Similar coding of freely chosen and externally cued intentions in a fronto-parietal network

David Wisniewski [a,b,*], Thomas Goschke [b], John-Dylan Haynes [a,c]

[a] Bernstein Center for Computational Neuroscience Berlin, Berlin Center for Advanced Neuroimaging, Cluster of Excellence NeuroCure, Department of Neurology, Charité Universitätsmedizin Berlin, Germany
[b] Department of Psychology and Neuroimaging Center, Collaborative Research Center 940 "Volition and Cognitive Control", Technische Universität Dresden, Germany
[c] Berlin School of Mind and Brain, Department of Psychology, Humboldt-Universität zu Berlin, Germany

ARTICLE INFO

ABSTRACT

Intentional action is essential to human behavior, yet its neural basis remains poorly understood. In order to identify neural networks specifically involved in intentional action, freely chosen and externally cued intentions have previously been contrasted. This has led to the identification of a fronto-parietal network, which is involved in freely choosing one's intentions. However, it remains unclear whether this network encodes specific intentions, or whether it merely reflects general preparatory or control processes correlated with intentional action. Here, we used MVPA on fMRI data to identify brain regions encoding non-motor intentions that were either freely chosen or externally cued. We found that a fronto-parietal network, including the lateral prefrontal cortex, premotor, and parietal cortex, contained information about both freely chosen and externally cued intentions. Importantly, MVPA cross-classification indicated that this network represents the content of our intentions similarly, regardless of whether these intentions are freely chosen or externally cued. This finding suggests that the intention network has a general role in processing and representing intentions independent of their origin.

© 2016 Published by Elsevier Inc.

1. Introduction

Intentional action is an essential part of everyday human behavior (Goschke, 2013; Haggard, 2008). In cognitive neuroscience, two types of intentions are often contrasted: internally vs. externally guided intentions (Beck et al., 2014; Brass et al., 2013; Cunnington et al., 2002; Forstmann et al., 2006; Gilbert et al., 2009; Jahanshahi et al., 1995; Mueller et al., 2007; for a recent meta-analysis see Rae et al., 2014). Internally guided or "free" intentions are generated in the absence of direct external trigger stimuli and result from an internal choice process. Externally guided or "cued" intentions in contrast are generated in direct response to external stimuli. Note that when we speak of free intentions, we do not mean to imply that these intentions are less causally determined, but that their direct cause is not an external stimulus. In typical experiments, subjects can either freely choose which of two tasks to perform (Soon et al., 2013), or they are externally cued as to which of two tasks to perform (Monsell, 2003; Ruge et al., 2013). By comparing the neural representations of free and cued intentions it is possible to assess whether they are processed similarly in the brain or not (Deiber et al., 1991; Forstmann et al., 2006; Passingham et al., 2010; but see Nachev and Husain, 2010).

Previous research using functional magnetic resonance imaging (fMRI) suggests that different networks might be involved in processing free and cued intentions, with e.g. the dACC (Bengtsson et al., 2009; Forstmann et al., 2006; Mueller et al., 2007) or preSMA (Bengtsson et al., 2009; Rae et al., 2014) being more strongly activated while processing free intentions. However, regions found to be associated with free intentions have also been found to be associated with general preparatory processes (Fedorenko et al., 2013), such as conflict monitoring (Botvinick et al., 2001). Whenever intentions are freely chosen, two comparable alternatives need to be maintained and conflict between them resolved (Brass et al., 2013). This conflict resolution might explain increased activation in the dACC as well, although in contrast to other conflict paradigms (Eriksen, 1995; Stürmer et al., 2002) there is no "correct" or "incorrect" response for free choices. Furthermore, working memory demands might also play a role (Lau et al., 2004b).

A solution to ruling out unspecific processes when comparing free and cued intentions, is to use multivoxel pattern analysis (MVPA; Haynes and Rees, 2006; Haynes, 2015; Kriegeskorte et al., 2006). Here, spatial activation patterns which encode the content of specific free (or cued) intentions can be identified. Recent studies identified a fronto-parietal network which encoded cued intentions, including the anterior medial PFC (Gilbert, 2011), lateral PFC, and parietal cortex (Bode and Haynes, 2009; Momennejad and Haynes, 2013; Wisniewski et al., 2015a). A partly overlapping brain network was found to encode freely chosen intentions, including the dACC (Wisniewski et al., 2015b),

frontopolar cortex, precuneus (Soon et al., 2008), medial and lateral PFC (Haynes et al., 2007). However, it is still an open question whether free and cued intentions are represented similarly in the brain, although the overlapping networks seem to suggest this. Within a single region the same task might nonetheless have a different neural representation depending on whether it is free or cued. Thus, in order to identify regions where neural task representations under free and cued conditions are similar it is essential to directly compare the specific patterns coding individual intentions under both cueing and free conditions. Furthermore, comparing results from previous studies is complicated by the different tasks, stimuli and designs used. One recent study, which compared free and cued intentions within-subjects using the same task (Zhang et al., 2013), demonstrated that a fronto-parietal intention network represents free and cued intentions. Different parts of this network were functionally specialized, with the premotor and parietal cortex representing both free and cued intentions, whereas the lateral PFC only represented free intentions. However, the tasks in this experiment were based on *attending* to different features of one stimulus, making it difficult to exclude attentional confounds in task coding. Moreover, it remains unclear whether results generalize to more abstract intentions, which are not specified in terms of direct stimulus–response-mappings between perceptual features and motor responses, but rather refer to more abstract cognitive tasks such as mental calculation as used here (see Discussion for details).

Here, we report an experiment in which we directly compared the representations of free and cued intentions by applying MVPA to fMRI data in a mental calculation task. This research was motivated by two central questions: First, is the fronto-parietal intention network also involved in representing abstract, non-motor intentions especially when differences in feature-based attention can be ruled out? Second, does this network represent freely chosen and externally cued intentions similarly, suggesting a general role for the fronto-parietal network in intention processing? Or does this network exhibit functional specialization with respect to freely chosen vs. externally cued intentions?

2. Materials and methods

2.1. Participants

35 participants took part in the experiment (24 females). All subjects volunteered to participate and had normal or corrected-to-normal vision. Subjects gave written informed consent and received 25€ for participation. The experiment was approved by the local ethics committee. Subjects were right-handed, and no subject had a history of neurological or psychiatric disorders. Four subjects showed excessive head movements inside the MR scanner (>5 mm) and were excluded from further fMRI analyses.

2.2. Experimental paradigm

The experiment was implemented using Matlab Version 8.1.0 (The MathWorks) and the Cogent Toolbox (http://www.vislab.ucl.ac.uk/cogent.php). Trials started with the presentation of a single visual cue centrally on screen (Fig. 1). In half of the trials this cue specified one of two possible calculation task to be performed (adding or subtracting). This was the *cued* condition. In the other half of the trials, subjects were given the free choice between addition and subtraction (*free* condition). In half of the *cued* trials, subjects were cued to add, in the other half they were cued to subtract. In *free* trials, subjects received no explicit instruction on which task to perform in each trial.

The tasks (addition and subtraction) and intention types (free and cued) were orthogonalized in the experiment. The cues used were abstract line drawings that were designed to minimize a priori semantic associations to the subjects before the start of the experiment (see Wisniewski et al., 2015b; Reverberi et al., 2012 for a similar approach). Furthermore, two cues each were associated with the free, cued
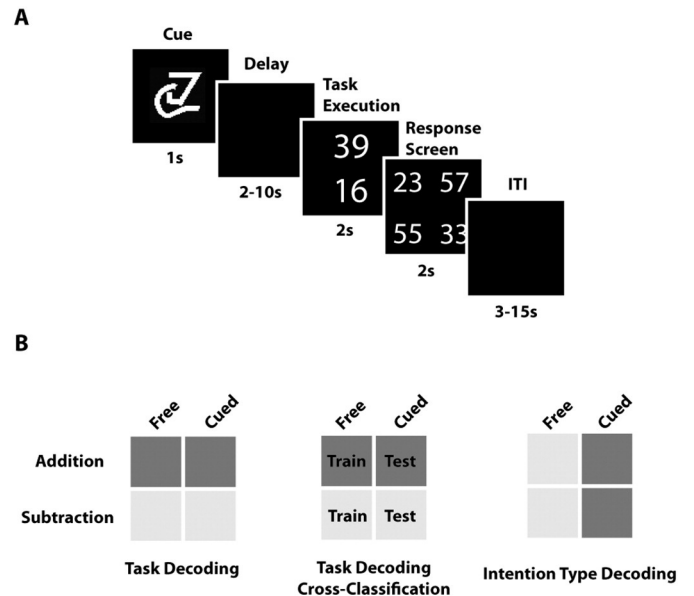

Fig. 1. A. Trial structure. At the beginning of each trial, subjects were presented with a cue indicating that they could either choose freely between the two tasks (free trials), or indicating which of the two tasks to perform (cued trials). After a variable delay, subjects were presented with two numbers on the screen and either added or subtracted them, depending on the current trial condition. The response screen was used to indicate the correct response, and in free trials the task performed was determined by subjects' responses. Trials were separated by a variable inter-trial-interval (ITI). B. Analyses. The three main analyses are presented. In the task decoding, addition (dark gray) and subtraction (light gray) trials were contrasted. In the task decoding cross-classification, a classifier was trained to distinguish addition and subtraction trials in the free condition only. Classifier performance was then tested on cued trials. Only brain regions in which tasks are represented similarly in free and cued trials will show above chance decoding accuracies. In the intention type decoding, free trials (light gray) and cued trials (dark gray) were contrasted.

addition, and cued subtraction conditions, respectively. This was done in order to allow dissociating the neural representation of the task choice from the visual identity of the cues (see below for details). Which of the two semantically identical cues was presented was pseudo-randomized across trials. The cue was presented visually for 1000 ms, after which a variable delay followed (between 2000 and 10,000 ms, mean duration 6000 ms, distributed uniformly in steps of 2000 ms). This delay allowed us to dissociate in time the cue presentation and intention maintenance phase from the task execution, which followed after the delay. It also made the time of the task screen onset unpredictable to the subjects, forcing them to maintain a task representation throughout the whole delay period (Haynes et al., 2007). Two numbers were presented on the task screen, one above and the other below the fixation cross. Depending on the current condition subjects either added or subtracted these two numbers. The numbers were randomly chosen in each trial, from a set of numbers between 11 and 59. Integer multiples of 10 were excluded, as calculations with these numbers would be too easy. The numbers were presented for 2000 ms. Then, a response screen was presented, giving subjects four different response options: the correct response for addition, the correct response for subtraction and two wrong responses. Response options were presented on four fixed positions on screen (Fig. 1), which were mapped onto four buttons which subjects operated using their left and right index and middle fingers. The response-mapping was pseudo-randomized in each trial, dissociating task execution from motor preparation processes. (This is in contrast with Zhang et al. (2013), where response-mappings were fixed for each subject, making a dissociation of task execution and motor preparation processes more difficult). The response screen was presented for 2000 ms, irrespective of the actual reaction time (RT) in each trial. Note, that in free trials the chosen task was inferred from the responses. If for instance subjects chose the correct