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# Q1 Individual attentional selection capacities are reflected in 2 interhemispheric connectivity of the parietal cortex

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## ABSTRACT

Modelling psychophysical data using the Theory of Visual Attention (TVA) allows for a quantification of attentional sub-processes, such as the resolution of competition amongst multiple stimuli by top-down control signals for target selection (TVA-parameter  $\alpha$ ). This fMRI study investigated the neural correlates of  $\alpha$  by comparing activity differences and changes of effective connectivity between conditions where a target was accompanied by a distractor or by a second target. Twenty-five participants performed a partial report task inside the MRI scanner. The left angular gyrus (ANG), medial frontal, and posterior cingulate cortex showed higher activity when a target was accompanied by a distractor as opposed to a second target. The reverse contrast yielded activation of a bilateral fronto-parietal network, the anterior insula, anterior cingulate cortex, and left inferior occipital gyrus. A psychophysiological interaction analysis revealed that the connectivity between left ANG and the left and right supramarginal gyrus (SMG), left anterior insula, and right putamen was enhanced in the target-distractor condition in participants with worse attentional top-down control. Dynamic causal modelling suggested that the connection from left ANG to right SMG during distractor presence was modulated by  $\alpha$ . Our data show that interindividual differences in attentional processing are reflected in changes of effective connectivity without significant differences in activation strength of network nodes.

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## Introduction

That multiple sensory inputs compete for processing resources has long been put forward on both behavioural and physiological grounds: According to influential theoretical accounts, the presence of multiple elements in a visual display triggers competitive parallel processing for access into visual short-term memory (VSTM) (Rumelhart, 1970), and for processing resources in the brain (Desimone and Duncan, 1995). Interestingly, although the elements are processed in parallel, certain elements can be processed more effectively than others. The Theory of Visual Attention (TVA; Bundesen, 1990) is a computational framework which is based on this biased competition account and which quantifies an element's competitive strength by its attentional weight. Higher attentional weights are assigned to elements that match a top-down description of currently relevant input (Duncan et al., 1999). Consequently, targets defined by a distinctive feature (such as, e.g., colour) receive higher attentional weights than

distractors—thereby biasing bottom-up competition and enabling efficient attentional selection.

These processes can be investigated with partial report paradigms involving categorization of elements (e.g., letters) in visual displays and, more specifically, resolution of the competition between targets and distractors for access to VSTM. In TVA, the ratio of the attentional weights between distractors and targets is defined as the top-down control parameter  $\alpha$ . The lower this ratio  $\alpha$ , the better the competition between targets and distractors can be resolved. Target report probabilities are known to degrade when bottom-up competition cannot be resolved at all. This is generally the case in situations where top-down bias is rendered inefficient, for instance when multiple targets need to be reported (e.g., Habekost and Bundesen, 2003). Besides attentional weights ( $\alpha$ ), TVA allows for a quantification of other parameters such as the number of elements which can maximally be stored in VSTM ( $K$ ), processing speed measured in items processed per second ( $C$ ), and the minimal exposure duration required for conscious perception ( $t_0$ ).

Modelling of these TVA parameters has been successfully applied in both healthy participants and brain damaged patients (Duncan et al., 1999; Habekost and Bundesen, 2003; Finke et al., 2005; Peers et al., 2005; Habekost and Rostrup, 2007). Peers et al. (2005) specifically investigated the lesion correlates of attentional weighting and observed that the only predictor of impaired attentional top-down control

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(reflected in the TVA parameter  $\alpha$ ) was lesion volume. Neurostimulation studies have highlighted the role of key attentional network nodes such as the posterior parietal cortex (Hung et al., 2005), intraparietal sulcus (IPS) (Moos et al., 2012), and the frontal eye fields (FEF) (Hung et al., 2011) for top-down attentional selection of targets amongst distractors as reflected in the TVA parameter  $\alpha$ . So far, only one functional imaging study has investigated the neural underpinnings of the different attentional components measured by TVA (Gillebert et al., 2012). While dorsal fronto-parietal regions showed higher activity when more targets entered VSTM in this study, activity was reduced in the left (and to a smaller extent also in the right) angular gyrus, medial posterior parietal cortex, and medial frontal areas when more targets entered VSTM. This finding is consistent with the above notion that multiple stimuli are not processed independently from each other but rather interact competitively in a mutually suppressive fashion (e.g., Kastner et al., 1998).

Individuals differ in their capacity to employ top-down control to resolve competition between targets and distractors. In TVA, the top-down control parameter  $\alpha$  is estimated for a given subject on the basis of his/her performance profile in a partial report task and hence allows for a quantitative assessment of interindividual differences in attentional selection. Gillebert et al. (2012) used correlation analyses to test for a relationship of TVA parameters and brain activity but did not find any significant association with the top-down control parameter  $\alpha$ . This null result may suggest that interindividual differences in implementing attentional top-down control to resolve competition do not rest upon differences in BOLD amplitudes (i.e., activation strength) in attentional network nodes. Alternatively, interindividual differences may rather be reflected in differential network connectivity, i.e., the degree to which information is passed on between the network nodes. It is well known that attentional modulation is reflected in altered connectivity patterns between brain regions and that the parietal cortex is critically involved in this process: Attending to a particular stimulus feature such as motion increases the connectivity from the parietal cortex to area MT/V5 (Friston and Büchel, 2000), and attending to a particular location in space modulates connectivity from IPS to visual areas (Vossel et al., 2012). The anticipation or presence of distractors affects the coupling between the temporoparietal junction (TPJ) and visual areas (Ruff and Driver, 2006), and TPJ and FEF (DiQuattro and Geng, 2011). While all these studies focused on manipulations of attentional factors within subjects, the present fMRI study aimed at investigating the origin of interindividual differences in attentional processing by relating a TVA-based assessment of behavioural performance in a partial report task to cortical connectivity patterns.

As noted above, target report probabilities were expected to be higher in target-distractor conditions than in conditions with two targets, since for the former competition for VSTM entry can be resolved by top-down control settings, i.e., a differential weighting of targets and distractors. Accordingly, our comparisons focused on the effect of the relevance of the accompanying item in two-item displays (a target accompanied by a distractor versus two-target displays), although single target displays were also realised for matters of completeness of the paradigm. More specifically, we contrasted trials with correct report of the target in the target-distractor (TD) condition with trials with correct report of one target in the target-target (TT) condition. This contrast is matched for sensory characteristics as well as for the number of targets entering VSTM and should reveal activation patterns that reflect implementation of top-down control to resolve competition (TD > TT) or competition of two equally weighted targets (TT > TD), respectively. We did not include trials in which both targets in the TT condition were correctly reported in this contrast, since these trials were rare and cannot be classified according to the position of the target that is reported. On the basis of the study by Gillebert et al. (2012), we expected higher activity in the TD (as compared to the TT) condition in the angular gyrus and frontal areas. Another candidate region for this contrast was the right temporoparietal junction, since this area has been shown to be involved in distractor preparation (Ruff and

Driver, 2006), and particularly in the filtering of distractors during visual search (Shulman et al., 2003, 2007). In contrast, dorsal fronto-parietal regions (IPS and FEF) were expected to show higher activity in the TT than in the TD condition. Moreover, since the parietal cortex modulates the activity of other brain regions during attentional modulation, and interfering with the posterior parietal cortex with TMS worsens attentional top-down control in this paradigm (Hung et al., 2005), we hypothesized that interindividual differences in the TVA parameter  $\alpha$  can be related to either BOLD amplitude differences in the above contrast, and/or to differential connectivity strength between the task-related areas.

## Materials and methods

### Participants

Thirty-two participants without a history of neurological or psychiatric disease and without psychopharmacological treatment participated in the study. Seven participants were excluded from further analysis due to significant head movement during fMRI scanning ( $n = 6$ , translation > 3 mm or rotation > 3°) or technical failure of response logging ( $n = 1$ ), resulting in data from twenty-five participants (17 males, 8 females, mean age 26.6 years, range 21–35 years). The experiment was realised in accordance with the Declaration of Helsinki and had been approved by the local ethics committee of the medical faculty of the University of Cologne. All participants gave written informed consent and received monetary allowance for their participation.

### Partial report paradigm

The participants performed a variant of a partial report task initially introduced by Sperling (1960) (see also Bundesen, 1990; Duncan et al., 1999), in which letters (subtending 0.5° visual angle) were presented and subjects were asked to report only a subset of these letters. In particular, they were asked to selectively report digits in a relevant colour, but not those in an irrelevant colour (Hung et al., 2005). The target-defining colour (red or green) was varied across different experimental blocks. When target letters were red, then distractors were green and vice versa. Letters for targets and distractors were randomly chosen from the set AJKLPTWXYZ. The letters were presented on a black background in the corners of a virtual square (4.7° × 4.7°) centred on a fixation cross.

Stimulus arrays could contain either one or two letters, arranged in rows or columns, resulting in five different experimental conditions (see Fig. 1A): targets in left and right hemifields could be presented alone (Ta condition), or accompanied by a second item. The second item could be either a distractor (TD), or a second target (TT) appearing in the same or other hemifield, respectively. In sum, there were 16 different display conditions. The number of targets presented at each of the 4 locations was held constant across the different display conditions.

Fig. 1B illustrates the stimulus sequence of a single trial. The trials started with a 200 ms presentation of the cue (red or green square) indicating the target colour. Subsequently, one of the stimulus arrays (cf. Fig. 1A) appeared in randomized order with a subject-specific exposure duration. Stimuli were followed by a mask of superimposed red and green digits presented for 300 ms. Immediately following each mask display, the participants were asked to enter two responses, reporting the perceived target letters. Each response involved the selection of the potential target letter from a vertical array of letters containing all set letters and a hyphen (–). Using the index and middle finger of the right hand, participants were able to move the array until the perceived letter appeared within a box centred on fixation. They then confirmed their choice by pressing a button with the left index finger. Participants were instructed to avoid guessing. To keep the number of answers constant amongst Ta, TD, and TT conditions, participants were asked

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