37, p = .504). Median difficulty and vividness ratings for all conditions were = 2.

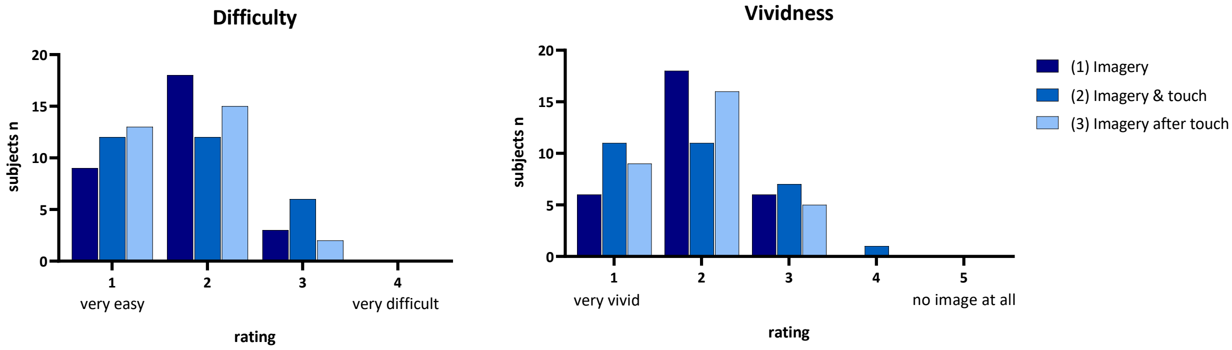

Figure 11. Frequency distributions of Likert-type scale ratings for difficulty and vividness during the three conditions of experiment 2.

3.2 FMRI results

3.2.1 Experiment 1

Final sample

In experiment 1, successful imagery was of critical importance, particularly regarding the unfamiliar objects. Therefore, the two participants that failed to meet recognition criteria in a post-experimental quiz (see 3.1.1) were excluded from the fMRI analysis. Due to a technical error of the fMRI scanner, five participants' data could not be taken into consideration for analysis. As the technical error affected the data of one participant that failed the quiz, a total of six participants had to be excluded, resulting in the analysis of 24 participants' data (12 of which were female).

Whole-brain analyses

Contrasts of imagery of familiar objects (F) vs unfamiliar objects (U) revealed no significant differences on the FWE-corrected significance level of p < .05, that withstood q(FDR) < .05. The reverse contrast (U > F) revealed no significant activations either. Comparing visual imagery while exploring objects with either the left or right hand revealed additional activation in the respective contralateral somatomotor and somatosensory areas, as well as the ipsilateral cerebellum *(see Table 2)*. Aside from these expectable anatomical representations of the sensorimotor system, no significant differences were detected at p(FWE) < .05.

Table 2. WBA results of experiment 1 at cluster-level p(FWE) < .05. Contrasted are imagery creation based on familiar objects (F) and unfamiliar objects (U), as well as imagery creation based on left-handed tactile exploration (L) and right-handed tactile exploration (R). Reported are significantly activated clusters including coordinates of peak voxels and comprised anatomical regions ordered by extent, where applicable.

contrast	brain region	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
F > U	-							
U > F	-							
L > R	Post- & precentral gyrus	R	267	45	-22	59	10.31	6.24
	Cerebellum (IV-VI)	L	140	-15	-55	-19	9.31	5.94
	Posterior insula, Putamen	R	10	36	-7	-4	7.50	5.28
R > L	Post- & precentral Gyrus	L	224	-45	-19	50	8.50	5.66
	Cerebellum (IV-VI)	R	54	15	-55	-22	7.58	5.31

Note: F = Familiar object imagery, U = unfamiliar object imagery, R = right, L = left, coordinates in Montreal Neurological Institute (MNI) space, T = T-statistics reported on peak-level, z = z-statistics reported on peak-level.

At the more explorative significance level of p(uncorrected) < .001, restricted to q(FDR) < .05, additional activation was found during familiar compared to unfamiliar object imagery. These additionally activated areas during familiar object imagery comprise large clusters in the right and left postcentral gyri *(Table 3, Figure 12).* For the reverse contrast of unfamiliar > familiar object imagery, no significant voxels were found. Concerning laterality, the comparison of left-hand based vs. right-hand based imagery creation revealed additional, albeit exploratory, insights: besides the somatosensory regions that were already showing significant additional activation in the stricter p(FWE) < .05 analysis, additional activation during LH imagery was observed in the right midcingulate cortex (MCC), as well as in the right rolandic operculum and the left caudate nucleus. The reverse contrast (R > L) revealed additional BOLD signal increases in the middle temporal gyri of both hemispheres, as well as in the left midcingulate cortex (MCC), and left rolandic operculum.

Table 3. WBA results of experiment 1 at cluster-level p < .001. Contrasted are imagery creation based on familiar objects (F) and unfamiliar objects (U), as well as imagery creation based on left-handed tactile exploration (L) and right-handed tactile exploration (R). Reported are significantly activated clusters including coordinates of peak voxels and comprised anatomical regions ordered by extent, where applicable.

contrast	brain regions	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
F > U	Postcentral Gyrus, inferior parietal lobule	R	1389	48	-31	59	6.63	4.91
	Postcentral Gyrus, inferior & superior parietal lobule	L	425	-60	-19	38	5.68	4.45
U > F	-							
L > R	Post- & precentral gyrus	R	1020	45	-22	59	10.31	6.24
	Rolandic Operculum	R	460	36	-7	-4	7.50	5.28
	Cerebellum (IV-VI)	L	447	-15	-55	-19	9.31	5.94
	Caudate Nucleus	L	64	-18	-31	26	5.43	4.31
	MCC	R	52	9	-19	50	5.66	4.44
R > L	Post- & Precentral Gyrus	L	801	-45	-19	50	8.50	5.66
	Cerebellum (IV-VI)	R	385	15	-55	-22	7.58	5.31
	Rolandic operculum	L	99	-42	-22	17	5.19	4.18
	MCC	L	85	-6	-25	44	5.78	4.50
	Middle Temporal Gyrus	L	66	-51	-61	8	5.97	4.59
	Middle Temporal gyrus	R	63	60	-61	14	5.90	4.56

Note: F = Familiar object imagery, U = unfamiliar object imagery, R = right, L = left, MCC = Midcingulate Cortex, coordinates in Montreal Neurological Institute (MNI) space, T = t-statistics, z = z-statistics, both reported on peak-level.

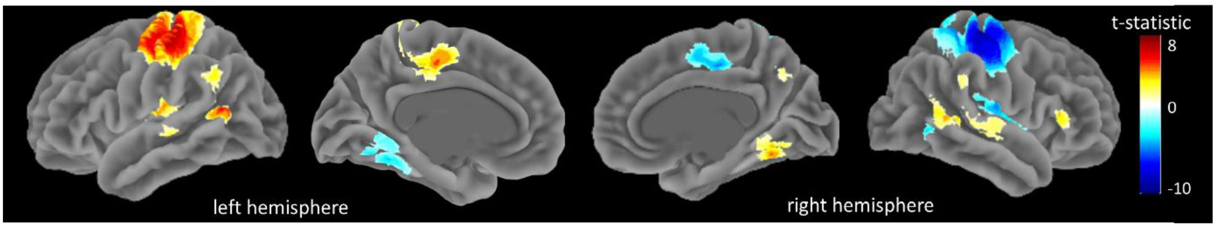

Figure 12. BOLD signal differences when contrasting imagery creation based on left- vs. right-handed tactile exploration at p < .001. Right-handed exploration led to additional activation in the left pre- and postcentral gyri, right cerebellum, bihemispheric middle temporal gyri, left midcingulate cortex (MCC), and left operculum (displayed in red shades). Left-handed exploration-based imagery led to additional activation in right hemispheric pre- & postcentral gyri, left cerebellum, right MCC, and Rolandic operculum (displayed in blue shades).

ROI analysis

Parameter estimates (β-values) derived from the WBA full-factorial design were used to compute ROI analyses of experiment 1. For each of the eleven predefined structural ROIs, paired t-tests have been calculated to identify significant differences in parameter estimates between imagery of familiar (F) and unfamiliar (U) objects on the one hand, and imagery based on left- and right-handed exploration (LH/RH) of these objects on the other hand (*Figure 13*).

In the calcarine region (left and right hemisphere; L&R), analyses neither revealed significant differences in parameter estimates between familiar and unfamiliar objects (t (23) = 0.825, p = .418), nor between left- and right-handed exploration (t (23) = 1.02, p = .319). Activity in the middle occipital cortex (MOC; L&R) also did not differ significantly between F and U (t (23) = 1.91, p =.069), or LH and RH (t (23) = 0.058, p = .954). In the left postcentral gyrus, a significant difference was found between imagery of familiar and unfamiliar objects (t (23) = 2.17, p = .040), with higher β-values for familiar object imagery. In this ROI, the comparison of left- and right-handed exploration serves as a control and is indeed highly significant with higher activation estimates in the left postcentral gyrus during right-handed exploration (t (23) = 5.72, p < .001), reflecting neuroanatomical structures. Paired t-test of parameter estimates of the right postcentral gyrus also revealed significant differences regarding both experimentally manipulated factors. Parameter estimates were significantly higher during familiar object imagery compared to unfamiliar object imagery (t (23) = 5.04, p < .001), and, in line with the laws of neuroanatomy, parameter estimates were significantly higher during LH compared to RH (t (23) = 6.09, p < .001). Precentral gyrus β-value analyses over the left hemisphere revealed no significant difference between F and U (t (23) = 1.43, p = .167), while, expectedly, there was a highly significant difference with higher parameter estimates for RH vs. LH (t (23) = 4.27, p < .001. Activation estimates of the right precentral gyrus differed significantly between F and U conditions, with higher parameter estimates for imagery of familiar objects (F) (t (23) = 4.46, p < .001). As expected, RH and LH also differed significantly with greater activation in the LH condition (t (23) = 5.56, p < .001). Parameter estimates of the parahippocampal cortex (L&R) revealed no significant difference between F and U (t (23) = 1.14, p = .265), as well as between LH and RH (t (23) = 0.255, p = .801). Similarly, parameter estimates of the precuneus (L&R) revealed no significant differences, neither between F and U (t (23) = 0.081, p = .936), nor between left- and right-handed tactile exploration-based imagery (t (23) = 1.77, p = .090). Activation in the left superior parietal cortex was significantly higher for familiar compared to unfamiliar object imagery (t (23) = 3.37, p = .003), while there was no significant difference between LH and RH in this region (t (23) = 0.875, p = .391). Parameter estimates within the left supplementary motor area (SMA, L) differed significantly with regards to the familiarity of imagined objects (t (23) = 2.51, p = .019). Here, β-values were higher for familiar object imagery compared to unfamiliar object imagery. Between LH and RH, there was no significant difference in activation estimates of the left SMA (t (23) = 1.06, p = .301). Mirroring the left SMA, the right SMA also revealed a significant difference between higher parameter estimates for F and lower estimates for U (t (23) = 2.76, p = .011), while LH and RH did not differ significantly (t (23) = 1.90, p = .070).

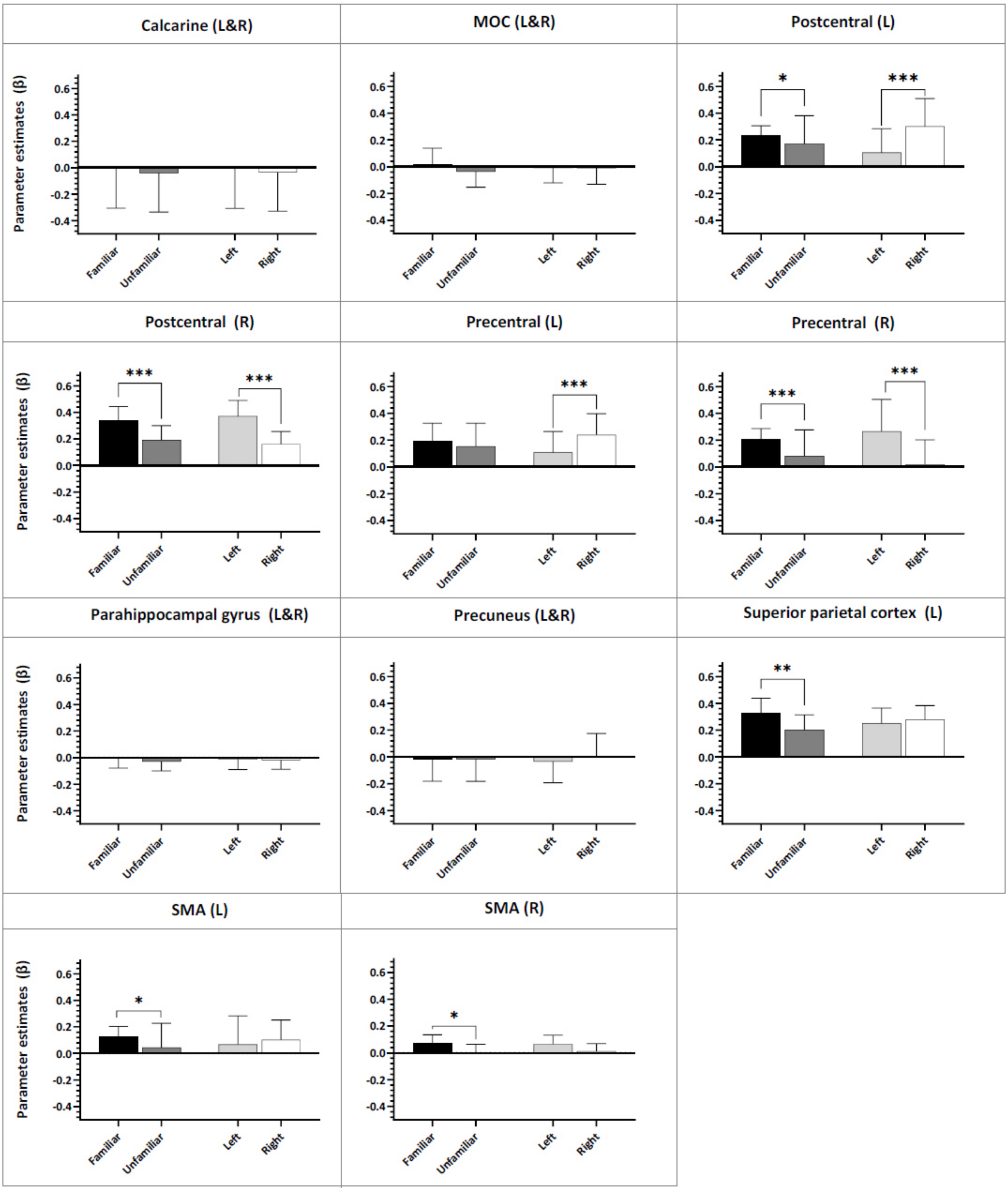

Figure 13. ROI analysis results of experiment 1, in regions relevant to visual imagery processing. Results were computed by paired t-tests based on parameter estimates of familiar vs. unfamiliar object imagery, as well as left-handed and right-handed tactile exploration-based imagery. Note: MOC = middle occipital cortex, SMA = supplementary motor area, L = left, R = right; error bars: 95% confidence interval (CI); Significance levels: * = p < .05, ** = p < .01, *** = p < .001.

In addition to the structural ROI analyses described above, the middle temporal gyri (MTG) were identified as an additional ROI worth investigating based on the WBA results. Accordingly, functional ROI analyses were computed based on spheres of 5mm radii around the MNI coordinates of the peak voxels located in both MTG, as identified during WBA *(Figure 14*). Paired t-tests were performed revealing no significant difference between familiar and unfamiliar object imagery for both right MTG (t (23) = 0.503, p = .620), and left MTG (t (23) = 1.10, p = .281). However, MTG parameter estimates during right-handed exploration-based imagery were found to be significantly less negative, than those of left-hand based imagery in the left MTG (t (23) = 5.40, p < .001), as well as in the right MTG (t (23) = 5.33, p < .001).

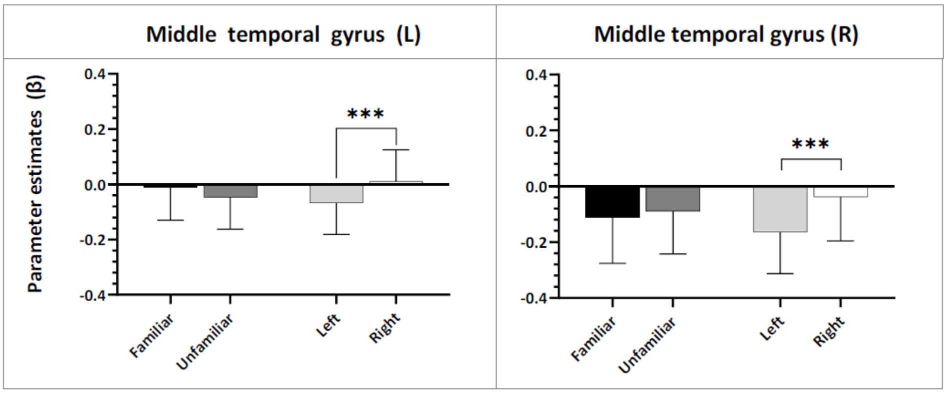

Figure 14. Functional ROI analysis of the middle temporal gyri (MTG). Paired t-tests were computed for left and right hemispheric MTG, and for familiar vs. unfamiliar object imagery, as well as for left- and right-hand tactile exploration-based imagery. L = left, R = right; error bars: 95% CI; significance levels: * = p < .05, ** = p < .01, *** = p < .001.

3.2.2 Experiment 2

Final sample

In addition to the five subjects discarded from analyses due to a technical error during scanning (see 3.2.1), two subjects had to be excluded from analysis for the second experiment due to technical errors in logfile recording and data storage. Eventually, 23 participants' data (12 of which were female) was used for analyses.

Whole-brain analysis

Subtraction analyses were conducted to identify differences and similarities between the three conditions of experiment 2. A significant difference in the activation pattern was observed when contrasting condition 1 (imagery only; I) to condition 2 (imagery creation with simultaneous tactile exploration; I&T; *see Table 4*). The areas additionally activated in condition 1 (I) were a cluster located in the postcentral gyrus, spreading onto the precentral gyrus, with peak voxels corresponding to somatosensory as well as motor hand areas (Blatow et al., 2011). Additionally, there were suprathreshold clusters located in the right cerebellum, as well as in the supplementary motor areas (SMA) located in the posterior medial frontal gyrus of both hemispheres. Additionally, a cluster was located in the left superior frontal gyrus.

Table 4. WBA results of experiment 2 at cluster-level p(FWE) < .05. Contrasted are conditions **1 (I) > 2 (I&T).** Clusters with higher activation during imagery of objects without tactile input (I) compared to tactile exploration and simultaneous imagery (I&T) are reported including peak-voxel coordinates and anatomical labels, ordered by extent where applicable.

contrast	brain region	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
I > I&T	Post- & precentral gyrus	L	369	-48	-25	53	11.44	6.47
	Cerebellum VI	R	90	24	-55	-19	8.98	5.77
	SMA	L	20	-6	-4	53	7.91	5.39
	Superior Frontal gyrus	L	10	-18	-7	68	7.80	5.35
	SMA	R	9	9	-1	53	7.90	5.38

Note: SMA = supplementary motor area, coordinates in Montreal Neurological Institute (MNI) space, T = t-statistics, z = z-statistics, both reported on peak-level.

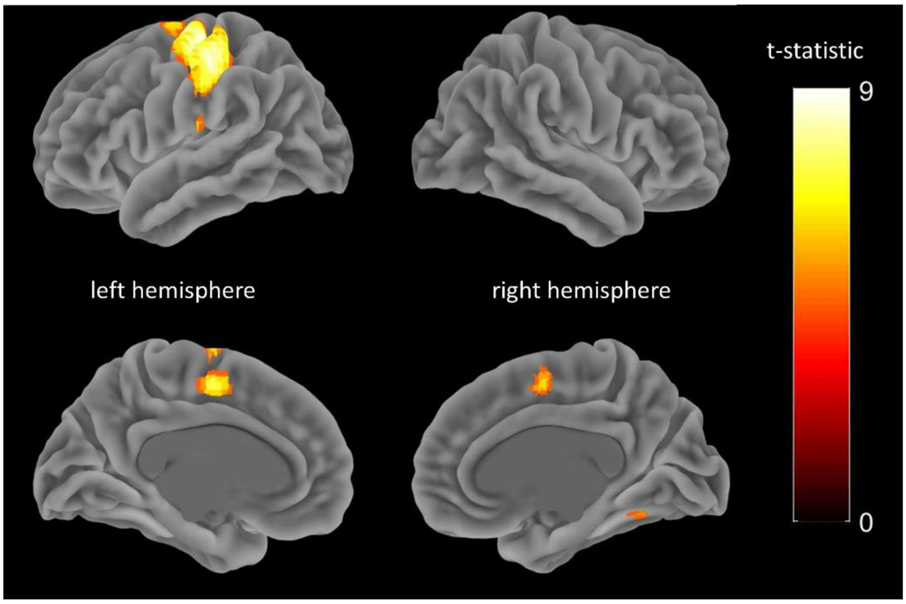

Figure 15. Additionally activated brain regions when comparing imagery creation without tactile input (I) to imagery creation with simultaneous tactile input (I&T) at p(FWE) < .05 on cluster-level. Regions comprise parts of the left post- and precentral gyrus, left superior frontal gyrus, bihemispheric supplementary motor areas, as well as the cerebellum (not depicted here).

None of the remaining contrasts revealed further significant BOLD signal changes at p(FWE) < .05 considering a cluster level qFDR < .05, including the reverse contrast of multimodal imagery (I&T) > imagery without external input (I). Similarly, no additionally activated brain areas were found when contrasting simultaneous imagery & touch (I&T) to imagery after a preceding period of tactile exploration (I/T) in both directions of comparison. Likewise, contrasts of mere imagery creation (I) and imagery creation after preceding tactile exploration (I/T) revealed no significant results at p(FWE) < .05 in both directions of comparison.

Additional contrasts were calculated for subcomponents of condition 3 (I/T) at the p(FWE) < .05 level, to examine efficacy of the paradigm (*Table 5, Figure 16*). The temporal succession and similar duration of the tactile exploration and imagery phases allowed to contrast the two subcomponents to control whether the imagery disruption during the tactile exploration phase, i.e. the bright fixation screen, actually led to disruption of visual imagery. Indeed, the visual cortex showed higher activation during the imagery period compared to the antecedent tactile exploration, pointing towards successful suppression of visual cortex activity during tactile exploration by the applied distraction paradigm. Comparisons of the tactile exploration period to the subsequent imagery period revealed no additional BOLD signal changes at the p(FWE) < .05 level.

Table 5. WBA results contrasting subcomponents of condition 3 (I/T > T). Analyses at p(FWE) < .05 on cluster-level. Contrasted were the subsequent imagination period to the preceding tactile exploration period, which coincided with visual distraction. Reported are significantly activated clusters including coordinates of peak voxels and comprised anatomical regions ordered by extent, where applicable.

contrast	brain region	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
I/T > T	Calcarine & lingual gyri	L + R	29	3	-88	-1	6.40	4.53
	Lingual & fusiform gyrus	L	22	-24	-88	-10	6.60	4.85

Note: L = left, R = right, coordinates in Montreal Neurological Institute (MNI) space, T = t-statistics, z = z-statistics, both reported on peak-level.

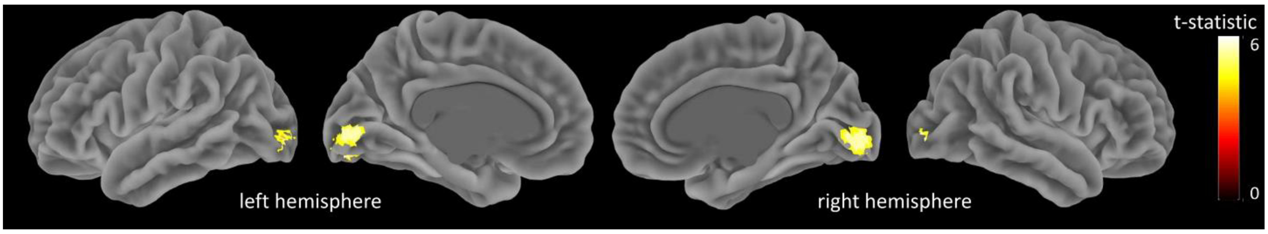

Figure 16. Control contrasts of imagery after preceding tactile object exploration at p(FWE) < .05. Contrasting imagery (I/T) to the tactile exploration period (T) during which visual imagery was aimed to be suppressed by a bright screen revealed additional activation in visual cortical areas (lingual, calcarine, fusiform gyri), indicating successful visual suppression during (T).

For exploratory reasons, the results of the contrasts described above were also examined at p(uncorr.) < .001, while accounting for the high likelihood for false positives by only considering those clusters with a qFDR < .05 on the cluster level. For the comparison of condition 1 (I) to condition 2 (I&T), suprathreshold clusters largely mirrored those obtained at the stricter level of p(FWE) < .05, with additional cluster components in the right Rolandic operculum. On this more liberal significance level, the reverse contrast (I&T > I) revealed additional clusters in the left and right middle occipital gyri (*Table 6, Figure 17*).

Table 6. WBA results of experiment 2 at cluster-level p < .001 (I; I&T). Contrasted are imagery creation based on verbal cues (I) and imagery creation based on tactile object exploration (I&T). Reported are significantly activated clusters including coordinates of peak voxels and comprised anatomical regions ordered by extent, where applicable.

contrast	brain region	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
I > I&T	Post- & precentral gyrus	L	1614	-48	-25	53	11.84	6.47
	Cerebellum VI	R	344	24	-55	-19	8.98	5.77
	Postcentral gyrus, Rolandic Operculum	R	222	60	-16	32	6.04	4.59
I&T > I	Middle occipital gyrus	R	281	39	-85	8	5.43	4.28
	Middle occipital gyrus	L	209	-33	-85	26	6.16	4.65

Note: L = left, R = right, coordinates in Montreal Neurological Institute (MNI) space, T = t-statistics, z = z-statistics, both reported on peak-level.

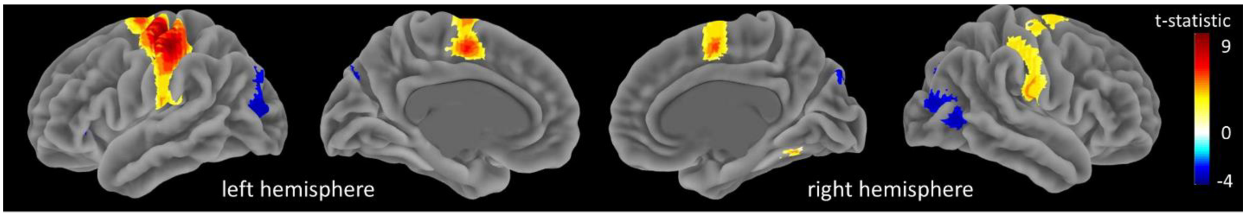

Figure 17. BOLD signal differences when contrasting imagery creation of objects with and without tactile exploration at p < .001 on cluster-level. Imagery without tactile input (I, red shades) led to additional activation in the left and right pre- and postcentral gyri, right operculum, and right cerebellum. Imagery created during simultaneous tactile exploration (I&T) led to additional activation in the left and right middle occipital gyri (displayed in blue shades).

Next, differences of the two tactile exploration-based imagery conditions (I&T = imagery with simultaneous tactile exploration and I/T = imagery creation after preceding tactile exploration) were analysed at p(uncorr.) < .001. Here, the simultaneity of tactile input (I&T) led to BOLD signal increases in the right inferior temporal gyrus, as well as bihemispheric occipital cortices. When imagery was created temporally segregated from tactile exploration (I/T), BOLD signal differences were observed in the left pre- and postcentral gyri and right cerebellum *(Table 7, Figure 18)*.

Table 7. WBA results of experiment 2 at cluster-level p < .001 (I&T; I/T). Contrasted are imagery creation based on simultaneous tactile exploration (I&T) and imagery creation based on preceding tactile object exploration (I/T). Reported are significantly activated clusters including coordinates of peak voxels and comprised anatomical regions ordered by extent, where applicable.

contrast	brain region	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
I&T > I/T	Superior occipital gyrus, calcarine gyrus	R	286	24	-88	26	4.79	3.92
	Middle occipital gyrus	L	260	-36	-79	14	4.59	3.81
	Inferior temporal gyrus	R	90	42	-76	-1	5.18	4.14
I/T > I&T	Pre- & postcentral gyrus	L	626	-30	-13	65	7.03	5.04
	Cerebellum (VI)	R	98	33	-52	-28	5.17	4.14

Note: L = left, R = right, coordinates in Montreal Neurological Institute (MNI) space, T = t-statistics, z = z-statistics, both reported on peak-level.

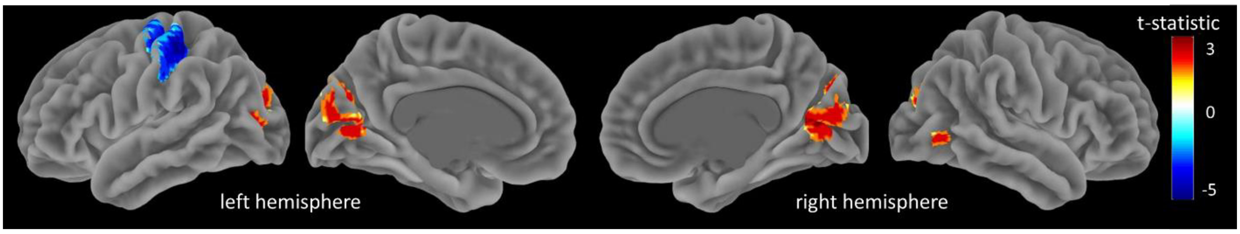

Figure 18. BOLD signal differences when contrasting imagery creation of objects with simultaneous tactile exploration and imagery (I&T) and with imagery after tactile exploration (I/T) at p < .001 on cluster-level. I&T (red shades) led to additional activation in various parts of the occipital cortex, while in the reverse contrast, I/T (blue shades) led to BOLD signal increases in the pre- & postcentral gyri and right cerebellum.

Lastly, object imagery without tactile input was compared to imagery when the object had been tactilely explored right before the imagery task, but not simultaneously (I > I/T). At the liberal cluster significance level of p(uncorr.) < .001, BOLD signal differences for this contrast were observed in the left postcentral gyrus, left temporal pole, and superior temporal gyrus, clusters comprising the right rolandic operculum and precentral gyrus, and bihemispheric SMAs. The reverse contrast (I/T > I) revealed additional signal changes in the left middle frontal gyrus, and in a cluster containing the left angular gyrus and left superior parietal lobule (*Table 8, Figure 19*).

Table 8. WBA results of experiment 2 at cluster-level p < .001 (I; I/T). Imagery without tactile input is contrasted with imagery creation based on preceding, yet temporally segregated tactile exploration (I/T). Reported are significantly activated clusters including coordinates of peak voxels and comprised anatomical regions ordered by extent, where applicable.

contrast	brain region	hemisphere	cluster size (voxel)	coordinates			T	z
				x	y	z		
I > I/T	Postcentral gyrus	L	285	-54	-25	47	4.39	3.68
	Temporal Pole, superior temporal gyrus	L	100	-54	8	-7	5.23	4.17
	Precentral gyrus	R	91	60	8	5	5.75	4.45
	SMA	R + L	81	9	-4	53	4.75	3.90
	Rolandic Operculum	R	72	57	-16	17	5.42	4.27
I/T > I	Middle frontal gyrus	L	142	-42	11	56	5.18	4.14
	Angular gyrus, superior parietal lobule	L	92	-30	-73	47	4.99	4.04

Note: L = left, R = right, coordinates in Montreal Neurological Institute (MNI) space, T = t-statistics, z = z-statistics, both reported on peak-level.

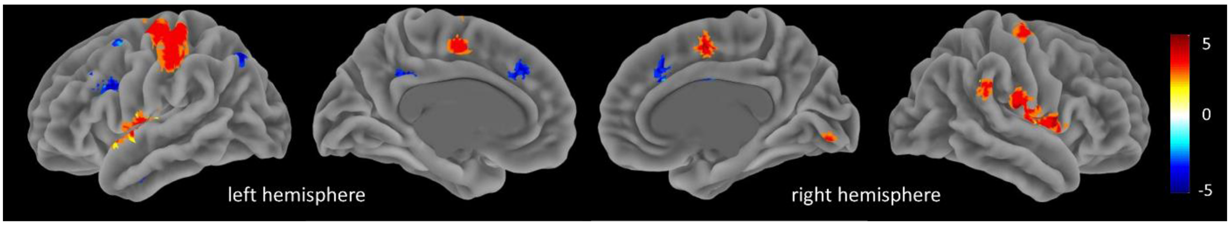

Figure 19. BOLD signal differences for the comparison of imagery without tactile input (I) with imagery after tactile exploration (I/T) at p < .001 on cluster-level. I > I/T (red shades) led to additional activation post- and precentral gyri, SMA, rolandic operculum, and temporal regions, while the reverse contrast I/T > I (blue shades) revealed BOLD signal increases in the left middle frontal, and angular gyrus as well as the superior parietal lobule.

ROI analysis

For experiment 2, structural region of interest analyses of predefined anatomical ROIs were performed using repeated measures one-way ANOVAs to examine the effect of the three different conditions on parameter estimates (β) within the ROIs (*see Figure 20*). No additional WBA findings were selected for further functional ROI analyses.

The ANOVA of the Calcarine sulcus (L&R) revealed no significant difference of parameter estimates between the three conditions (F (2,44) = 3.206, p = .05). Statistical analysis of the middle occipital cortex (MOC, L&R) showed significant differences (F (2,44) = 3.417, p = .042). However, Tukey's corrected post-hoc tests revealed that higher MOC-parameter estimates in condition 3 (I/T) compared to condition 2 (I&T) were only approaching significance (p = .05), while the other comparisons between conditions were insignificant (condition 1 & 2: p = .461, condition 1 & 3: p = .335). In the left postcentral gyrus, the ANOVA revealed significant differences between conditions (F (2,44) = 9.795, p < .001). Post-hoc tests showed that this effect is based on larger parameter estimates in condition 1 (I) compared to both condition 2 (I&T, p < .001) and condition 3 (I/T, p = .030). Conditions 2 (I&T) and 3 (I/T) did not differ significantly (p = .195). Mean parameter estimates also differed significantly between conditions in the left precentral gyrus (F (2,44) = 3.675, p = .033). This effect was driven by the difference between conditions 1 (I) and 2 (I&T, p = .028). Other comparisons did not yield significant results (condition 1 and 3: p = .613; conditions 2 and 3: p = .207). There was no significant difference between conditions in ROI Parahippocampal gyrus (L&R) (F (2,44) = 1.457, p = .24), nor in the precuneus (L&R) (F (2,44) = 1.19, p = .313). ROI analysis of the left superior parietal cortex revealed no significant differences between the three experimental conditions (F (2,44) = 0.179, p = .836). Repeated measures ANOVA for the left SMA revealed significant differences between parameter estimates in the three conditions (F (2,44) = 4.45, p = .017). Post-hoc analyses showed that condition 1 (I) has higher estimates than condition 2 (I&T), (p = .017). Other comparisons (condition 1 & 3: p = .092, and condition 2 & 3: p = .755) were not significantly different regarding their mean parameter estimates. For the right hemispheric SMA, there was no significant difference between conditions (F (2,44) = 2.562, p = .089).

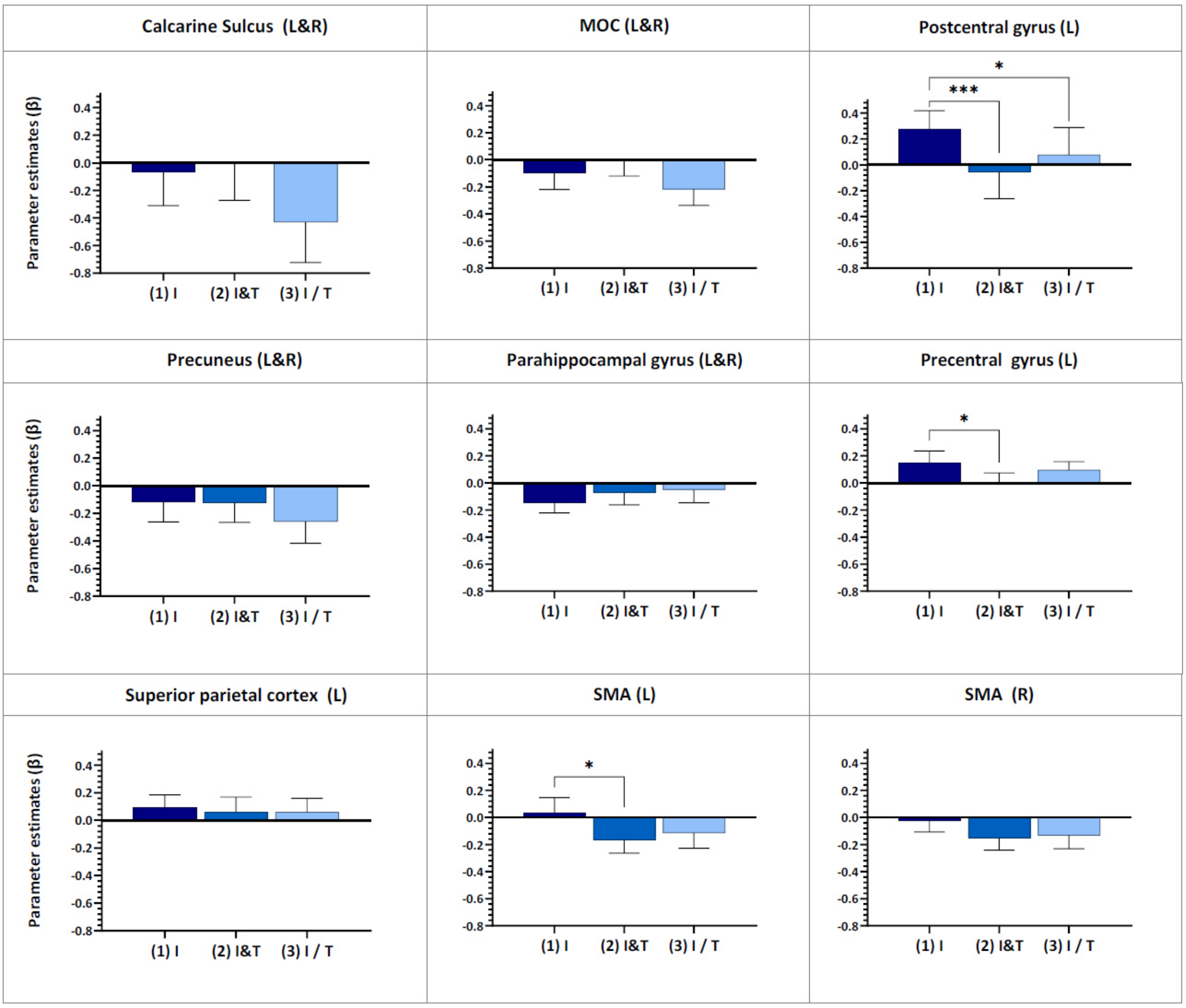

Figure 20. ROI analysis results of experiment 2. Results were computed in ROIs relevant for visual imagery processing by paired t-tests based on mean parameter estimates of imagery without tactile input (condition 1, I), imagery with simultaneous tactile input (condition 2, I&T), and imagery after preceding tactile object exploration (condition 3, I/T). MOC = middle occipital cortex, SMA = supplementary motor area, L = left, R = right; error bars = 95% CI; Significance levels: * = p < .05, ** = p < .01, *** = p < .001.

4 Discussion

4.1 Overview

Visual imagery is of central importance for the execution of numerous cognitive tasks, ranging from remembering to being creative. Yet, to date, knowledge on the specific determinants of visual imagery creation remains scarce. Therefore, this study was designed to investigate the cognitive process of mental image creation, focussing on the interplay of internal priors and external stimuli. Using fMRI, in a first experiment, we studied how visual imagery of objects is influenced by familiarity, i.e. predefined knowledge and memories. The results point towards a strong preference and processing advantage for imagery creation of familiar objects compared to unfamiliar objects. This finding is supported by the dominance of familiar imagery over unfamiliar imagery on the behavioural level and by stronger involvement of relevant neurofunctional fMRI correlates. In a second experiment, we investigated the effect of tactile stimulus exploration on the creation of visual imagery of objects. Our results provide insights into multisensory processing and show an inhibitory effect of tactile input on visual imagery, represented by somatosensory rather than visual cortex activity. Behaviourally, however, we observed no differences in experienced vividness or difficulty of the imagined stimuli, pointing towards metamodal processing in imagery creation. In the remainder of this chapter, these findings will be discussed in more detail before limitations of the study are evaluated and a research outlook is provided.

4.2 Familiarity directs mental image creation

We investigated the influence of familiarity on visual imagery processing and hypothesised a dominance of imagery based on familiar objects over imagery based on novel, unfamiliar objects. Our findings provide evidence to support this hypothesis. Specifically, the behavioural data collected in our study clearly indicates that imagery created during tactile exploration of familiar objects is perceived to be more vivid than imagery created while tactilely exploring unfamiliar objects. At the same time, the creation of imagery based on familiar tactile stimuli is rated to be significantly less difficult than imagery of unfamiliar tactile input. While our study has, to the best of our knowledge, been the first to directly compare the process of mental imagery creation based on tactile stimuli using familiar and unfamiliar objects, our findings add to previous evidence on the dominance of familiarity over novelty in cognitive processing. For instance, familiar faces are recognised more efficiently and robustly compared to unfamiliar faces, even under limited attentional capacities (Gobbini et al., 2013; Visconti Di Oleggio Castello et al., 2017). The same applies to familiar name processing (Nijhof et al., 2021). Within the domain of imagery, it was shown that motor imagery was more accurately computed for familiar than unfamiliar movements, as measured by similar durations in imaginative and executed movement patterns (Rieger, 2012). In the visual imagery domain, prospective imagery of future events was observed to be more clear and detailed when familiar surroundings were imagined compared to imagery based on novel cues (Szpunar & McDermott, 2008). Notably however, the distinction in familiar and unfamiliar categories in Szpunar & McDermott's experiment has its pitfalls, as surroundings defined to be 'novel' (e.g. the jungle, the north-pole) have an implied semantic meaning and, most likely, corresponding mnemonic imagery patterns despite being less familiar than the control settings. In contrast, our paradigm allowed the investigation of the effect of familiarity independent of verbal semantic cues and implying truly novel, unfamiliar, and abstract stimuli. By investigating the direct translation of tactile, sensory input to imagery, we avoided priming and predetermination of participants with verbal or visual semantic information. Because the sensory content on the basis of which imagery could be created by bottom-up processing was equally available in both object types, the clear behavioural performance benefit of familiarity for imagery creation is particularly compelling.

Consequences of the higher vividness of mental imagery of familiar objects over unfamiliar objects are implied, as more vivid imagery is known to influence cognitive processes stronger than less vivid imagery. Evidence includes studies on the positively correlated effect of imagery vividness on emotions such as desire and cravings for food (Tiggemann & Kemps, 2005) or sports activities (May et al., 2008). Notably, prior research suggests a greater influence of more vivid imagery on visual perception as tested using a binocular rivalry paradigm (Pearson et al., 2011), where more vivid imagery led to higher detection rates of the imagined patterns in subsequently presented binocular rivalry tasks. This effect of imagery vividness on priming points towards the variety of further cognitive processes potentially influenced by more familiar, and hence more vivid imagery.

Our behavioural findings regarding the influence of familiarity on vividness and difficulty of imagery creation suggest the possibility of differential neurocognitive processing pathways. In fact, neurofunctional correlates of visual imagery creation show distinct differences in activation patterns between familiar and unfamiliar object imagery. While we hypothesised that unfamiliar, non-semantic objects lead to more tactile activity during the attempt to create imagery, represented by increased BOLD signal activation in the somatosensory cortices, this assumption is not affirmed by our data. On the contrary, when participants are asked to explore and imagine familiar objects, they engage both top-down and bottom-up networks more, than when unfamiliar stimuli are imagined. Concerning bottom-up processing, postcentral gyrus activity, particularly in the somatotopic hand region, was higher when participants explored and imagined familiar objects compared to unfamiliar objects. Notably, the postcentral gyrus in the parietal cortex also contains numerous functions exceeding somatosensory perception, including somatosensory imagery (McNorgan, 2012; Schmidt et al., 2014). From the top-down perspective, additional superior parietal cortex activation was observed in relation to familiar imagery creation, a region known to facilitate attentional components of imagery creation (Winlove et al., 2018). Importantly, ROI analyses show that visual cortex activation remains scarce in all four conditions (familiar/unfamiliar, and left-/right-handed exploration), pointing towards a dominance of tactile input in the multimodal imagery required in our specific task-setting. Previous studies have related the lack of visual cortex involvement in imagery to less detailed imagery (for a recent meta-analysis see Winlove et al., 2018). However, our results suggest that the degree of detail or vividness of imagery might not only be related to visual cortex activation but can also be supplied by primary cortical areas of other sensory modalities. Flexibility in sensory modality-independent processing is known from research on blind subjects, where cortical plasticity across primary sensory processing areas is evident (Bridge et al., 2012b; Cacciamani & Likova, 2016; von Trott zu Solz et al., 2017). However, without the need for reorganisation due to structural or functional impairments, and within a temporally dynamic and short-term mechanism, such modality-switching is remarkable. Grounded or embodied cognition can offer an explanatory model for such modality-switches in sensory processing. Its central proposition is, that processing of internal information is facilitated via the same routes as incoming perceptual information (Barsalou, 2010). This concept will be discussed in more detail in relation to the findings of experiment 2 (*see 4.3*).

Notably, the inferior parietal lobule (IPL) is additionally activated when comparing familiar object-based imagery to imagery creation of unfamiliar objects. The left IPL was previously suggested as an area related to semantic processing (Binder et al., 2009; Numssen et al., 2020), and additionally found to be related to multisensory processing (Gentile et al., 2011). Correspondingly, the general lack of additional activation in the reverse contrast (U > F) might underline the involvement of more elaborate processing mechanisms when familiar imagery is processed and mnemonic correlates, prior expectations, and semantic memory of the object-to-imagine are available. Findings of our ROI analyses support a processing benefit of familiar imagery by significant differences in favour of higher BOLD signals during familiar imagery throughout somatomotor and somatosensory areas, including higher associative processing correlates such as the SMA. Importantly, participants did not just resign from imagining the more difficult unfamiliar objects as indicated by their high recognition rates of these objects after the experiments. Further, vividness ratings as applied in our study are valid and reliable indicators of good imagery (Cui et al., 2007; McKelvey, 1995; McKelvie, 1995).

Conceptually, the observed processing advantage of imagery creation in light of familiarity might be explained by the general need of humans to make sense of the world, using anticipation and expectation. A familiarity bias as indicated by our data can provide a benefit by facilitating the creation of a stable representation of the world around us, and us within it (Zhou et al., 2016). By highlighting the dominating role of familiar pathologic imagery over novel, more physiologic imagery, our findings may provide an explanation of why change in consolidated imagery patterns is so hard to achieve (Bell et al., 2015). This is of clinical relevance for psychotherapeutic techniques such as imagery rescripting in depression, PTSD, or phobias (for a review see Ji et al., 2021). In depression, for instance, negative imagery outweighs positive imagery and such imagery is overgeneralised, contributing to the classical cognitive triad of negative views about the self, the world, and the future (Beck et al., 1979). However, traditionally, psychotherapy has mainly been based on verbal techniques, such as cognitive behavioural therapy (CBT), although it has been shown that working with imagery can have a greater impact on emotion than working with verbal processing (Holmes et al., 2016; Holmes & Mathews, 2010). Holmes & Matthew argue that imagery mediates access to autobiographic memories and thereby includes self-relevant, personal events along with sensory information, while verbal, semantic demands lead to less personal and hence less emotional involvement. In PTSD, knowledge of the central importance of intrusive imagery (flashbacks) has led to therapeutic attempts to rescript underlying traumatic visual memories. While such imagery rescripting has proved to be a promising therapeutic tool, knowledge on the underlying neurobiological processes remains scarce (Arntz, 2012; Blackwell, 2019).

To advance fundamental knowledge on imagery rescripting and other techniques in a variety of mental disorders, we need to understand how mnemonic correlates underlying (pathologic) imagery can be accessed and altered. Interestingly, in our study, differential patterns of involvement of cortical structures related to memory retrieval were found in dependence of laterality, i.e. left- or right-handed tactile exploration. In contrast to somatosensory activations that were similar for both left-and right-handed tactile exploration-based imagery, BOLD signal increases are observed in the middle temporal gyri (MTG) when contrasting right-handed to left-handed exploration. The MTG is known to be involved in memory processing, particularly semantic processing and object representation (Binder et al., 2009; Hoffman et al., 2012; Whitney et al., 2011). Mnemonic correlates might thus be involved more strongly when the dominant right hand leads tactile exploration. Such hemispheric differences in imagery processing related to familiar images might be of use when attempting to access and modify existing memories. However, further evidence is required, particularly in light of the apparent global lack of activation in ROIs related to episodic memory retrieval (precuneus) and memory retrieval in relation to imagery in general (area PH; Winlove et al., 2018). Additional ROI analyses of the MTG provide negative BOLD signals and are therefore difficult to interpret, stressing the need for further research. The observed neural correlates are paralleled by a significant behavioural difference, namely that participants found imagery creation based on tactile object exploration with the left, non-dominant hand to be more difficult than right-handed exploration-based imagery. Interestingly however, the lack of a significant difference in vividness ratings between the dominant right and non-dominant left hand points out that although different processing strategies seem to be applied, effectively, the same goal of vivid imagery is achieved.

To conclude, a critical processing advantage of familiar imagery was revealed, leading to more vivid imagery and hence greater influence on other cognitive and psychological processes. Differential mnemonic processing in relation to left vs. right hemispheric involvement is observed, necessitating further research on the dynamics and details of imagery creation in light of prior beliefs and knowledge.

4.3 Differential inhibition of visual imagery by tactile input

In our second experiment, we investigated the influence of touch on mental image creation and hypothesised that tactile input would have an inhibitory effect on visual imagery. Indeed, differential neurocognitive processing patterns were observed indicating an inhibition of visual imagery as represented by lacking visual cortex activity in favour of somatosensory cortical activity. On the behavioural level however, participants rated imagery equally difficult and vivid in all the three conditions. This divergence of differential fMRI findings and equal behavioural results suggests the existence of different, yet efficient processing strategies when it comes to visual imagery creation in the realm of tactile input.

Interestingly, the inhibitory effect of tactile input on visual imagery emerges throughout the course of the entire experiment, rather than explicitly during the simultaneous imagery and touch condition (I&T). Here, when tactile input and imagery are performed at the same time, additional visual cortex involvement is observed when comparing it to the other two conditions. Particularly, additional activation includes clusters in the middle occipital gyrus with peak activation coordinates corresponding to the lateral occipital complex (LOC; compare Emberson et al., 2017), a region known to contribute to multimodal visuohaptic object recognition (for a review see Sathian, 2016). The LOC is thought to contain specific object representations, in particular of familiar objects as employed in our paradigm, that can be accessed by both top-down and bottom-up input of both the visual and haptic domain (Amedi et al., 2001; Lacey et al., 2009b). Similarly, when comparing simultaneous imagery and touch (I&T) to the temporally segregated I/T condition, where the imagery period follows after tactile exploration, additional middle and superior occipital, as well as calcarine cortex involvement might suggest a more detailed and vivid visual imagery (Dijkstra, Bosch, et al., 2017; Kosslyn & Thompson, 2003). However, this is not reflected by behavioural differences in experienced vividness. To explain this apparent discrepancy, these findings must be analysed in synopsis with the differential processing patterns found during the remaining contrasts of this experiment.

In both other conditions of imagery without tactile input (I) and with the temporally segregated preceding tactile input (I/T), the processing strategy employs cortical activity related to the tactile system rather than the visual (imagery) system. This substitution of visual imagery processing by cortical structures related to tactile processing is reflected by primary somatosensory cortex activity, predominantly in the postcentral gyrus' somatotopic hand region. Additional activations were observed in the primary motor cortex of the precentral gyrus and in the rolandic operculum, known to be related to tactile (working) memory processing (Bonda et al., 1996; Pasternak & Greenlee, 2005), as well as in the cerebellum. The cerebellum's role in cognition is widely accepted and relevant due to its interconnectedness in feedforward- and feedback loops to somatosensory areas, required for instance to predict somatosensory feedback as a consequence of our movements (Blakemore et al., 1999; Kilteni & Ehrsson, 2020). As no direct tactile exploration was involved in conditions I and I/T, these findings stand out. Overall, the results imply that the regular occurrence of tactile input during the experiment has occupied the cognitive machinery, despite the task to explicitly imagine the objects visually. Of note, this specifically applies to the two conditions where no direct external input is available, and imagery had to be created based on internal, top-down processing involving short- or longer-term mnemonic correlates.

Our findings have two implications. First, it may be a processing advantage to create imagery within the modality that has recently provided the most information on what is to be imagined. Second, the processing modality of imagery on the neural level might not influence the eventually experienced imagery type. Rather, imagery processing appears to be metamodal, and conscious impressions of the images created seem to be independent of unconscious sensory cortical processing employed to create the 'image' in mind. Our first conclusion goes in line with theories of grounded or embodied cognition (for a review see Barsalou, 2010). Grounded cognition rests on the idea that perceptual and cognitive processing rely on the same neural, sensory structures. In other words, mental representations are grounded in the same systems used for external perception. Evidence for grounded cognition is growing (Barsalou, 2016) and provides a possible theoretical background for our results, particularly by previous studies on sensory modality-switches. A synopsis of behavioural and EEG studies implies that when modality-switches are required by tasks, processing effort increases as reflected by larger reaction times and higher error rates (Anema et al., 2012; Bernabeu et al., 2017; van Dantzig et al., 2008). This applies to visual, auditory, and tactile domains alike. Thus, in our task, switching modality might have been too much effort, implying lower processing costs upon remaining in the perceptually dominating tactile modality. We conclude that tactile input inhibits visual imagery on the cortical level. We further suggest this inhibition to be based on processing preferences within the tactile domain, as well as a complexity reduction of the overall imagery task. However, when imagery and touch are to be executed at the same time, it is not somatosensory cortical activity that predominates, challenging theories of grounded cognition. As described above, visual cortical areas are more involved compared to imagery without concurrent tactile input (I, I/T). It therefore seems that upon aiming to form a mental representation of the bottom-up processed incoming tactile stimuli, participants use the complementary visual modality to increase information gain. Such complimentary processing might not be required in the relatively easy imagery tasks where imagery is created merely from top-down mnemonic input (I; I/T). But, once complexity levels rise such as in the I&T-task with its mixed modality and simultaneous processing demands, the increase in information by adding visual components to the tactile stimulus might facilitate successful task completion, which can be interpreted in line with the generative principle of complementarity in cognition (Bao et al., 2017).

Although we argue that touch does inhibit visual imagery processing from mnemonic correlates on a cortical level, the behavioural, conscious experience that participants report is unaffected by such inhibition. This is where our second conclusion of a multimodal, unconscious imagery process becomes relevant. As participants in our study believed to have created vivid visual images regardless of the cortical processing routes involved, one may conclude that the process of imagery creation is metamodal (Pascual-Leone & Hamilton, 2001). The modality of neural correlates of imagery creation appears to be independent of the sensory modality of the eventual conscious imagery. Of note, the phenomenal conscious experience of the generated imagery is congruent in modality to the task-specific goal. As stressed before, participants' successful creation of vivid visual images rests on valid and reliable rating scales (Cui et al., 2007; Marks, 1973; McKelvey, 1995), supported by high individual visual imagery ability. The question arises, when and where phenomenal conscious imagery evolves. Previous research on multisensory processing has centred largely around convergence zones that potentially integrate multisensory processing such as visual and tactile processing in the lateral occipital complex (e.g. Amedi et al., 2002; Lacey et al., 2009b; Lacey & Sathian, 2014). However, likely, the mere identification of multimodal regions of convergence cannot provide sufficient explanation for the domination of conscious experience by one of the domains represented in these convergence zones. Other neuronal or generally cortical mechanisms on network-level must come into play to provide explanation on unconscious and conscious processing networks. Such mechanisms might for instance include oscillations (Buzsáki et al., 2004; Pöppel, 1989), and oscillatory traveling waves (H. Zhang et al., 2018).

In summary, we found evidence for the inhibitory role of tactile input in visual imagery creation. The inhibition is represented by a lack of visual cortical involvement in favour of somatosensory processing when mnemonic correlates of touch contribute to the creation of imagery. We have further discovered a distinction between neural and behavioural processing of imagery, as sensorimotor cortical activity facilitated vivid *visual* imagery. In conjunction, our results suggest metamodal, unconscious processing of multisensory imagery and stress the necessity to investigate unconscious processing of (visual) imagery in general.

4.4 Limitations

Some methodological limitations apply to this study. First, the investigation of neurofunctional correlates by fMRI implies constraints of interpretability within the realms of assured knowledge on what fMRI imaging represents. Rather than representing specific neuronal spiking, the BOLD signal relies on summed mass activation represented by local field potentials (Logothetis & Pfeuffer, 2004). Therefore, the interpretability of BOLD contrasts is limited to undirected activity, including excitatory and inhibitory neuronal action alike. Especially when investigating inhibitory processes, this poses constraints on interpretability. Further, according to the principle of pure insertion applied in classic fMRI, only the additional variance added by a task to another (control) task or baseline, is observable, rather than the actual pattern of activation (K. J. Friston et al., 1996). While the origin of the positive BOLD signal is relatively well studied (see 2.5.1), there is no consensus for the interpretation of negative BOLD signals as obtained in parts of this study's ROI analyses (Goense et al., 2016). Suggested mechanisms of negative BOLD signals include cortical inhibition and neural activity decreases (Goense et al., 2012; Northoff et al., 2007; Shmuel et al., 2006), blood flow redistributions to neighbouring areas (Harel et al., 2002), and subcortical activity increases (Shih et al., 2009). Negative BOLD signalling varies over different macroscopic cortical regions (Ances et al., 2007; Schridde et al., 2008), microscopical cortical layers (Fracasso et al., 2018; Goense et al., 2016), and in relation to various cell-types including excitatory and inhibitory neurons as well as glial and vascular cells (Howarth et al., 2021). Albeit a conclusive and generalised understanding of negative BOLD is still lacking, one can conclude that neural activity in the affected regions might follow differential haemodynamic coupling and metabolic mechanisms, potentially suggesting differential processing routes. Further research is required to clarify the mechanisms underlying negative BOLD. Particular difficulty in researching visual imagery arises from the ubiquity of imagery in human processing, not only for task completion, but also during the resting state (Wang et al., 2008). Hence, neurofunctional correlates of imagery processing might be partially shadowed when compared to a generally computed baseline, as in our ROI analyses. Future studies could therefore advance the task paradigm by designing appropriate, distinguishable control tasks. Furthermore, when applying more explorative significance levels as in most parts of this fMRI study, the probability of false-positive findings must be acknowledged. Future replication and further investigation of these findings are of course required to gain certainty on the neurofunctional mechanisms involved.

4.5 Outlook

Generally, cognitive science lacks a clear taxonomy of functions (Pöppel & Ruhnau, 2011) in particular in the realm of predominantly internal processes such as imagery. Across imagery research, one observes that different branches of research work in parallel for a long time before concepts with different names yet similar underlying ideas are tentatively merged. As an example, debates on imagery have only recently considered grounded or enactive cognition (Palmiero et al., 2019; Schmidt et al., 2014), while in grounded cognition, theories of conceptual representations were referred to as "simulations" (e.g. van Dantzig et al., 2008), yet not extensively discussed in light of imagery research. Recently, Nanay (2021) has stressed the importance of unconscious imagery. Indeed, it is about time to move on and investigate imagery as the central means of thinking that it is, rather than as a single conscious phenomenon. By bringing together different branches of research, novel findings and eventually potential applications in clinical settings might become available at a much faster rate.

Besides further conceptual and systemic development in the research environments, future research on imagery also needs to address interindividual differences in imagery ability. Studies including the entirety and variety of the imagery spectrum are required to advance understanding of its role in cognitive processing. Harvesting findings of studies on aphantasia and hyperphantasia, the extreme ends of the imagery spectrum (Milton et al., 2021), can provide valuable insights into the specifics of visual imagery's role in cognition. Additionally, analysing connectivity and temporal dynamics of imagery processing, as well as using and combining multimodal imaging techniques, such as high-resolution fMRI, MEG, and EEG could provide more comprehensive insights on brain mechanisms underlying imagery, as well as related pathologies. Insights gained from these studies can, for instance, be used for fMRI neurofeedback, where first clinical studies indicate the potential of such targeted training strategies to help patients overcome the hardships related to imagery pathologies (Jaeckle et al., 2021; Skottnik & Linden, 2019). Currently, there is still a great need to advance basic understanding of elementary influences on visual imagery processing as attempted by the study at hand. Eventually, however, the effects of emotions, mood, and other more complex factors are of great interest in following the aim to understand individual mental image creation at the interface of external and internal realities.

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6 List of Figures

7 List of Tables

8 List of Abbreviations

ANOVA	Analysis of Variance
BOLD	Blood oxygenation-level dependent
CBF	Cerebral blood flow
CBV	Cerebral blood volume
CBT	Cognitive behavioural therapy
CI	Confidence interval
$CMRO_2$	Cerebral metabolic rate of oxygen
Deoxy-Hb	Deoxygenated haemoglobin
EEG	Electroencephalography
EPI	Echo-planar imaging
F	Familiar
FA	Flip angle
FEF	Frontal eye fields
fMRI	Functional magnetic resonance imaging
FOV	Field of view
FWE	Family-wise-error
I	Imagery
L	Left
LH	Left-handed
LMU	Ludwig – Maximilians- University of Munich
MCC	Midcingulate cortex
MEG	Magnetoencephalography
MNI	Montreal Neurological Institute
MOC	Middle occipital cortex
MTG	Middle temporal gyrus
PTSD	Post-traumatic stress disorder
R	Right
RF	Radio frequency
RH	Right-handed
ROI	Region of interest
SCEF	Supplementary and cingulate eye fields
SENSE	Sensitivity-encoding
SMA	Supplementary motor area
T	Touch
TE	Echo time
TR	Repetition time
U	Unfamiliar
V1	Primary visual cortex
WBA	Whole-brain analysis

9 Attachments

9.1 Bett’s shortened Questionnaire upon Mental Imagery

Mit diesem Test soll die Stärke Ihrer bildlichen Vorstellungskraft gemessen werden. Sie werden gefragt, sich bestimmte Dinge vorzustellen, und dann zu bewerten, wie klar und deutlich Sie diese Dinge vor Augen haben. Ein Beispiel: denken Sie an eine rote Ampel. Wenn das Bild, dass Sie dann vor Augen haben, beschrieben werden kann als

so klar und deutlich wie in der Realität	entscheiden Sie sich für (1)
sehr klar und beinahe so deutlich wie in der Realität	entscheiden Sie sich für (2)
mittelmäßig klar und deutlich	entscheiden Sie sich für (3)
nicht so klar und deutlich, aber doch erkennbar	entscheiden Sie sich für (4)
wage und unscharf	entscheiden Sie sich für (5)
sehr vage und kaum zu erkennen	entscheiden Sie sich für (6)
ich denke daran, aber ich habe kein Bild vor Augen	entscheiden Sie sich für (7)

Machen Sie bitte dasselbe mit den nun folgenden Dingen. Suche Sie die Bewertung, die mit der obigen Beschreibung übereinkommt, um auszudrücken, in welchem Ausmaß Ihre bildliche Vorstellung von jedem der folgenden Dinge klar und deutlich ist. Tragen Sie ihre Bewertung dann zwischen die Klammern hinter jedem Thema ein.

Denken Sie an einen Freund, eine Freundin oder einen Bekannten, den Sie regelmäßig sehen. Betrachten Sie das Bild, das Sie vor Augen haben, sorgfältig. Bewerten Sie dann, wie klar und deutlich Sie jedes der folgenden Dinge sehen:

1.die genauen Linien des Gesichtes, Kopfes, der Schultern und des Oberkörpers ( )
2. die Haltung von Kopf und Gesicht ( )
3. das genaue Verhalten beim Gehen (z.B. Schrittlänge) ( )
4. die verschiedenen Farben von zuletzt getragener Kleidung ( )

Wie klar und deutlich ist das Bild, das Sir vor Augen haben, wenn Sie denken an

5. eine untergehende Sonne ( )

Wie klar und deutlich können Sie sich das Geräusch vorstellen, wenn Sie denken an

6. das Pfeifen einer Dampflok ( )
7. die Hupe eines Autos ( )
8. das Miauen einer Katze ( )
9. das Geräusch von austretendem Dampf ( )
10. das Händeklatschen bei Applaus ( )

Denken Sie an das Gefühl, das beim Anfassen der folgenden Dinge entsteht. Wie klar und deutlich könne Sie sich das Gefühl vorstellen von

11. Sand ( )
12. Leinen ( )
13. Pelz ( )
14. einem Nadelstich ( )
15. der Wärme eines lauwarmen Bades ( )

Denken Sie daran, was Sie mit Armen, Beinen, Händen, Lippen etc. tun, wenn Sie die folgenden Aktivitäten ausführen. Wie klar und deutlich können Sie sich vorstellen, was Sie tun bei

16. eine Treppe hochlaufen ( )
17. über einen Balken springen ( )
18. einen Kreis auf Papier zeichnen ( )
19. sich nach einem Gegenstand auf einem hohen Regal recken ( )
20. etwas von den Füßen wegtreten ( )

Denken Sie an die folgenden Geschmackssorten. Wie klar und deutlich können Sie sich jeden Geschmack vorstellen ?

21. Salz ( )
22. weißer Kristallzucker ( )
23. Apfelsine ( )
24. Konfitüre ( )
25. Ihr Lieblingsgericht ( )

Denken Sie an jeden der folgenden Gerüche. Wie klar und deutlich können Sie sich den Geruch der folgenden Objekte vorstellen ?

26. ein muffiges Zimmer ( )
27. das Kochen von Rosenkohl ( )
28. das Braten von Fleisch ( )
29. frische Farbe ( )
30. Leder ( )

Denken Sie an jedes der folgenden Gefühle. Wie klar und deutlich können Sie sich jedes Gefühl vorstellen?

31. Müdigkeit ( )
32. Hunger ( )
33. Halsschmerzen ( )
34. Schläfrigkeit ( )
35. satt sein nach einem ausgedehnten Essen ( )

9.2 Edinburgh handedness inventory

Edinburgh Händigkeitsfragebogen

Bitte geben Sie an, welche Hand Sie bei den folgenden Aktivitäten bevorzugen. *Setzen Sie + in die entsprechende Spalte.* Sollte die Präferenz so stark sein, dass Sie nie - wenn nicht absolut notwendig - versuchen würden, die andere Hand zu benutzen, *setzen Sie ++.* Wenn Sie wirklich keine Präferenz haben, *setzen Sie + in beide Spalten.*

Manche Aktivitäten erfordern zwei Hände. In diesen Fällen ist der Aufgabenteil, oder der Objektteil, für welchen Handpräferenz abgefragt wird, in Klammern angezeigt.

Bitte versuchen Sie alle Fragen zu beantworten, und lassen sie eine Zeile nur dann leer, wenn sie überhaupt keine Erfahrung mit dem Objekt oder Aufgabe haben.

		LINKE(R)	RECHTE(R)
1	Schreiben		
2	Malen		
3	Werfen		
4	Schere		
5	Zahnbürste		
6	Messer (ohne Gabel)		
7	Löffel		
8	Besen (obere Hand)		
9	Streichholz zünden (Streichholz)		
10	Schachtel öffnen (Deckel)		
i	Mit welchem Fuß treten Sie bevorzugt einen Gegenstand?		
ii	Welches Auge benutzen Sie, wenn Sie nur eines benutzen?		

L.Q.		Bitte lassen Sie diese Felder leer	DEZIL	

9.3 Vividness of Visual Imagery Questionnaire

VVIQ

*Übersetzt ins Deutsche nach: Marks, D.F. (1973). Visual imagery in the recall of pictures. British Journal of Psychology, **64**, 17-24.*

Bitte stelle dir die folgenden vier Bilder vor. Beurteile die Lebhaftigkeit/Deutlichkeit/Klarheit jedes Bildes entsprechend folgender Skala:

1	2	3	4	5
Vollkommen deutlich und so lebhaft wie normales Sehen	Deutlich und ziemlich lebhaft	Mäßig deutlich und lebhaft	Vage und trüb	Kein Bild (sich lediglich bewusst sein, an das Objekt zu denken)

Denke an einen Verwandten oder Freund, den du regelmäßig siehst (der aber gerade nicht hier ist), und prüfe das Bild, dass vor deinem geistigen Auge erscheint, gründlich. Dann bewerte die folgenden Aspekte:

1	Die genaue Kontur von Gesicht, Kopf, Schultern und Körper.	
2	Charakteristische Kopf- und Körperhaltung etc.	
3	Die genaue Art zu gehen, mit Schrittlänge etc.	
4	Die verschiedenen Farben einiger bekannter Kleidungsstücke.	

Stelle Dir eine aufgehende Sonne bildlich vor. Betrachte das Bild, das vor deinem geistigen Auge erscheint. Dann bewerte die folgenden Aspekte:

5	Die Sonne erhebt sich über den Horizont in einen dämmrigen Himmel.	
6	Der Himmel erhellt sich und umgibt die Sonne in blauer Farbe.	
7	Wolken. Ein Sturm zieht auf, mit Blitzen.	
8	Ein Regenbogen erscheint.	

Denke an ein Laden-Schaufenster, an dem du oft vorbeigehst. Betrachte das Bild, das vor deinem geistigen Auge erscheint. Dann bewerte die folgenden Aspekte:

9	Das Gesamtbild des Ladens von der anderen Straßenseite aus betrachtet.	
10	Ein Schaufenster-Arrangement mit Farben, Formen und Details der ausgestellten Objekte.	
11	Du bist nahe des Eingangs. Die Farbe, Form und Details der Tür.	
12	Du betrittst den Laden und gehst zur Kasse. Die Kassiererin hilft dir, Geld wechselt den Besitzer.	

Denke zuletzt an eine Landschaft mit Bäumen, Bergen und einem See. Betrachte das Bild, das vor deinem geistigen Auge erscheint. Dann beurteile die folgenden Aspekte:

13	Die Umrisse der Landschaft.	
14	Die Farbe und Form der Bäume.	
15	Die Farbe und Form des Sees.	
16	Ein starker Wind bläst über Bäume und See hinweg und verursacht Wellen.	

9.4 Information sheet fMRI experiment

Info fMRT-Messung

Die ersten ca. 10 Minuten im Scanner wird eine sogenannte *Resting-State Aufnahme* gemacht, bei der du noch gar nichts tun musst, außer still zu liegen. Dabei solltest du die Augen schließen und versuchen, an nichts Bestimmtes denken.

Danach geht es mit dem Experiment los. Wir wollen das **Zusammenwirken von visueller Imagination und taktilen Eindrücken** untersuchen, deshalb enthalten die Aufgaben verschiedene Variationen von Ertasten und bildlichem Vorstellen. Es gibt zwei Aufgabenteile, Instruktionen werden Dir jeweils über einen Monitor angekündigt. Bitte prüfe deshalb direkt am Anfang, ob du den Monitor gut im Blick hast.

Damit die fMRT-Bilder auswertbar sind, ist es essentiell, dass Du dich (abgesehen natürlich von den Tastbewegungen deiner Hand) **nicht bewegst**! Gescannt wird zwar nur der Kopf, jegliche Bewegung des Körpers, z.B. der Füße oder Arme, stören die Messung aber auch. Wenn du es schaffst, dich gut zu konzentrieren und während des Scans nicht zu bewegen, werden wir dich mit **5€** extra belohnen!

Teil 1 / 2

Der erste Aufgabenteil wird Dir folgendermaßen angekündigt→

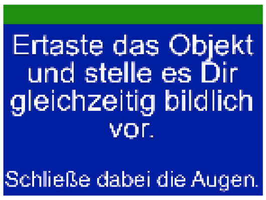
Während des Experiments wird stets jemand von uns an deiner Seite sitzen, um Dir die zu ertastenden & vorzustellenden Objekte in die Hand zu legen.

Teil 1 / 2

Dir wird jeweils ein Objekt in die linke oder rechte Hand gelegt.

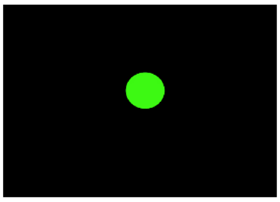
Ertaste das Objekt mit dieser einen Hand und versuche, es Dir dabei mit geschlossenen Augen genau vorzustellen.

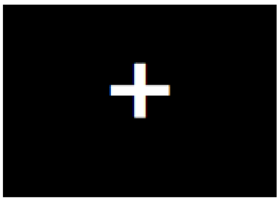
Deine Aufgabe ist es, jeweils das Objekt **gründlich zu ertasten und es Dir währenddessen so genau wie möglich bildlich vorzustellen**. Bitte halte das innere Bild des Objekts solange aufrecht, bis wir Dir das Objekt wieder wegnehmen. Höre bitte auch nicht, auf das Objekt mit deinen Händen zu erkunden, wenn du schon vor Ablauf der Zeit glaubst, dir ein Bild vom Objekt machen zu können. Ein einzelner solcher Durchgang sieht dann am Monitor folgendermaßen aus:



Ertaste das Objekt und stelle es Dir gleichzeitig bildlich vor.

Schließe dabei die Augen.





Während der Instruktion werden wir Dir das zu ertastende Objekt in eine Hand legen. Du kannst gleich damit beginnen, die **Augen zu schließen**, das Objekt mit der **einen Hand** zu ertasten und es Dir vorzustellen. Der **grüne Kreis** wird dann für die gesamte Dauer des Vorstellens (15 s) angezeigt, solange er sichtbar ist, dauert die Imaginationsaufgabe noch an (d.h. im Idealfall hast du immer die Augen geschlossen, während der grüne Kreis angezeigt ist).

Nach Ablauf der 15 s werden wir dir das Objekt wegnehmen. Du solltest nun die **Augen öffnen** und dich kurz erholen. Während der **Pause** wird stets ein **weißes Kreuz** eingeblendet (6 s).

Genau nach diesem Schema, nur mit unterschiedlichen Objekten verläuft die gesamte erste Aufgabe, und zwar für ca. 18 Minuten. Dabei werden die Farben der Bildschirme variieren, lass Dich hiervon einfach nicht stören und versuche über die gesamte Versuchsdauer konzentriert zu bleiben.

Teil 2 / 2

Hier wird es neue und häufiger wechselnde Aufgabenstellungen geben. Eine einleitende Instruktion →


Teil 2/2

Nun wird es verschiedene Aufgabenstellungen geben. Lies Dir also bitte die jeweiligen Anweisungen genau durch.

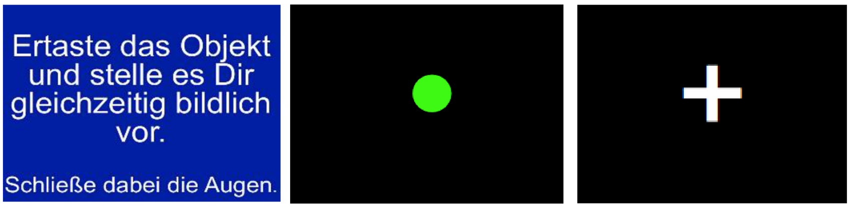
weist auf den Start des zweiten Aufgabenteils hin, der nur ca. 14 Minuten dauern wird.

Hier wirst Du entweder...

a) ... gleichzeitig tasten und dir das Objekt bildlich vorstellen. Die Pausen beginnen jeweils, wenn wir dir das Objekt wieder wegnehmen.
b) ... erst nur tasten (mit geöffneten Augen), dann werden wir dir das Objekt wegnehmen, und dich bitten dir das ertastete Objekt bildlich vorzustellen (hierzu schließt du die Augen wieder). Das Pausensignal wird hier eine eindeutige Handberührung (links) sein.
c) ... dir ohne taktilen Input ein geometrisches Objekt vorstellen. Als Pausensignal fungiert wieder die Handberührung.

Die entsprechenden Instruktionen sehen folgendermaßen aus:

a)


Ertaste das Objekt und stelle es Dir gleichzeitig bildlich vor.

Schließe dabei die Augen.

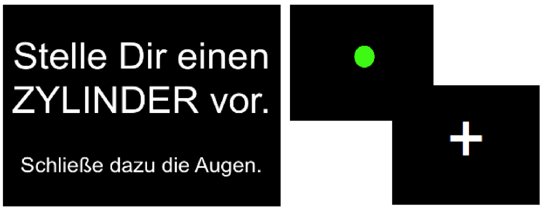
b)


Ertaste das Objekt mit geöffenten Augen und fixiere dabei den Stern.

Stelle Dir das gerade ertastete Objekt vor.

Schließe dazu die Augen.

c)


Stelle Dir einen ZYLINDER vor.

Schließe dazu die Augen.

Öffne bitte Deine Augen während der Pause nach jeder Aufgabe (nach der Wegnahme des Objekts (a) bzw. nach der Handberührung (b,c))

Wann immer Du aufgefordert wirst, Dir ein Objekt vorzustellen, dann versuche Dir bitte ein so klar und deutlich wie mögliches Bild des Objekts in den Geist zu rufen und zu aufrechtzuhalten!

Wichtig in beiden Aufgaben ist außerdem, dass Du während der Tast-Aufgaben nicht frühzeitig aufhörst, die Objekte taktil zu erkunden, auch wenn Du z.B. schon vorher glaubst, ausreichende Information ertastet zu haben, um Dir ein Bild vom Objekt machen zu können.

Nachdem der Scan vorbei ist, werden wir dir noch drei **Fragebögen** zum Ausfüllen geben. Einer davon wird beinhalten, die ertasteten Objekte **wiederzuerkennen**. Wenn du es schaffst, mind. 4 von 5 Objekten zu erkennen, werden wir dir noch einmal **5 €** extra bezahlen.

9.5 Post-experiment difficulty and vividness ratings

Bitte erinnere Dich **an Aufgabenteil 1/2.** Wie schätzt du jeweils die Bilder ein, die Du dir während des Ertastens der Objekte vorgestellt hast?

	sehr klar und so lebendig wie normales Sehen	klar und ziemlich lebendig	mittelmäßig klar und lebendig	vage und schemenhaft	überhaupt kein Bild (nur das Bewusstsein, dass du an ein Objekt denkst)
Tasten mit der linken Hand	○	○	○	○	○
Tasten mit der rechten Hand	○	○	○	○	○
Ertasten einfacher, bekannter Formen	○	○	○	○	○
Ertasten komplexerer, abstrakter Formen	○	○	○	○	○

Bitte erinnere Dich **an Aufgabenteil 1/2**. Wie leicht/schwer fiel es Dir jeweils, Dir ein inneres Bild des Objektes vorzustellen?

	Sehr schwer	eher schwer	eher leicht	sehr leicht
Tasten mit der linken Hand)	○	○	○	○
Tasten mit der rechten Hand	○	○	○	○
Ertasten einfacher, bekannter Formen	○	○	○	○
Ertasten komplexerer, abstrakter Formen	○	○	○	○

Bitte erinnere Dich an Aufgabenteil 2/2.Wie schätzt du jeweils die Bilder ein, die Du dir vorgestellt hast?

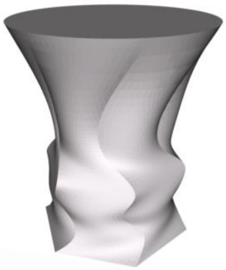
	sehr klar und so lebendig wie normales Sehen	klar und ziemlich lebendig	mittelmäßig klar und lebendig	wage und schemenhaft	überhaupt kein Bild (nur das Bewusstsein, dass du an ein Objekt denkst)
Reine Imagination ohne Tasten	○	○	○	○	○
Gleichzeitiges Ertasten und Vorstellen	○	○	○	○	○
Vorstellen erst NACH dem Ertasten	○	○	○	○	○

Bitte erinnere Dich an **Aufgabenteil 2/2**. Wie leicht/schwer fiel es Dir jeweils, Dir das Objekt bildlich vorzustellen?

	sehr schwer	eher schwer	eher leicht	sehr leicht
Reine Imagination ohne Tasten	○	○	○	○
Gleichzeitiges Ertasten und Vorstellen	○	○	○	○
Vorstellen erst nach dem Ertasten	○	○	○	○

9.6 Post-experiment object recognition quiz

Erkennst du die Objekte wieder, die du eben ertastet hast? Pro Zeile ist ein Objekt tatsächlich Bestandteil des Experiments gewesen, bitte kreuze es an! (1 Kreuz/Zeile)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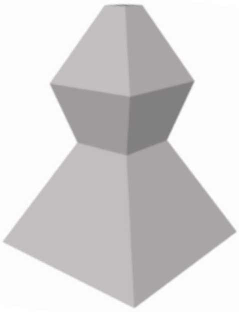
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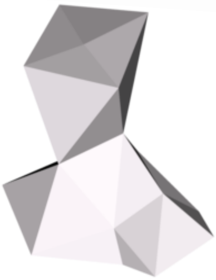
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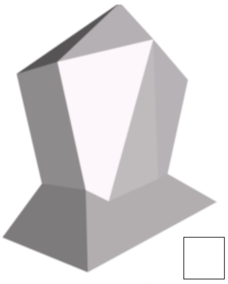
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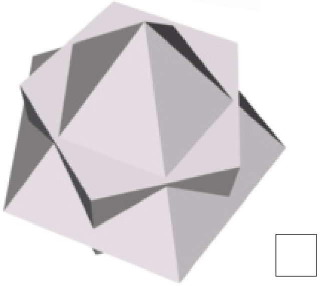
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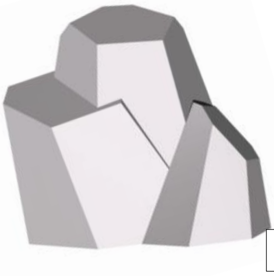
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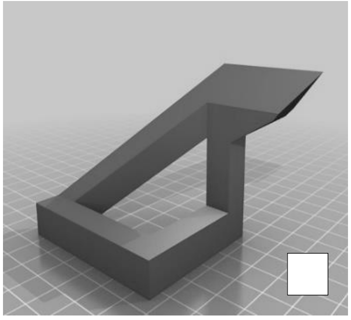
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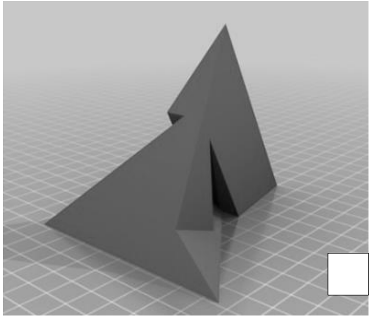
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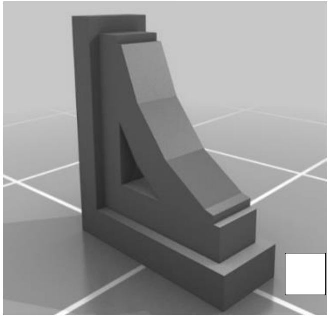
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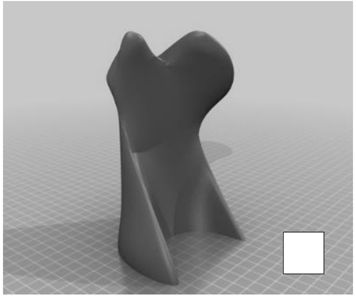
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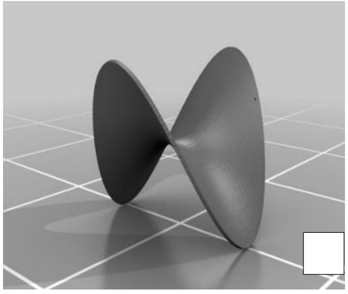
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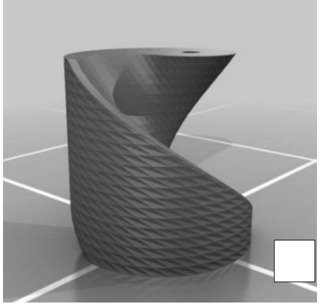
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Affidavit

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