

Information Flow Between Ventral and Dorsal Streams During Complex Tool Use

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Table of Contents

Introduction	3
Background and Context	3
Problem Statement	4
Research Questions	5
Relevance and Importance of the Research	5
Literature Review	5
Key Concepts, Theories, and Studies	5
Key Debates and Controversies	12
Gaps in Existing Knowledge	13
Research Design and Methods	14
Participants	14
Materials	14
Design and Procedure	15
MEG Data Acquisition and Preprocessing	16
MEG Data Analysis	16
Practical Considerations	18
Implications and Contributions to Knowledge	18
References	19

Introduction

Background and Context

The range of possible interactions that animals and humans have with their surroundings can be extended using tools. The different affordances (Gibson, 1986) that a tool has increase creatures' power to act within their environment. Even a simple tool like a stick makes it possible to act in ways that are not possible beforehand because its usage modifies one's perception of the world by extending one's peripersonal space. In this respect, Maravita and Iriki (2004) demonstrated that tool use alters monkeys' visual receptive field of intraparietal neurons. In this way, monkeys could manipulate objects that were not near their bodies and were beyond their grasping distance. Even though these objects were in the monkeys' extrapersonal space before using a tool for reaching, meaning they could be visually perceived already, using a stick modified their visual receptive field and presented them with more possibilities for action.

The usage of more complex tools starting with hominids introduced to humans and their ancestors, further means to engage with their environments. An axe, a bow, a knife, a hammer, or a pair of scissors presented us with more possibilities for action, given that we know how to use them. The knowledge of their usage that has been cultivated in our culture over time made complex tools special and differentiated them from simple ones. The semantic information associated with a complex tool is essential because it comes down to a simple tool when used merely based on its intrinsic physical properties and out of its appropriate context. For instance, using a knife for reaching rather than cutting reduces it to its perceptible parts. The lack of semantic knowledge associated with its usage deprives a knife of being a complex tool, and it cannot enable advanced ways to interact with the environment. Thus, the contextual information related to complex tools provides us with further opportunities for action that we cannot perform otherwise.

Problem Statement

The research on complex tool use in humans up to now has demonstrated that this distinctive property necessitates the integration of semantic knowledge about object use stored in the ventral stream with the online sensory-motor representations in the dorsal stream. The left supramarginal gyrus (SMG) was shown to be functionally connected to both ventral and dorsal pathways by integrating the conceptual knowledge of tools and their associated actions computed in the ventral stream with the volumetric and structural representations of tools operated in the dorsal stream (Garcea & Buxbaum, 2019). Some studies found reciprocal connections between dorsal and ventral visual pathways (Chen et al., 2018), but the literature predominantly suggests that tool manipulation knowledge in the parietal cortex is contingent on the identity of the tool processed in the temporal cortex. However, because the research has been performed almost wholly using functional magnetic resonance imaging (fMRI), the presented findings lack the temporal precision to assess that they are conclusive. If similar experimental designs have been done using brain imaging methods with millisecond temporal resolution corresponding to the time domain of neural activities, the functional connectivity between two visual streams could reveal further information unnoticed previously.

Thanks to the high spatial resolution of magnetoencephalography (MEG) compared to other brain imaging techniques such as Electroencephalography (EEG), we can have precise information on where and when the integration occurs between ventral and dorsal streams. More importantly, we can come up with a definitive answer to reveal the direction of information flow between these two streams in the different stages of action for several experimental conditions. Based on the directed influences that we might observe within the Tool Processing Network (Garcea & Mahon, 2014), we can construct functional hierarchies that dynamically change as the action unfolds for the different stages, such as resting, action planning, and execution. Moreover, we can assess the frequency domain of feedforward and feedback influences within the network.

Research Questions

The research proposed in the current paper aims to answer how the Tool Processing Network's functional and effective connectivity changes precisely between the different stages of action, such as during the resting state, action planning, and execution. Most importantly, we aim to conclude where and when the ventral and dorsal stream exchange information and the direction of information flow between them during tool use for different experimental conditions. Besides, we plan to investigate the disassociation between the ventro-dorsal and dorso-dorsal streams (Sakreida et al., 2016) to question their involvement in complex tool use in humans.

Relevance and Importance of the Research

We expect to reveal the precise dynamics between the ventral and dorsal visual streams and their hierarchical organization. The different experimental conditions will consider the importance of semantic information from the ventral stream, monitoring the online control of objects in the dorso-dorsal pathway, and the known object manipulations in the ventrodorsal stream. Our study's results will be relevant to ongoing research on vision and motor cognition by answering the common questions about the integration and dissociation between two visual streams and the parietal cortex's role in their neuronal communication. Our research is worth doing because there is a lack of evidence considering the precise temporal dynamics during complex tool use in humans. Thanks to its high temporal and relatively well spatial resolution, MEG can offer further insights into the Tool Processing Network.

Literature Review

Key Concepts, Theories, and Studies

The idea that the visual cortex in the primate brain processes qualitatively different kinds of information in the ventral and dorsal pathways is first put forward by Ungerleider and Mishkin (1982). Later, Mishkin et al. (1983) provided further justification from ablation studies that observed monkeys' behavioral changes in object or landmark discrimination tasks, respectively, after removing cortical areas from the ventral or dorsal stream. Mishkin et al.

(1983) claimed that while the ventral stream identifies objects ('what' pathway), the dorsal stream is responsible for their spatial information ('where' pathway). After recasting their theory, Goodale and Milner (Goodale et al., 1994b; Goodale & Milner, 1992; Milner & Goodale, 2008) separated these two streams based on the purpose of information processing rather than the type of information that operates, as pointed out by van Polanen and Davare (2015). They stated that the ventral stream processes visual information to perceive objects' properties ('what' pathway), and the dorsal stream computes visual information to guide actions ('how' pathway). The studies performed with the well-known patient DF (Goodale et al., 1994b), who had bilateral damage in the ventrolateral occipital region, provided strong evidence for their research. They observed that the patient DF could easily grasp objects by properly arranging her fingers, but she could not identify them. They concluded that different neuronal pathways subserve the perception of objects and the actions directed at them.

Additional studies with the participation of patient DF revealed more insights into ventral and dorsal streams. Goodale et al. (1994a) question whether imposing a delay between the brief presentation of an object and the imitation of grasping, as if the object was still there, affects the grip size of the patient DF in comparison to control subjects. They found that the control group's grip size correlated with the object width until 30 seconds. However, the patient DF's grip size and the object width did not correlate after 2 seconds. They reasoned that to pantomime the action for grasping, the participants needed to access the stored perceptual information in their ventral stream. Because the patient DF had damage in the ventrolateral occipital region, her dorsal stream could not receive the necessary information. The insufficiency of the dorsal pathway alone during delayed actions made it evident that these two streams do not process the visual information always in parallel. However, the dorsal stream is most likely contingent on the knowledge stored in the ventral stream. The more recent studies replicated these results in healthy subjects by using transcranial magnetic stimulation (TMS). While TMS's application to the dorsal stream distorted the execution of both immediate and delayed actions, its implementation to the ventral stream disrupted only

delayed actions (Cohen et al., 2009). These findings indicate the dorsal stream alone computes 'here and now' (Milner, 2017) during visuomotor behaviors. The ability to pantomime an action after a delay period depends on the perceptual representations stored in the ventral stream. As we will discuss in the following paragraphs, the dorsal stream also necessitates semantic knowledge about tools from the ventral stream during complex tool use to utilize it in the right context.

The evidence from neuropsychological and neuroimaging studies shows actions directed at objects (e.g., to grasp a knife) and skillful actions performed with them (e.g., to peel an orange using a knife) are separable (Almeida et al., 2010). Because grasping an object only requires the coordination of a series of movements according to the target object's intrinsic attributes, whereas using an object skillfully necessitates stored semantic knowledge about the object's identity, function, and associated motor behaviors (Frey, 2007). In this context, patients with optic ataxia have difficulties reaching or grasping objects compared to healthy people. However, they may manipulate them according to their functions once they canprehend. In contrast, patients with apraxia cannot execute skillful actions associated with objects' purposes. However, they may reach and perform optimal grasp towards objects as well as healthy people. To this respect, Mahon et al. (2013) indicated that the behavioral impairments observed in optic ataxic and apraxic patients could explain the integration between visual pathways during complex tool use. Importantly, neuroimaging studies on these patients revealed that the lesions at the intersection of the ventral and dorsal streams, i.e., the left parietal cortex are responsible for these neuropsychological disorders. While the lesions to the left posterior and superior parietal cortex were observed in patients with optic ataxia (Goodale & Milner, 1992; Pisella et al., 2006), the lesions in the left inferior parietal structures were associated with apraxia of object use (Johnson-Frey, 2004).

To indicate the neural foundation of complex tool use in humans, Johnson-Frey (2004) made a further distinction between conceptual and ideomotor apraxia. He emphasized that patients with conceptual apraxia commit 'errors of content,' meaning they could perform skilled

actions but out of their functional context. For example, Ochipa et al. (1989) reported a patient who tried to use a toothbrush for eating. He could recognize that the object was a toothbrush but failed to use it in the right context. In contrast, patients with ideomotor apraxia were aware of the context in which tools are supposed to be used and their associated actions. However, even though they could grasp and manipulate tools, they could not perform the motor skills linked with those actions. In light of these findings, Johnson-Frey (2004) concluded that distinct neural pathways within the left parietal lobe underlie semantic knowledge and motor skills associated with complex tools.

Frey (2007) stated that researchers must reveal how semantic knowledge represented partly in the ventral stream is integrated with sensory-motor representations processed by the dorsal stream to comprehend tool use. To that end, Almeida et al. (2013) utilized the selective projections of parvocellular and koniocellular channels, respectively, to ventral and dorsal streams to investigate the representation of tool manipulation knowledge in the brain. They presented participants with tool images chromatically defined to be exclusively visible to either ventral or dorsal stream during fMRI. They expected that the stimuli biased toward being processed by the parvocellular channels (P-biased) would indicate differential blood oxygen level-dependent (BOLD) in the ventral stream (Merigan & Maunsell, 1993). In contrast, the images biased toward being processed by the koniocellular channels (K-biased) would lead to differential BOLD responses in the dorsal stream via the visual motion area MT/V5 (Sincich et al., 2004). Importantly, they observed that P-biased stimuli activated inferior parietal regions, whereas K-biased stimuli drove the BOLD response in superior and posterior parietal areas in the left hemisphere. Afterward, they proved their assumption on parvocellular and koniocellular channels' selectivity by computing functional connectivity between the regions reported in the left parietal cortex and the two visual streams. The tool-preferring regions in the left inferior parietal cortex were shown to have more robust functional connectivity with the medial fusiform gyrus than MT/V5. On the contrary, the tool-preferring areas in the left posterior/superior parietal cortex had greater functional connectivity with MT/V5 than the

medial fusiform gyrus. Mahon et al. (2013) reaffirmed these findings with a similar experimental design and indicated an inferior-to-superior organization in the left parietal cortex. On the whole, these findings pointed out the integrative function of the left parietal lobule between the ventral and dorsal streams and implied that the tool manipulation knowledge is contingent on the information computed by the ventral pathway.

In light of its integrative function, Garcea et al. (2014) aimed to parcellate the left parietal cortex into its subregions, accordingly, its functional connectivity to the rest of the Tool Processing Network. They presented subjects with the images of tools and from other baseline categories during fMRI. Later, they used k-Means clustering over fMRI data to classify the voxels in the parietal cortex based on how similar their functional connectivity is to other regions of the network. They specifically decided to limit the number of k clusters to three because they were particularly interested in the inputs from the ventral and dorsal streams to the parietal cortex and the outputs from the parietal cortex to the motor system. They found that the first cluster of voxels in the inferior parietal cortex with a differential BOLD response to the tool images had stronger functional connectivity with the left ventral premotor cortex. The second cluster of voxels near the anterior intraparietal sulcus had more robust functional connectivity with the left medial fusiform gyrus. The third cluster from the superior parietal cortex was exclusively functionally connected to the left dorsal occipital cortex. To verify their results, they repeated the same analysis using the left posterior middle temporal gyrus as a ventral stream seed rather than the left medial fusiform gyrus. They observed a similar pattern of functional connectivity between the parietal and extra-parietal regions. They proved that the left posterior middle temporal gyrus was part of the ventral stream rather than the dorsal stream regarding its functional connectivity during viewing tool images. Additionally, they performed hierarchical clustering analysis to compare their results to the anatomically based parcellations of the left parietal cortex reported before (Caspers et al., 2013; Ruschel et al., 2014) and found that the functional parcellation of the left parietal cortex was consistent with the anatomical ones. After considering these results, they emphasized that apraxia and optic

ataxia might not only be caused by damage to the parietal cortex but could also be caused by disconnections between the parietal cortex and visual streams.

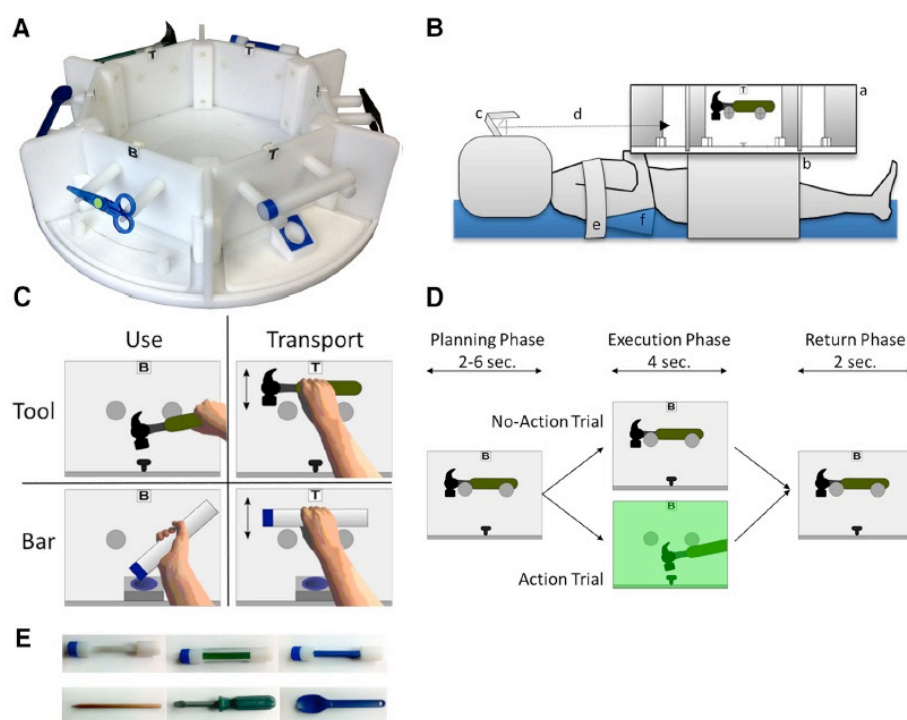
The study by Chen et al. (2017) drew attention to the effect of elongation on brain activations during viewing tool images. Because graspable tools are mostly elongated rather than being stubby, they questioned the extent to which the differential BOLD responses to the images of tools resulted from their toolness, i.e., the property of merely being a tool rather than elongation. In this respect, they first asked their participants to view grayscale images of elongated tools, elongated nontools, stubby tools, and stubby nontools during fMRI. Later, To compute context-dependent changes in the effective connectivity between ventral and dorsal streams, they applied psychophysiological interaction (PPI) (Friston et al., 1997) and dynamic causal modeling (DCM) (Friston et al., 2003) analysis. PPI indicated that the interaction between ventral and dorsal streams was robustly regulated by the processing of toolness rather than elongation. Furthermore, DCM revealed that viewing both elongated and stubby tools' images boosted the connectivity between these two streams. However, only seeing the images of elongated tools increased reciprocal connectivity between them. Together with the previous findings, these results suggested that different connectivity patterns between two visual streams subserved the property of elongation and toolness. They claimed the dorsal stream could operate the information on elongation without the ventral stream's involvement, but manipulation knowledge associated with tools was contingent on the inputs from the ventral stream.

Unlike the studies discussed so far, Brandi et al. (2014) investigated complex tool use in humans by asking participants to use and manipulate actual objects from a 'Tool Carousel' they designed (Figure 1). In this way, they came up with an experimental setting in which humans were actively using tools during fMRI rather than passively viewing their images. In general, they observed that the BOLD response during the action planning phase was robustly lateralized to the left brain and continued to do so during the action execution phase. Moreover, the contrast between the fMRI activity maps for different experimental conditions

emphasized the dissociations within the dorsal stream reported before (Binkofski & Buxbaum, 2013). They revealed that a dorso-dorsal pathway, including the superior occipital gyrus, superior parietal lobule, and dorsal premotor area, was responsible for monitoring the online control of movements directed at objects independently from their identity. In contrast, a ventro-dorsal pathway consisting of the middle occipital gyrus, inferior parietal lobule, and ventral premotor area was involved in operating known object manipulations such as tools. Additionally, along the same line with the previous research, the ventral stream was responsible for processing semantic information associated with tools.

Figure 1

The "Tool-Carousel" and Experimental Design



Note. (A) The "Tool-Carousel." (B) The experimental setup. (C) Illustration of the four experimental conditions: tool use, tool transport, bar use, and bar transport. (D) Time course of a trial. (E) Example stimuli in the experiment. Reprinted from "The Neural Correlates of Planning and Executing Actual Tool Use," by M. L. Brandi, A. Wohlschläger, C. Sorg, and J. Hermsdörfer, 2014, *Journal of Neuroscience*, 34(39), 13183–13194.

Sakreida et al. (2016) evaluated the results discussed in the previous paragraph in light of the idea of affordances proposed by Gibson (1986). They stated that the ventro-dorsal stream comprehends stable affordances related to the information on objects' constant features, that is to say, its associated functions. In contrast, the dorso-dorsal stream picks up variable affordances linked to objects' changing properties, such as size, shape, weight, or orientation. Concerning this, they asserted that the ventro-dorsal pathway has high working memory capacity but can slowly operate while processing stored object knowledge from the ventral stream. On the contrary, although the dorso-dorsal path has a low working memory load, it can function fast while monitoring online interactions with objects. Soon afterward, Garcea and Buxbaum (2019) demonstrated the left SMG's role concerning the ventro-dorsal and dorso-dorsal streams after questioning the qualitative functional difference in the Tool Processing Network during tool use and tool transport gesturing. They asked participants to view the tool images, plan their actions, and pantomime them in both tool use and tool transport trials during fMRI. In this way, they aimed to emphasize the difference in BOLD response regarding functional manipulation and structure-based grasping, respectively, during tool use and tool transport gesturing. Based on the evidence they gathered from the task-based functional connectivity analysis, they indicated the left SMG is a point of connection between the dorso-dorsal and ventro-dorsal visual pathways. After considering the previous studies' results, they proposed that the left SMG is a hub region between the ventral, ventro-dorsal, and dorso-dorsal pathways by combining conceptual knowledge processed in the ventral stream with the online visuomotor information computed in the dorsal one.

Key Debates and Controversies

The research thus far indicates there are two main theoretical views on complex tool use in humans called the Embodied Hypothesis of Tool Recognition (Gallese & Lakoff, 2005; Martin et al., 2000; Noppeney et al., 2006) and the Grounding by Interaction Hypothesis (Mahon & Caramazza, 2008a, 2008b). The Embodied Hypothesis of Tool Recognition claims that the knowledge associated with object manipulations is computed independently from the

ventral stream projections. Consequently, they believe the differential activation in the parietal cortex for tools results from the dorsal stream's operations alone. On the contrary, the Grounding by Interaction Hypothesis argues that the information linked to object manipulations requires an object's identity and associated function. Hence, they claim that the computation of visuomotor information depends on the inputs from the ventral pathway. Therefore, they expect to observe an information flow from the ventral stream to the tool-preferring regions in the parietal cortex. Additionally, another view by Arbib et al. (Arbib, 2008; Fagg & Arbib, 1998) opposes the Embodied Hypothesis of Tool Recognition, having regard to the notion of affordances (Gibson, 1986). They point out that an object's recognition confines the set of affordances that is based on its intrinsic physical properties, according to its associated manipulations. Thereby, they emphasize the contingency of the dorsal stream onto the ventral stream.

The studies presented in the current review provide evidence that the ventral stream contributes to the visuomotor processing of tool use in the dorsal stream via its projections to the parietal cortex. The functional connectivity, PPI, and DCM analysis demonstrate a link between two visual streams in the parietal lobe. In this respect, the research proposed in the current paper will try to gather further evidence for the Grounding by Interaction Hypothesis.

Gaps in Existing Knowledge

Most researchers could study complex tool use in humans by presenting subjects with tool images due to mobility limitations during fMRI. In this regard, several studies reported that actual tool use during brain imaging could offer further insight into the functional connectivity within the Tool Processing Network. For instance, Garcea and Mahon (2014) stated that by asking subjects to free-view tool images, pantomime tool use, and use actual tools, we could reveal the dynamic changes in the network for different tasks. In this respect, the current proposal suggests that MEG, compared to fMRI, provides more opportunities for designing an experiment. Furthermore, it provides higher temporal resolution than fMRI and better spatial resolution than EEG, both of which are valuable for data analyses. In this way, we can have

more insight into the precise time of interaction between the ventral and dorsal streams, their location and the direction of information within the Tool Processing Network, and the dissociation within the dorsal pathway.

Research Design and Methods

Participants

We plan to analyze the MEG data of twenty-five participants, as in the study by Garcea and Mahon (2014). However, to make provision for the possible exclusion of some subjects due to the strong head movements, which was the case for the experiment by Brandi et al. (2014), we aim to have thirty participants in our study in exchange for payments. Subjects will have normal or corrected-to-normal vision, no history of neurological disorders, and be right-handed. The study will be approved by the Center for Mind/Brain Sciences (CIMeC) ethics committee.

Materials

To present the experimental stimuli during MEG, we will build a "Tool Carousel" similar to the experiment by Brandi et al. (2014) (Figure 1A). We will make it from materials compatible with MEG and install it in the most productive way to make participants comfortable during the experiment to prevent head movements. We will fixate the subjects' upper arms with a belt to restrain the movements of the upper arm and shoulder. Each compartment of the carousel will be divided by a partition so that subjects will see only one part of it at a time.

We plan to put the same tools used by Brandi et al. (2014) into the Tool Carousel. However, they can be revised in light of further discussions. For now, we will select ten kinds of tools based on how often they are used in daily life. These tools are a hammer, scissor, tweezers, pen, screwdriver, knife, spoon, key, bottle opener, and lighter. We will also place ten neutral objects that have different colors and shapes. In general, they will have a shape similar to a bar, but they will be designed to correspond to each tool in the first set to minimize the visual and tactile differences. For instance, a bar's handle will have a small diameter when

it is designed to match a pen and a flat shape when it is formed to correspond to a knife. Also, they will have matching colors with their designated tools (Figure 1E).

Additionally, the tools will have corresponding hangers to hold them and specific recipients to perform their associated actions, such as a nail for the hammer or a screw for the screwdriver. In this way, participants will be able to manipulate tools according to their functions. However, as emphasized by Brandi et al. (2014), goal attainment may not be possible in some cases. For example, while subjects will turn a screw using a screwdriver, they may not hammer a nail into the carousel or light a candle with a lighter. In this respect, Brandi et al. (2014) point out that the Tool Carousel is not designed to address goal attainment but actual tool manipulation. Therefore, it still fulfills our research goal.

Design and Procedure

Our experiment will utilize three distinct experimental manipulations for two possible trials, as in Brandi et al. (2014). These manipulations will be related to the kind of object, the type of action performed, and the hand used. We will ask subjects to either use objects from the carousel according to their typical functions or transport them, that is to say, return them to their hanger after grabbing and lifting them. Subjects will participate in two runs of MEG, in which they will be asked to use only their right or left hand throughout the recording. The order in which hand they will use in each run will be randomized across the subjects, and the tools' handles will be placed accordingly. While using the bars, they will be expected to place the bar's blue marked side into the blue opening on the bottom (Figure 1C). For half of the trials, the blue sign will be on the left, and for the other half, it will be put on the right. To indicate which task they need to perform, either for tools or bars, we will place a letter at each compartment. The letter 'U' will imply the usage of objects, and the letter 'T' will imply their transportation. Ultimately, we will have four experimental conditions called tool use, tool transport, bar use, and bar transport.

We plan to use an event-related design with 200 trials for each run, similar to Brandi et al. (2014). For each experimental condition, we will have 40 trials. Consequently, each tool

or bar will be repeated four times in one trial. In total, subjects will participate in 160 trials for four experimental conditions and also 40 control trials. In the control condition, a compartment of the carousel will be presented as empathy. We will randomize the order of trials for each run. Each trial has a planning phase, an execution phase, and a return phase, respectively, with 2-6, 4, and 2 seconds. During the planning phase, subjects will be presented with an object and a cue for action (U or T). During the execution phase, they will act if a green light appears in the beginning. The return phase will start when the green light is turned off, during which participants will return the object to its hanger (Figure 1D). The green light will appear for half of the trials. The order of action and no-action trials and the onset of the green light (2-6 seconds) will be randomized to prevent participants from making predictions about their order. Importantly, participants will fill in a questionnaire to control their familiarity with the usage of objects in the carousel. We will make sure that they understand the experimental procedure. We will also videotape the experiment to evaluate their performance according to the guidelines explained in Brandi et al. (2014).

MEG Data Acquisition and Preprocessing

We will use a 306-channel whole-head MEG system at a sampling rate of 1000 Hz to measure subjects' brain activity and preprocess data using the Fieldtrip toolbox (Oostenveld et al., 2010) as in Tucciarelli et al. (2015).

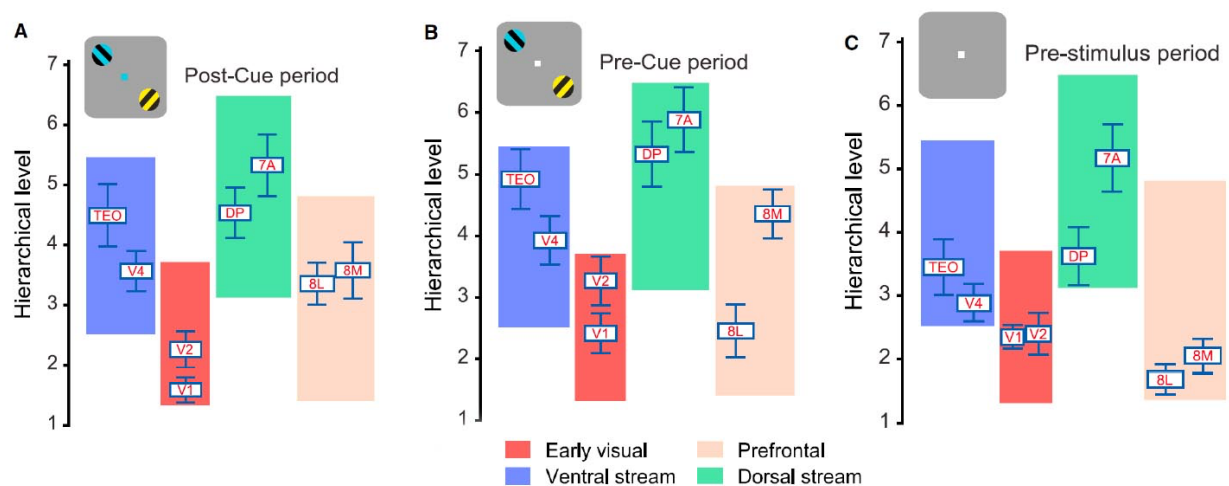
MEG Data Analysis

Firstly, we will apply multivariate decoding analysis iteratively for source parcels in a searchlight fashion (van Ede et al., 2019) to demonstrate the source level topography as a function of time for the kind of object, the type of action performed, and the hand used. For the second part, we will implement Granger causality analysis (Seth et al., 2015) by following the steps in Bastos et al. (2015) to identify directed functional interactions within the Tool Processing Network for each trial. In the first step, we will compute the interareal synchronization between different regions within the Tool Processing Network by using the coherence metric (Bastos & Schoffelen, 2016). In the second step, we will calculate Granger-

causal (GC) influences between all those areas to find the frequency-specific directed influences within the network. Additionally, we will construct a functional hierarchy for each experimental phase to observe how it changes across different task periods. To this end, we will first calculate a directed influence asymmetry index (DAI) based on GC (Bastos et al., 2015). Secondly, we will compute the multifrequency band DAI (mDAI) by averaging the DAIs across the frequency spectrums that we will find. Thirdly, the mDAI values that will range from -1 to +1 will be rescaled into a range -x to +x after multiplying it with half of the number of regions (2x) we would like to include. Fourthly, the rescaled mDAI values of all source areas will be shifted such that they will range from 0 to 2x. Lastly, the functional-hierarchical levels computed will be averaged across all target areas and the twenty-five subjects. In the end, we will reveal how the functional hierarchy changes across different task phases for each experimental condition (Figure 2).

Figure 2

Functional Hierarchy Between Different Task Periods



Note. An example illustration of the dynamics of the functional hierarchy with cognitive context across three main periods of the task. Reprinted from "Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels," by A. M. Bastos, J. Vezoli, C. A. Bosman, J. M. Schoffelen, R. Oostenveld, J. R. Dowdall, P. De Weerd, H. Kennedy, and P. Fries, 2015, *Neuron*, 85(2), 390–401.

Practical Considerations

We are aware that building the Tool Carousel might be challenging. However, we believe it is quite possible to construct it since the latest developments in 3D printing. Thanks to 3D printing, we will easily design the tools and carousel in its software and print them with MEG-compatible materials such as plastic. Additionally, we are concerned that the upper arm and shoulder might decrease our data's signal-to-noise ratio during action trials. However, we think that fixing the subjects' upper arms with a belt will prevent unwanted movements during the experiment. Afterward, we can also use electromyography (EMG) to reject artifacts while preprocessing the data.

Implications and Contributions to Knowledge

The proposed project is important because it promises to fill the gaps in the existing knowledge. We believe multivariate decoding analysis as a function of time will provide conclusive results on the dynamics between the ventral and dorsal visual streams during actual tool use, thanks to MEG's high temporal resolution. Additionally, Granger causality analysis will demonstrate how the Tool Processing Network's functional and effective connectivity changes between the different phases of action, such as planning and execution. It will reveal the direction of information flow between ventral and dorsal streams for complex tool use in humans. Also, we will find out which frequency channels subserve the feedforward and feedback influences between them. Moreover, thanks to our experimental design, we hope to provide further insights into the dissociation within the dorsal stream, that is to say, between ventro-dorsal and dorso-dorsal pathways.

We believe that our work will strengthen the Grounding by Interaction Hypothesis and challenge the Embodied Hypothesis of Tool Recognition. It will create a basis for further research on vision and motor cognition and the parietal cortex's role in the brain. Ultimately, it will make MEG an attractive option as a functional neuroimaging technique for studying complex tool use in humans.

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